MOOSE (*ALCES ALCES*) BROWSE AVAILABILITY AND USE IN RESPONSE TO POST-FIRE SUCCESSION ON KANUTI NATIONAL WILDLIFE REFUGE, ALASKA

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Abstract

I examined post-fire moose habitat dynamics on Kanuti National Wildlife Refuge in interior Alaska with the objective of increasing understanding of local moose habitat characteristics. I estimated browse density, biomass, and summer browse use in a 2005 burn, 1990 burn, 1972 burn, and an unburned area. I revisited each site the following spring to estimate browse availability and removal during winter. In addition to evaluating browse production and use, I estimated proportional habitat use of varying-aged burns by 51 VHF-collared moose. I found that summer browse production and winter browse availability were highest in the 1990 and 2005 burns. I found that summer and winter browse use was highest in the 1990 burn. Collared moose generally avoided recently burned stands and demonstrated preference for >30 year old stands in both summer and winter. Moose demonstrated preference for unburned stands during calving. Although biomass production and availability were highest in 11 – 30 year old stands, disproportionate use of food resources in burns was evident. This disproportionate use of burns and food resources could be due to a variety of reasons including resource type, historic moose distribution patterns, and predation avoidance strategies.
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INTRODUCTION

Kanuti National Wildlife Refuge

Kanuti National Wildlife Refuge (NWR) was established by Congress in 1980 with passage of the Alaska National Interest Lands Conservation Act (ANILCA). The legal purposes of the Refuge are to:

1) Maintain the natural diversity of the Refuge's fish, wildlife and habitat,

2) Comply with international treaties,

3) Provide continued opportunity for subsistence to rural residents, and

4) Ensure water quality and quantity needed by the fish, wildlife, and habitats of the Refuge (US Congress 1980).

The 2008 Kanuti NWR Revised Comprehensive Conservation Plan (CCP) established goals to fulfill these Refuge purposes. Goal 1 directs the US Fish and Wildlife Service (USFWS) to “conserve the Refuge’s diversity of wildlife, fish, and habitats, while allowing natural processes, including wildland fire and the natural hydrologic cycle, to shape the environment” (USFWS 2008). Twenty-five programmatic objectives were outlined under this goal. Objective 5 directs USFWS to “obtain baseline information about late winter availability and use of moose (Alces alces) forage” to increase understanding of the potential for the Refuge to support growth in the moose population. Objective 7 acknowledges the role of wildfire in maintaining Refuge diversity, and directs USFWS to “participate in local and regional fire ecology research during the life of [the CCP]” (USFWS 2008).

Resources important to subsistence use (such as moose) are of special concern on Kanuti NWR. The third purpose of Kanuti NWR, as set forth by Section 302(4) (B) of ANILCA, is “. . . to provide . . . the opportunity for continued subsistence by local residents” (USFWS 2008). This provision is specifically designed to address the subsistence needs of four village communities,
Allakaket, Alatna, Bettles, and Evansville, adjacent to the Refuge boundary. Additionally, ANILCA Section 812 directs Federal agencies to “undertake research on fish and wildlife . . . on the public lands [in support of subsistence management]” (US Congress 1980).

**Wildfire**

Kanuti NWR lies within the boreal forest, where wildfire, flooding, permafrost dynamics, and other climatic and physiographic variables create a mosaic of vegetation patterns on the landscape. Wildfire is the primary disturbance in upland areas and inactive floodplains (Chapin *et al.* 2008). Natural fire maintains plant communities at various stages of vegetative succession. Changes in species composition and stand structure due to disturbances such as wildfire alter wildlife habitat and, consequently, impact wildlife populations. Impacts to wildlife vary depending on species-specific habitat needs. It is commonly accepted that fire is beneficial to moose because it maintains the presence of deciduous shrubs, which are an important winter food resource (MacCracken and Viereck 1990).

Post-fire succession is impacted by multiple variables, including pre-fire vegetation composition, topography and hydrology, timing of burn, and fire behavior characteristics such as fire severity (Epting *et al.* 2005, Johnstone and Chapin 2006, Johnstone *et al.* 2010). Vegetative succession generally follows one of two pathways based on these variables: 1) self-replacement or 2) relay floristics (Dyrness *et al.* 1986). Self-replacement is characterized by re-establishment of similar pre-fire species and vegetation communities. Conversely, relay floristics is when a site is colonized by herbaceous plants immediately post-fire, and ultimately results in a site dominated by deciduous shrub and tree species such as willow (*Salix* spp.) and birch (*Betula neoalaskana*). Johnstone (2003) found that stands subject to higher fire severity resulting in
removal of the organic layer are more likely to undergo relay floristics and be colonized by deciduous species, which can be advantageous to moose (Lord and Kielland 2015).

With few exceptions, Kanuti NWR is managed under a natural fire regime with minimal effort to directly suppress lightning-caused fires. Several large fire scars are present within the Refuge boundary. An important objective for Refuge staff is to understand how the vegetation and habitat quality within these burns, particularly those that are accessible from villages, will change through time. By coupling understanding of habitat change with data from semi-annual moose surveys, land and game managers can anticipate local changes in moose density over the next 3-5 decades.

Moose

Moose are an important part of the landscape and ecology of the boreal forest in interior Alaska. They are a primary food source for multiple predators, and are one of the most important big game animals in the state (Gasaway et al. 1983). Their feeding patterns, particularly in areas with dense moose populations, can have dramatic impacts on vegetation re-establishment, stand architecture, and range quality (DeJager et al. 2009, Danell and Ericson 1986, Persson et al. 2005, Boertje et al. 2000). They are a vital subsistence resource for rural communities in interior Alaska (Nelson et al. 2008). Considerable state and federal resources are expended to monitor regional populations and fulfill established population and habitat objectives, particularly for populations that are heavily hunted.

Local and regional moose populations are impacted by interactions between various density-dependent and density-independent factors. At high densities, limited habitat quantity and quality can impact individual health and limit production (Messier and Crête 1984, Van Ballenberghe 1987, Boertje et al. 2000). High predation rates often maintain moose populations at low densities, and overharvest of bull moose may result in decreased production due to
reduced pregnancy rates (Gasaway et al. 1992, Bishop and Rausch 1974). In addition, climatic factors, specifically snow accumulation, can have short and long term impacts on moose populations (Mech et al. 1987). Climate related disturbances such as wildfire impact moose populations both directly as moose move to escape fire, and indirectly due to changes in vegetation and habitat over time. It is difficult to predict how many moose an area can support because of complex and changing interactions among habitat, predation, hunting pressure and climate that are unique to each population (Franzmann and Schwartz 2007).

The moose density on Kanuti NWR (0.8 moose/km²) is considered moderate. Calf production is high, but adult recruitment is low. This pattern is consistent with population dynamics described by Gasaway et al. (1992), where predation limits moose populations at densities well below habitat carrying capacity (Craig and Stout 2014). Moose habitat on Kanuti is considered excellent based on incidental observation (Stout 2010). Twinning rates are high, indicative of good nutrition, and individual moose are generally in good health. Moose management in Game Management Unit 24B focuses on monitoring population size and cohort recruitment (Stout 2010). However, habitat dynamics on the Refuge have not been well studied. Paragi et al. (2008) conducted winter browse surveys on the Refuge in 2007 to determine if winter browse resources were limited, and Maier et al. (2005) used data from Kanuti NWR moose surveys to evaluate moose densities in burned areas. Beyond these studies local moose-habitat relationships on the Refuge are not well documented.

**Moose and wildfire**

Moose have been linked to post-fire habitats since the 1940s (Aldous and Krefting 1946). Much work has been done to refine the concept of “ideal” post-fire habitat characteristics. Numerous studies have documented the important role of stand age in producing quality habitat.
Loranger et al. (1991) observed that moose densities were highest 17-26 years post-fire and were followed by abrupt declines. Similarly, Schwartz and Franzmann (1989) reported that moose density peaked 15 years after fire, although the response was noticeably lessened when wolves and bears were present. Kelsall et al. (1977) argued that the optimal post-burn stand age for moose was 11 – 30 years post-fire in the boreal forest. This was corroborated by Maier et al. (2005), who modeled winter cow moose density in interior Alaska and found that high moose densities in November are positively correlated with areas that burned 11 – 30 years ago.

Mid-seral stands are important to moose for a number of reasons. Multiple studies demonstrated that woody browse biomass production is higher in early seral stands than in older stands (LeResche et al. 1974, Bangs and Bailey 1980, MacCracken and Viereck 1990, Loranger et al. 1991). Nutritional quality of moose browse is higher in mid-seral stands as well (Oldemeyer 1974, Oldemeyer et al. 1977, Kielland and Osborne 1998). Cowan et al. (1950) found that carbohydrate and protein content of vegetation in a 20 – 30 year old burn were higher than in a 70 year old burn. Wolff (1978) documented that young shrubs and trees are more nutritious because they have a higher nutrient to fiber ratio; they are easily digestible and are thus higher quality browse resources for moose. Additionally, the physical structure of mid-seral stands enables access to food resources. Vegetation in early seral stands is often unavailable to moose during the presence of seasonal snow cover; likewise deciduous species such as mature birch and Bebb’s willow in late seral stands are often inaccessible due to their height in excess of 3.0 m (Danell and Ericson 1986, Wolff and Zasada 1979).

Recent work on the relationship between moose and wildfire has focused on exploring characteristics of habitat in individual burns, particularly those that are accessible by hunters. Lord and Kielland (2015) found that fire severity influenced succession, which in turn impacted
browse availability in an interior Alaska burn scar. Brown et al. (2015) continued to monitor changing browse availability in this burn, and explored these changes in the context of a comprehensive “moose-hunter system” by investigating simultaneous changes in moose density and human use patterns. Many of these studies are driven by State mandates to project and maximize sustained yield of moose in heavily hunted areas over time. Consequently, moose-habitat relationships in remote areas with low hunting pressure, such as Kanuti NWR, are not well studied.

Objectives and hypotheses

The purpose of this study was to contribute to the mandated purposes of Kanuti NWR by increasing the understanding of moose-habitat relationships on the Refuge. The goal of this study was to explore the relationship between time since fire and seasonal food resources and resource use by moose on the Refuge. Specific objectives of this research were to 1) quantify summer browse production and winter browse availability in different aged burn scars, 2) quantify summer and winter browse use, and 3) explore proportional use of burned areas by collared moose on the Refuge.

In this thesis, I report and discuss the results of late summer and winter browse surveys conducted between 2012 and 2014. I also discuss proportional use of burns by collared moose. I hypothesized that summer and winter browse production and availability would be highest in areas that burned 11-30 years ago (consistent with Weixelman et al. 1998). I predicted that browse use by moose would occur in proportion to its availability. Similarly, I hypothesized that collared moose would demonstrate preference for 11-30 year old stands (Maier et al. 2005 Loranger et al. 1991). Chapter 1 is formatted for submission to the journal Alces.
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CHAPTER 1: MOOSE (*ALCES ALCES*) BROWSE AVAILABILITY AND USE IN RESPONSE TO POST-FIRE SUCCESSION ON KANUTI NATIONAL WILDLIFE REFUGE, ALASKA

*Abstract:* Wildfire is a prominent landscape-level disturbance in interior Alaska. Vegetation change as a result of wildfire affects moose habitat quantity and quality. These changes are of interest to land managers responsible for managing habitat, and wildlife managers responsible for ensuring sustained yield of game species such as moose (*Alces alces*). We explored post-fire moose habitat dynamics on Kanuti National Wildlife Refuge in interior Alaska to increase understanding of local habitat characteristics to fulfill these objectives. We visited 34 sites of various stand ages (2005 burn, 1990 burn, 1972 burn, and unburned in the last 80 years) in August 2012 and 2013 to estimate summer browse density, biomass production, and browse use. We revisited each site the following March to estimate winter browse availability and offtake. We used VHF data from 51 collared moose to explore their use of burns on Kanuti National Wildlife Refuge. We found that summer density and biomass were highest at sites in the 1990 burn. Use of burns by moose varied seasonally. Despite high biomass in the 2005 burn, collared moose avoided burns <11 years old in summer and demonstrated preference for older (>30 years old) stands. Winter browse offtake was highest in the 1990 and 1972 burns, despite relatively high biomass available in the 2005 burn. This disparate use of burns could be due to browse species composition, predator avoidance strategies, or historic moose distribution patterns.

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INTRODUCTION

Vegetation changes related to wildfire are of interest to scientists tasked with management of wildlife populations and their habitat. Fire regime in interior Alaska is changing as a result of climate change. This regime change is characterized by shorter fire return interval, an increase in late-season fires, increased frequency of large (>1,000 km$^2$) fires, and higher severity fires (Kasischke and Turetsky 2006, Kasischke et al. 2010). These changes impact post-fire vegetation patterns at both local and landscape scales. Specifically, higher fire severity results in deeper burning of the surface organic layer. This has been shown to increase establishment of deciduous species, thereby negatively impacting recruitment of black spruce (*Picea mariana*) (Johnstone 2006). Increased prevalence of high severity fires could result in a major vegetation shift from coniferous black spruce communities to vegetation communities dominated by deciduous species (Johnstone et al. 2010b). Landscape-scale changes in vegetation impact wildlife habitat and, consequently, wildlife populations. Impacts to wildlife populations can be positive or negative depending on species-specific habitat needs.

Changes in the boreal forest fire regime are anticipated to be generally beneficial to moose (*Alces alces*) because it is hypothesized that plant communities dominated by deciduous species will increase (Chapin et al. 2008, Johnstone et al. 2010a). In addition to aquatic vegetation, moose feed on willow (*Salix* spp.), birch (*Betula neoalaskana*), and aspen (*Populus tremuloides*) regrowth maintained on the landscape by natural disturbance such as wildfire. Maier et al. (2005) showed that during November moose preferentially use recently burned forests, stands where fire occurred between 11 and 30 years ago, and where quantity and quality of available browse is higher (Oldemeyer 1974, Oldemeyer et al. 1977, MacCracken and Viereck 1990, Lord and Kielland 2015). Additionally, the physical structure of 11 - 30 year old stands enables access to
food resources; vegetation in early seral (<11 year old) stands is often unavailable to moose during the presence of seasonal snow cover. Likewise, deciduous species such as mature birch and Bebb’s willow (*S. bebbiana*) in late seral (>30 years old) stands are often inaccessible due to their height in excess of 3.0 m (Wolff and Zasada 1979, Danell and Ericson 1986). Moose populations respond to disturbance and vegetative succession in a number of ways. Individual animals can actively immigrate into recently disturbed areas (Peek 1974b), or moose densities in these areas can change through time (Loranger *et al.* 1991).

Wildfire and flooding are the primary natural disturbance agents on Kanuti National Wildlife Refuge (NWR). Fire behavior depends on abiotic conditions such as topography and weather in addition to fuel type (Dyrness *et al.* 1986, Kasischke *et al.* 1995). Much of the Refuge is dominated by black spruce communities that are disturbed by large, severe stand-replacing wildfires. In Alaska, large fires have been well documented since 1942 (Drury and Grissom 2008, Alaska Interagency Coordination Center 2014). The fire return interval in interior Alaskan black spruce communities is 36 - 130 years (Kasischke *et al.* 2010). Fire history on the Refuge is varied, resulting in many forest stands of differing sizes and ages.

We sought to examine moose habitat characteristics in stands at various stages of post-fire succession. Much is known about moose and their response to fire on a general level. In particular, the role of wildfire in areas with dense moose populations and specific management concerns regarding habitat degradation and carrying capacity is particularly well studied (Boertje *et al.* 2000, Boertje *et al.* 2009, Lord and Kielland 2015). The moose population in the upper Koyukuk River drainage, including Kanuti NWR, is primarily regulated by predation (Stout 2010). Although habitat is not thought to inhibit the size of the moose population in this area, it is important to continue to explore habitat dynamics and the disturbance regimes that influence
them to understand whether moose distribution is influenced by specific disturbance events. Additionally, there is a continual need to understand how fire regime changes will impact moose habitat. Here we evaluated summer and late winter browse availability and use in multiple burn scars within the Refuge. We also used Very High Frequency (VHF) radio collar location data to explore use of burns by collared moose. We predicted that seasonal browse availability and use would be highest in 11 - 30 year old stands. Moreover, we predicted that moose would exhibit a seasonal preference for 11 - 30 year old stands in winter.

**STUDY AREA**

The study took place on Kanuti NWR in interior Alaska. The federal lands managed as Kanuti NWR include approximately 3.2 million roadless hectares (1.3 million acres) located between 65° 59’ to 66° 53’ N, and between 150° 58’ to 152° 58’ W. It is typical of the boreal forest biome, which is characterized by plant diversity and vegetation patterns dictated by climate, hydrology, and wildfire. The climate is cold and continental, with short, hot summers and long, cold winters. Mean monthly temperatures range from -20.5°C in January to 69.3°C in July (Western Region Climate Center, http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak0761, accessed 20 October 2014). The growing season is short, generally beginning in late May and ending in August.

Physiographically, the Refuge is the broad lowland flats between the Koyukuk and Kanuti Rivers. The Kanuti basin is characterized by poor drainage and riparian wetlands that are created and maintained by seasonal flooding and the presence or absence of permafrost. Vegetation patterns on the Refuge reflect drainage patterns, with lowland permafrost areas dominated by black spruce forests and tussock tundra. Well-drained slopes are dominated by deciduous stands of aspen, birch, and upland shrubs such as willow and alder (*Alnus* spp.). Large white spruce
(Picea glauca) and riparian shrub species dominate permafrost-free riparian areas, where secondary succession is a consequence of flood patterns and frequency along river corridors (Payette 1992, Nowacki et al. 2001).

Moose densities on Kanuti NWR range from 0.57 - 0.76 moose/km² (Stout 2010). The Kanuti population has fluctuated between 500 – 1,000 moose since 1999 (Stout 2010). The last reported Refuge population estimate was 551 ± 141 (90% confidence interval) moose in 2013 (Craig and Stout 2014). Hunting pressure on the population is light, and is localized near villages and along navigable rivers. Moose on Kanuti are large and healthy. Twinning rates are high (35 - 60%) in Game Management Unit (GMU) 24B, indicative of good nutrition (Stout 2010, Franzmann and Schwartz 1985). Despite adequate bull: cow ratios (46 - 70 bulls: 100 cows) and high pregnancy rates (96% from 2006 to 2009), fall recruitment is consistently low (33 calves: 100 cows in November, 2010) (Stout 2010). Low recruitment is purportedly due to high calf and yearling mortality caused by predation (Saperstein et al. 2009, Craig and Stout 2011). Adequate production but low adult recruitment is consistent with observations in similar low density moose populations across the state (Bertram and Vivion 2002, Lake et al. 2013).

METHODS

Site description

We established four burn age strata across fire scars on the Refuge based on seasonal landscape use patterns by moose documented by Maier et al. (2005): 1) <11 year old stands, 2) 11 - 30 year old stands, 3) 30 - 80 year old stands, and 4) stands that were unburned in the past 80 years of recorded fire history (hereafter: Unburned). We selected three fire scars to represent burn age strata 1-3: a 2005 fire (F-05), a 1990 fire (F-90), and a 1972 fire (F-72) (Fig. 1). Additionally, unburned sites were visited to represent burn stratum 4.
We measured abiotic characteristics in F-05, F-90, F-72, and Unburned. We used a digital elevation model (DEM) to determine the mean, minimum, and maximum elevations, and used the ArcMap 10.1 (Esri, Redlands, CA) Spatial Analyst extension to determine slope and aspect from the DEM. Slope was averaged across plots within each burn stratum and classified as flat, gentle (<10°), medium (10 - 30°), or steep (> 30°). We used photos to evaluate fire severity at each plot. We classified fire severity as low, moderate, or high.

The Alaska LANDFIRE vegetation map (2008) was used to quantify vegetation types and stand height classes in each burn strata. Much of the Refuge is dominated by black spruce vegetation communities, which are considered low quality moose habitat, so we chose to exclude black spruce communities from site selection. Instead, we selected vegetation types preferentially used by moose (Appendix A). We isolated vegetation types by adjacent pixel groups of three or more (areas >30 m²) and generated different lists for randomly derived boat/floatplane accessible and helicopter accessible sites. In 2012, field work was restricted to areas accessible by float plane or by boat from the Kanuti River; in 2013, the use of a helicopter facilitated access to more remote areas within a burn. For the boat/floatplane accessible sites, a 200 m buffer was created around the Kanuti River and Tachlodaten Lake (a lake approximately 12 miles north of the Kanuti River; Fig. 1) and random points were generated within 300 m outside the buffer. The <200 m buffer was implemented to avoid sampling in the floodplain, which is subject to flood disturbance dynamics. Eleven boat/floatplane accessible sites were visited in the summer of 2012 and spring of 2013 and 23 helicopter sites (eight Unburned, nine in F-72, eight in F-90, and nine in F-05) were visited in the summer 2013 and spring of 2014 for a total sample size of 34 sites (Fig. 1). The digital vegetation classification used in site selection pre-dated F-05. Lacking current, post-burn vegetation class information, we selected six of the
nine F-05 sites post-hoc while conducting field work. We classified vegetation within post-hoc sites using the classification scheme developed by Viereck et al. (1992).

**Summer field work and analyses**

A 30 m diameter plot was established at each site and was flagged to facilitate relocation for winter browse surveys. The following information was collected at each plot: vegetation community type, slope (°), aspect, elevation, average tree canopy height (m), and shrub height (m). Vascular and nonvascular plant species were inventoried and classified based on browse preference by moose. This study focused on moose browse consisting of deciduous trees and shrubs. We defined “preferred” tree and shrub species based on the literature (Bryant and Kuropat 1980, Oldemeyer et al. 1977, Wolff and Zasada 1979) (Appendix B). We did not consider birch to be preferred browse in summer.

Two 30 m transect lines were established in each plot. We counted individual preferred plants 1 m of each side of the transect line to estimate browse species density (individuals/ha) and evidence of past browsing (individuals browsed/ha) in the 120 m² transect area. Evidence of browsing was determined by leaf stripping and the presence of dead stems. Stems within 10 cm of each other were defined as one plant. We counted stems between 0.5 - 3.0 m above ground level, which defines the forage heights for moose (Danell and Ericson 1986, Wolff 1978).

We established a second plot at the center of the 30 m plot to measure browse biomass. The size of the sub-plot varied depending on browse plant density and vegetation homogeneity. Within this sub-plot, current annual growth (CAG) on preferred browse was removed and oven dried at 110°C for 48 hours. Stem and leaf material were weighed separately. Leaf material was used to estimate summer biomass (kg/ha).
We evaluated normality for all datasets prior to analysis. Data were not normally distributed, and were not easily transformed. Therefore, we used the non-parametric Kruskal-Wallis one way analysis of variance to detect differences in browse density, biomass, and browsed plant density among burn strata. We used the Mann-Whitney U test to detect pairwise differences between groups when the Kruskal-Wallis test indicated significance. Alpha was set at 0.05 for all tests. Median values are reported, as well as the first (25th) and third (75th) quartiles.

**Winter field work and analyses**

We followed the methods described in Paragi *et al.* (2008) and Seaton *et al.* (2011) to evaluate winter woody browse biomass availability and use in the four burn strata (Unburned, F-72, F-90, and F-05). Sites established in 2012 were revisited in late March, 2013 and sites established in summer 2013 were revisited in late March, 2014.

We re-established plot boundaries in the winter by delineating a 30 m diameter circle in the snow. Within each plot, we recorded slope (°), aspect, and snow depth (m), and documented preferred and non-preferred browse species. Although birch was not considered a preferred species in summer, we classified it as a preferred species in winter (Paragi *et al.* 2008). We counted the number of preferred plants present in the plot. In plots with high, relatively uniform densities of preferred browse, we counted individuals in one quadrat of the 30 m circle and used these data to estimate the number of plants in the entire plot area (707 m²).

We randomly selected three plants of each preferred browse species in the plot. We selected all available specimens if there were less than three plants of a species present. We recorded the species, plant height, number of CAG stems (0.5 – 3.0 m above ground level), and classified each plant as having no (0%) dead CAG stems, <50% dead, and >50% dead CAG stems. An architecture class was assigned to each plant as well: unbrowsed (no evidence of browse),
browsed (<50% of CAG stems were from lateral stems produced from browsing), and broomed
(>50% of CAG stems were from lateral stems). We measured CAG diameter (mm) on a random
sample of 10 twigs/plant using dial calipers. If a twig was browsed, the diameter at point of
browsing (DPB) was measured and recorded. Winter sampling effort (stems/plot measured) is
listed in Appendix C.

Data were entered into a Microsoft Access database and processed using software written in R
(Microsoft Corporation, Redmond, WA, R Project for Statistical Computing, http://www.r-
2008) for each browse species were used from sample twigs gathered on Kanuti NWR in 2007
and provided by the Alaska Department of Fish and Game (ADF&G) (T. Paragi, ADF&G,
personal communication). We calculated winter browse biomass availability and offtake using
these mass:diameter relationships, and our estimates of plant density (individuals/ha) and CAG
twigs/plant with the following formula:

\[
\hat{B} = \sum_j \frac{M_{jk}}{m_{jk}} \sum_i \frac{N_{ijk}}{n_{ijk}} \sum_h z_{hijk}
\]

Where \( \hat{B} \) denotes estimated plot biomass, twigs are denoted by \( h \), plants \( i \), species \( j \), and sites, \( k \).
\( M \) denotes total plants in each plot, \( m \) denotes sampled plants, and \( N \) and \( n \) denote total and
sampled twigs. \( z \) denotes individual twig biomass (g). The R output provided estimates of
biomass production and removal at the plant, species, plot, and study area levels. We estimated
proportional biomass removal (%) per area (kg/ha).

**Habitat use**

ADF&G, the U.S. Fish and Wildlife Service (USFWS), the National Park Service (NPS), and
the Bureau of Land Management (BLM) initiated a GMU 24 moose radiotelemetry study in
2008. One hundred and twenty moose were outfitted with VHF radio collars using techniques
described by Joly et al. (2015). Cooperatively funded Federal and State telemetry flights to locate collared moose were conducted monthly or as weather allowed from 2008 – 2013. Moose were observed when possible to determine presence or absence of calves and document vegetation type. Of the 120 moose originally collared, 51 moose ranged at least partially within the Refuge boundary. Capture efforts occurred throughout the Refuge and were not confined to specific habitat types (e.g. burns) (Table 1). We used radio collar location data from these moose to evaluate use of burn strata in Kanuti NWR. We assumed independence between locations (Dunn and Gipson 1977).

The VHF dataset we used was characterized by small (< 50 locations) sample sizes for each collared animal. Appropriate methods for analyzing habitat use with these samples sizes are limited compared to more robust datasets. We used methods described by Neu et al. (1974) to examine general use of burn strata by moose in Kanuti NWR. Habitat use by individual moose was difficult to assess due to sample size. Therefore, we combined all locations within the Refuge boundary for analysis.

We used a chi-square goodness-of-fit test to determine whether moose were exhibiting seasonal patterns of habitat use that deviated from proportional habitat availability. We first determined proportional availability of burn strata within the Refuge by dividing the number of hectares within each burn class by the total Refuge area. We designated two seasons: “winter” (October – April) and “summer” (May – September). Additionally, we designated a “calving” season (May 28 – June 23; Joly et al. 2015). We then compared the observed number of seasonal moose locations in each stratum to the expected number based on each stratum’s proportional availability. If $P < 0.05$, we determined that seasonal use did not occur in proportion to availability.
Where use of burn strata did not occur in proportion to availability \((P < 0.05)\), we determined whether moose were demonstrating preference (observed number of locations > expected proportion) or avoidance (observed < expected). We determined preference/avoidance and the degree to which they were demonstrated using confidence intervals developed by Neu et al. (1974). Confidence intervals were constructed for the proportion of times an animal used each habitat type. The interval used was:

\[
\tilde{p}_i - z_{(1-\alpha/2k)} \sqrt{\frac{\tilde{p}_i(1-\tilde{p}_i)}{n}} \leq \tilde{p}_i \leq \tilde{p}_i + z_{(1-\alpha/2k)} \sqrt{\frac{\tilde{p}_i(1-\tilde{p}_i)}{n}}
\]

Where \(\tilde{p}_i\) is the proportion of moose locations in the \(i^{th}\) burn stratum, \(n\) is the number of locations, and \(z_{(1-\alpha/2k)}\) is the lower standard normal variate corresponding to a probability tail area of \(\alpha/2k\) where \(k\) is the number of burn strata (4). The \(2k\) denominator was used because multiple confidence intervals were being computed simultaneously. We identified the degrees of freedom (df) as the number of available habitat types \((k)\) minus 1. If the proportion of available habitat was included in the confidence interval, we concluded that preference for or avoidance of a burn stratum was not exhibited. If the value of the lower bound of the confidence interval was greater than the proportion of available habitat, then we concluded that preference was exhibited. Alternatively, if the value of the upper bound was less than the proportion of available habitat, then we concluded that avoidance was exhibited.

**RESULTS**

**Site description**

The burns we selected for study each exceeded 80,000 ha. F-90 and F-05 burned during two of the biggest fire seasons on record. Abiotic characteristics of the burns are summarized in Table 2. The F-72 burn perimeter contains both flat wetlands and uplands with gentle (<10°), south-
facing slopes. Mean elevation in F-72 was 213 m. F-90 was also characterized by gentle slopes, although much of the burn scar was > 300 m in elevation and was dominated by upland vegetation types. The southern perimeter of F-05 abuts the foothills of the Ray Mountains. However, most of the burned area consists of wetlands and permafrost-rich soils. Fire severity in F-05 varied, but was generally moderate to high (Table 3).

Deciduous vegetation types dominated F-72, although over 30% of the vegetation was classified as being evergreen or mixed evergreen-deciduous (Appendix A). While shrub cover types were present in F-72, shrub cover was not as dominant in F-72 as in other burns. F-90 vegetation consisted mostly of deciduous and tall shrub vegetation types. Less than 1% of the vegetation was classified as dwarf shrub. F-05 was also dominated by deciduous and shrub vegetation types prior to burning. The proportion of dwarf shrub and graminoid cover types was highest in F-05 prior to burning. Unburned contained a wide variety of vegetation types and was not dominated by a specific cover type. Deciduous shrubland and evergreen cover were highest in this stratum.

Vegetation types documented at the plot for each study site are listed in Table 4. Forest vegetation communities were encountered most frequently in Unburned and F-72. The occurrence of vegetation communities dominated by woody shrubs was highest in F-90 and F-05, and lowest in F-72. Herbaceous vegetation communities were not observed in older (Unburned and F-72) stands, and were encountered infrequently in F-90 and F-05. Spruce forest was the most common vegetation type observed in Unburned and F-72 plots, and low shrub was most common in F-90 and F-05.

Canopy height varied considerably among burn strata (Table 2). Over 80% of the vegetation in F-72 was classified as > 10 m tall. Similarly, 65% of the vegetation in F-90 was > 5 m tall.
However, 33% of the vegetation in F-90 (compared to 18% in F-72) was classified as shrubs between 0.5 – 1.5 m tall. Half of the vegetation in F-05 was classified as shrubs > 1.5 m tall. Most of the vegetation > 5 m tall was concentrated in riparian areas. 45% of Unburned consisted of trees > 5 m tall. Forest height < 5 m was highest in Unburned due to the high occurrence of old growth black spruce stands throughout this study area.

**Availability and use of browse during summer**

We documented three preferred browse species in Unburned, three in F-72, five in F-90, and five in F-05 (Table 5). The number of preferred browse species among sites ranged from one to five.

Relative abundance (based on the number of individuals) of browse species and birch varied among strata (Fig. 2). Of the six browse species identified, two (S. arbusculoides, and P. tremuloides) were rarely observed. Willow species (S. pulchra, S. glauca, and S. bebbiana) dominated Unburned, F-72, and F-90.

Density of summer browse (excluding birch) ranged from approximately 500 – 18,000 individuals/ha across burn strata. Kruskal-Wallis analysis of variance indicated that median (mdn) values differed significantly. Mann-Whitney U pairwise comparisons among strata indicated that browse densities in F-90 and F-05 (mdn = 10,084 and 6,833 individuals/ha respectively) were greater than densities in F-72 and Unburned (mdn = 2,000 and 5,666, $U = 6$ - 31, $P = 0.01 – 0.04$) (Fig. 3). We did not detect differences in plant density between Unburned and F-72 ($P > 0.05$) or F-90 and F-05 ($P > 0.05$).

Browse use (individuals browsed/ha) in summer was highest in F-72 and F-90 ($U = 10 – 13$, $P = 0.008 – 0.03$) (Fig. 3). The proportion of individuals showing evidence of browse did not differ among Unburned, F-72, and F-05 ($P > 0.05$). The proportion of individuals showing evidence of
browse did not differ among F-72 and F-90 ($P > 0.05$), however, F-90 exhibited significantly higher proportion of browse than Unburned and F-05 ($U = 9$, $P = 0.03$ and $U = 10$, $P = 0.02$ respectively).

Leaf biomass (excluding birch) in summer ranged from approximately 40 kg/ha to over 400 kg/ha (Fig. 4). Biomass in F-90 and F-05 (mdn = 143 and mdn = 189 kg/ha respectively) was significantly higher than Unburned and F-72 (mdn = 16 and mdn = 9 kg/ha respectively, $U = 10 - 20$, $P = 0.001 - 0.03$). These patterns are consistent with those observed for density.

**Availability and use of browse during winter**

Available biomass in winter ranged from approximately 2 kg/ha – 30 kg/ha across study sites (Fig. 5). Winter biomass was highest in F-90 and lowest in Unburned (mdn = 28 and mdn = 24 kg/ha respectively, $U = 9 - 12$, $P = 0.02 - 0.04$). F-05 was dominated by birch, while woody browse in the other burn strata consisted primarily of willow. Sixty-one percent of available biomass in F-90 consisted of willow. In contrast, 10% of available winter biomass in F-05 was willow (Fig. 6).

The total removal rate of woody biomass across all burn strata was 5.4% (95% confidence interval 3.9 – 6.9%; Fig. 5). The highest removal rate was 6% in F-72 and the lowest was 4.5% in Unburned and F-05. Moose removed more woody browse (2.2 kg/ha) in F-72 and F-90 than in Unburned and F-05 ($df = 3$, $P = 0.001$). Additionally, moose generally took larger bites on willow twigs measured in F-90 and Unburned and smaller bites in F-05 (Fig. 7a). These burns were dominated by willow, whereas F-05 was dominated by birch. Browsing on birch was not observed during winter browse surveys, despite increases in the proportional availability of birch as a potential winter food source in F-90 and F-05 (Figs. 5, 7b).
Habitat use

Of the 120 moose collared as part of the GMU 24B study, 51 collared moose ranged at least partially within the boundary of Kanuti NWR from 2008 - 2013. Of these 51 moose (n = 1,356 relocations), three were bulls (n = 213) and 48 were cows (n = 1,142). Relocations per animal ranged from 31 – 56. The mean number of relocations per animal was 45.

Initial capture locations of collared moose did not appear to impact the results of the habitat use analysis. Although the largest number of moose (25) was collared in unburned areas, the habitat use analysis did not suggest that moose preferred these areas exclusively. Alternatively, only six moose were captured in burns >30 years old, but collared moose demonstrated preference for this stratum in both summer and winter. As such, preference or avoidance was likely not an artifact of sampling bias.

During the “summer” season, collared moose exhibited preferential use of burns >30 years old and demonstrated avoidance of burns <11 years old ($\chi^2 = 17.675, df = 3, P < 0.001$) (Fig. 8a). Collared moose did not appear to actively select or avoid unburned areas or 11 – 30 year old burns ($P > 0.05$) during this timeframe. Upon further investigation of locations during calving (28 May – 23 June; n = 120), we found that collared cows prefer unburned stands ($\chi^2 = 11.766, df = 3, P = 0.01$) (Fig. 8b). In winter, collared moose demonstrated preference for stands 11 – 30 years old and avoidance of stands <11 years old ($\chi^2 = 36.074, df = 3, P < 0.001$) (Fig. 8c). Collared moose used unburned areas and stands >30 years old in proportion to their availability in winter.

DISCUSSION

We found that density and biomass of summer browse were highest in F-90, consistent with the general understanding that moose habitat quality peaks between 11- 30 years after fire.
However, density and biomass in F-05 were high as well. Despite high biomass in F-05, use of browse in summer was low. Browsing frequency was highest in F-90 and F-72. Similarly, collared moose avoided <11 year old stands and preferred >30 year old stands in summer. This suggests that moose are not taking advantage of food resources in young burns; rather, use is focused in burns >11 years old. Collared moose avoided burns <11 years old in summer and demonstrated preference for older (>30 years old) stands.

Median values for available browse in winter ranged from < 1 kg/ha to approximately 26 kg/ha across burn strata. While this is consistent with a browse survey done in 2007, which reported an average of 22 kg/ha in GMU 24B, these values are low compared to other areas in interior Alaska (Paragi et al. 2008). Winter browse estimated in studies within GMUs 19, 20, and 21 frequently averages > 200 kg/ha, and local biomass > 400 kg/ha has been reported. While browse removal rates in these areas vary, they are high compared to the < 5% removal rate documented as part of this study. Removal rates were > 20% and ranged as high as 49% in areas where biomass abundance was > 200 kg/ha (Paragi et al. 2008). Although winter food availability appears to be much lower in our study area (GMU 24B) compared to other areas, low removal rates and consistently high twinning rates do not suggest that moose are negatively impacted by this apparent low browse biomass (Craig and Stout 2014).

We found that available browse in winter was highest in F-90, as it was for summer biomass. This supports our original hypothesis. Winter offtake was highest in F-90 and F-72. While considerable food resources (primarily birch) were present in F-05, the majority of browsing during winter was concentrated in older stands. This observation paralleled the habitat use of collared moose in both summer and winter.
Selective feeding on higher quality food resources is demonstrated through this study. While winter biomass in F-05 was high relative to F-72 and Unburned, it is important to note that estimated browse removal in this stratum was extremely low (< 0.5 kg/ha). We observed that the relative abundance of birch compared to willow in F-05 was much higher than in other burns. Despite birch dominance in F-05, browsing on birch was not observed, suggesting that, although birch is accessible and relatively plentiful in this burn, moose do not appear to be using it as a winter food resource. Rather, they are preferentially feeding on willow species, which are nutritionally superior to birch (Hjeljord et al. 1982). Digestibility declines as twig diameter increases because the ratio of digestible material (bark) to undigestible material (wood) decreases with twig size. We found that the DPB of sampled willow twigs was smaller in F-05 than other burns. This suggests that moose are maximizing food resources in older stands by taking larger bites, but are doing so at the expense of nutritive value.

While the results generally support our hypothesis that 11 – 30 year old would have high relative biomass, use of browse resources did not occur in proportion to their availability. Areas <11 years old had relatively high biomass, but moose were not using browse resources in these areas, nor were collared moose actively spending time in recent burns. It is likely that browse species composition is contributing to the patterns we observed, but historic moose distribution patterns and predation avoidance strategies may further explain this disparity.

This study demonstrated that the Kanuti moose are exhibiting selective feeding behavior by way of consuming a higher relative proportion of willows compared to birch. They forego feeding on birch even in winter, when available food resources are restricted to a few species of deciduous trees and shrubs. They avoid recent burns despite the food resources that are available to them in these areas. When they do feed in recent burns, they take smaller bites. This is likely a
consequence of population density. Moose densities are moderate in GMU 24B. As such, competition for habitat and resources is low. Browse pressure on food resources is minimal. Thus, these moose can afford to be highly selective not only as they are making specific decisions while feeding, but as they make broader decisions about habitat selection within their home range.

This study suggests that moose are not taking advantage of areas that have burned in the last decade, despite adequate food resources. Gasaway et al. (1989) found that immigration rates in low and moderate density populations are low, as these populations are generally not constrained by limited space or food resources. Similarly, Schwartz and Franzmann (1989) documented delayed and moderated density responses to disturbance in moose populations limited by predation. Historically high density populations have shown local density changes in as little as 2 years post-fire, but moose density in F-05 has remained low (Peek 1974a, Craig and Stout 2014). We hypothesize that this delayed population response will persist. Moose in Kanuti are not pressured to take advantage of new habitat created by wildfire because they are not limited by habitat. Given that their food resource needs are generally fulfilled, habitat selection is more likely to be a result of other factors such as predation avoidance.

Predation on calves and yearlings in the upper Koyukuk River drainage is high. ADF&G (2012) estimates that 74% of calves die between spring parturition surveys and November population surveys. Twenty-two percent of yearlings die each year, primarily due to wolf (Canis lupus) predation. Previous studies have found that moose, particularly cows with calves, preferentially inhabit forest stands dominated by conifers that offer greater protection from wolves and other predators (Mech 1966, Peterson 1977, Poole et al. 2007). Our results support this, as collared cows demonstrated preference for unburned stands during the calving season and
>30 year old stands throughout the summer. Vegetation in the F-05 burn was characterized by homogeneous stands of early seral vegetation. Present avoidance of burns <11 years old due to lack of vegetative cover and consequent increased predation risk is plausible.

The conclusions we are able to draw are limited due to our small sample size and lack of replication among burn strata. Paragi et al. (2008) suggest that a minimum of 30 plots per stratum are needed to minimize inter-plot variability and draw robust conclusions from winter browse survey data. Adequate sample size is important in areas with low moose densities, as herbivory could be highly localized and biomass removal potentially under or overestimated as a result. We sought to explore relationships between stand age and moose habitat, but access was limited to 3 large burn scars on the Refuge, and further confined to boat/floatplane accessible sites during 2012 field work.

The characteristics of the vegetation in F-05 are likely to change considerably in the next 5 years. However, given the population characteristics of moose in GMU 24B, it may be a number of years before moose begin regularly using F-05 and other recent burns, and establishing core home ranges within their perimeters. Semi-annual moose surveys will continue to be conducted on Kanuti NWR to quantify population changes and distribution shifts through time. These surveys will help managers understand the nuances of moose reestablishment in recent burns, in addition to documenting changes in Refuge-wide population dynamics and addressing broader moose management issues in GMU 24B.

Continued study of habitat and population change through time is particularly relevant in light of climate change. As relay floristics becomes the dominant paradigm for upland succession in interior Alaska, implications for moose and other species must continue to be explored. While research thus far suggests that an increase in deciduous species will benefit moose, the nutritive
value of deciduous trees and shrubs varies. Studying successional change at both large (landscape) and local (e.g. individual burns) scales, specifically as it relates to moose habitat, will improve understanding of habitat under this new fire regime.

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REFERENCES


Table 1. Capture locations of collared moose within burn strata in the vicinity of Kanuti NWR.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Moose captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unburned</td>
<td>25</td>
</tr>
<tr>
<td>&gt;30 years old</td>
<td>6</td>
</tr>
<tr>
<td>11 – 30 years old</td>
<td>10</td>
</tr>
<tr>
<td>&lt;11 years old</td>
<td>10</td>
</tr>
</tbody>
</table>
Table 2. Elevation, slope, dominant aspect, and vegetation characteristics of burn strata based on a digital elevation model (DEM) and LANDFIRE data.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Unburned</th>
<th>F-72</th>
<th>F-90</th>
<th>F-05</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>224</td>
<td>213</td>
<td>332</td>
<td>261</td>
</tr>
<tr>
<td>Min</td>
<td>121</td>
<td>116</td>
<td>160</td>
<td>151</td>
</tr>
<tr>
<td>Max</td>
<td>1068</td>
<td>459</td>
<td>809</td>
<td>889</td>
</tr>
<tr>
<td>Slope (°)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>2.06</td>
<td>2</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Flat</td>
<td>12</td>
<td>31</td>
<td>16</td>
<td>46</td>
</tr>
<tr>
<td>Gentle (&lt;10°)</td>
<td>24</td>
<td>66</td>
<td>76</td>
<td>46</td>
</tr>
<tr>
<td>Medium (10-30°)</td>
<td>32</td>
<td>2</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>Steep (&gt;30°)</td>
<td>32</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dominant aspect</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Canopy height (m)</td>
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<td></td>
</tr>
<tr>
<td>Mean</td>
<td>9</td>
<td>8</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max</td>
<td>12</td>
<td>10</td>
<td>5</td>
<td>4</td>
</tr>
</tbody>
</table>

*a* percent of burn in each slope class
Table 3. Fire severity classifications in F-05.

<table>
<thead>
<tr>
<th>Site</th>
<th>Severity</th>
</tr>
</thead>
<tbody>
<tr>
<td>F-05 - 1</td>
<td>Low</td>
</tr>
<tr>
<td>F-05 - 2</td>
<td>Low</td>
</tr>
<tr>
<td>F-05 - 3</td>
<td>Moderate/High</td>
</tr>
<tr>
<td>F-05 - 4</td>
<td>Moderate/Low</td>
</tr>
<tr>
<td>F-05 - 5</td>
<td>High</td>
</tr>
<tr>
<td>F-05 - 6</td>
<td>Moderate</td>
</tr>
<tr>
<td>F-05 - 7</td>
<td>High</td>
</tr>
<tr>
<td>F-05 - 8</td>
<td>Moderate</td>
</tr>
</tbody>
</table>
Table 4. Vegetation types\textsuperscript{a} observed in each burn stratum. Vegetation types are ranked based on their observed frequency in burn strata.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Vegetation code</th>
<th>Vegetation type</th>
<th># Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unburned</td>
<td>I.A</td>
<td>Needleleaf forest</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>II.C</td>
<td>Low shrub</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>I.B</td>
<td>Deciduous forest</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>I.C</td>
<td>Mixed forest</td>
<td>1</td>
</tr>
<tr>
<td>F-72</td>
<td>I.A</td>
<td>Needleleaf forest</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>I.B</td>
<td>Deciduous forest</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>I.C</td>
<td>Mixed forest</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>II.D</td>
<td>Dwarf shrub</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>II.C</td>
<td>Low shrub</td>
<td>1</td>
</tr>
<tr>
<td>F-90</td>
<td>II.C</td>
<td>Low shrub</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>I.B</td>
<td>Deciduous forest</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>I.C</td>
<td>Mixed forest</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>II.B</td>
<td>Tall shrub</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>II.D</td>
<td>Dwarf shrub</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>III.A</td>
<td>Graminoid herbaceous</td>
<td>1</td>
</tr>
<tr>
<td>F-05</td>
<td>II.C</td>
<td>Low shrub</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>II.D</td>
<td>Dwarf shrub</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>I.B</td>
<td>Deciduous forest</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>III.A</td>
<td>Graminoid herbaceous</td>
<td>1</td>
</tr>
</tbody>
</table>

\textsuperscript{a} The Alaska Vegetation Classification (Viereck \textit{et al.} 1992)
Table 5. Preferred browse species (trees and shrubs) documented in each burn stratum.

<table>
<thead>
<tr>
<th>Preferred</th>
<th>Unburned</th>
<th>F-72</th>
<th>F-90</th>
<th>F-05</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. neoalaskana\textsuperscript{a}</td>
<td>B. neoalaskana\textsuperscript{a}</td>
<td>B. neoalaskana\textsuperscript{a}</td>
<td>B. neoalaskana\textsuperscript{a}</td>
<td></td>
</tr>
<tr>
<td>S. bebbiana</td>
<td>S. bebbiana</td>
<td>S. arbusculoides</td>
<td>S. arbusculoides</td>
<td></td>
</tr>
<tr>
<td>S. glauca</td>
<td>Salix glauca</td>
<td>S. bebbiana</td>
<td>S. bebbiana</td>
<td></td>
</tr>
<tr>
<td>S. pulchra</td>
<td>S. pulchra</td>
<td>S. glauca</td>
<td>S. glauca</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>S. pulchra</td>
<td>S. pulchra</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. tremuloides</td>
<td>S. scouleriana</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P. tremuloides</td>
<td></td>
</tr>
<tr>
<td>Non-preferred</td>
<td>A. crispa</td>
<td>A. crispa</td>
<td>A. crispa</td>
<td>A. crispa</td>
</tr>
<tr>
<td>A. tenufolia</td>
<td>B. glandulosa</td>
<td>B. glandulosa</td>
<td>B. glandulosa</td>
<td></td>
</tr>
<tr>
<td>B. glandulosa</td>
<td>B. nana</td>
<td>B. nana</td>
<td>B. nana</td>
<td></td>
</tr>
<tr>
<td>B. nana</td>
<td>B. neoalaskana\textsuperscript{b}</td>
<td>B. neoalaskana\textsuperscript{b}</td>
<td>B. neoalaskana\textsuperscript{b}</td>
<td></td>
</tr>
<tr>
<td>B. neoalaskana\textsuperscript{b}</td>
<td>P. balsamifera\textsuperscript{b}</td>
<td>P. balsamifera\textsuperscript{b}</td>
<td>P. mariana</td>
<td></td>
</tr>
<tr>
<td>S. bebbiana\textsuperscript{b}</td>
<td>S. bebbiana\textsuperscript{b}</td>
<td>S. bebbiana\textsuperscript{b}</td>
<td>P. tremuloides</td>
<td></td>
</tr>
<tr>
<td>P. glauca</td>
<td>P. glauca</td>
<td>P. tremuloides\textsuperscript{b}</td>
<td>R. acicularis</td>
<td></td>
</tr>
<tr>
<td>P. mariana</td>
<td>P. mariana</td>
<td>P. glauca</td>
<td>S. beauverdiana</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. mariana</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{a} preferred browse species in winter only
\textsuperscript{b} mature individual (>3 m tall)
Figure 1. Sample site locations and age of fire scars visited, Kanuti National Wildlife Refuge, Alaska.
Figure 2. Relative abundance (based on the number of individuals) of preferred browse species and birch during summer. BENE denotes *Betula neoalaskana*, SAPU denotes *Salix pulchra*, SAGL denotes *S. glauca*, and SABE denotes *S. bebbiana*. “Other” denotes *Populus tremuloides* and *P. balsamifera*. 
Figure 3. Total and browsed plant densities (individuals/ha) for preferred browse during summer (excluding *Betula neoalaskana*). The lower bound represents the 1st (25%) quartile, center lines indicate median values, and upper bound represents the 3rd (75%) quartile. Letters denote significantly different groups based on Kruskal-Wallis analysis of variance and Mann-Whitney U post-hoc pairwise comparisons.
Figure 4. Summer leaf biomass (kg/ha) of preferred browse by burn strata. The lower bound represents the 1st (25%) quartile, center lines indicate median values, and upper bound represents the 3rd (75%) quartile. Letters denote significantly different groups based on Kruskal-Wallis analysis of variance and Mann-Whitney U post-hoc pairwise comparisons.
Figure 5. Winter biomass and removal\textsuperscript{a} (kg/ha) of preferred browse by burn strata. The lower bound represents the 1\textsuperscript{st} (25\%) quartile, center lines indicate median values, and upper bound represents the 3\textsuperscript{rd} (75\%) quartile. Letters denote significantly different groups based on Kruskal-Wallis analysis of variance and Mann-Whitney U \textit{post-hoc} pairwise comparisons.

\textsuperscript{a} browsed \textit{Betula neoalaskana} was not observed; reported values of removed biomass are exclusively \textit{Salix} spp.
Figure 6. Relative abundance of browse (based on biomass) during winter. BENE denotes *Betula neoalaskana*, SA SPP. denotes *Salix* spp.
Figure 7a. Willow CAG (current annual growth) and DPB (diameter at point of browsing) frequency distributions for each burn stratum.
Figure 7b. BENE (*Betula neoalaskana*) CAG (current annual growth) diameter frequency distributions for each burn stratum. Browsing of birch was not observed.
Figure 8a. Selection (use/availability) of burn age classes by collared moose during summer (May – September), Kanuti National Wildlife Refuge, Alaska, 2008 – 2013. Values indicate proportion of relocations observed in each stratum. Confidence intervals (95%) >1 indicate preference, whereas values <1 indicate avoidance. Confidence intervals overlapping 1 indicate that use of strata occurred in proportion to availability.
Figure 8b. Selection (use/availability) of burn age classes by collared cow moose during calving (28 May – 23 June), Kanuti National Wildlife Refuge, Alaska, 2008 – 2013. Values indicate proportion of relocations observed in each stratum. Confidence intervals (95%) >1 indicate preference, whereas values <1 indicate avoidance. Confidence intervals overlapping 1 indicate that use of strata occurred in proportion to availability.
Figure 8c. Selection (use/availability) of burn age classes by collared moose during winter (October - April), Kanuti National Wildlife Refuge, Alaska, 2008 – 2013. Values indicate proportion of relocations observed in each stratum. Confidence intervals (95%) >1 indicate preference, whereas values <1 indicate avoidance. Confidence intervals overlapping 1 indicate that use of strata occurred in proportion to availability.
Appendix A. LANDFIRE classification of vegetation types in burn strata. Note that the vegetation types for F-05 reflect the composition prior to burning.

<table>
<thead>
<tr>
<th>% Class</th>
<th>Unburned</th>
<th>F-72</th>
<th>F-90</th>
<th>F-05</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed tree canopy</td>
<td>28</td>
<td>50</td>
<td>55</td>
<td>15</td>
</tr>
<tr>
<td>Dwarf shrubland</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Herbaceous - grassland</td>
<td>11</td>
<td>9</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>Non-vegetated</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Open tree canopy</td>
<td>21</td>
<td>13</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>Shrubland</td>
<td>30</td>
<td>23</td>
<td>34</td>
<td>53</td>
</tr>
<tr>
<td>Sparse tree canopy</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sparsely vegetated</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>% Sub-class</th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Aquatic</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Deciduous</td>
<td>16</td>
<td>19</td>
<td>38</td>
<td>25</td>
</tr>
<tr>
<td>Deciduous dwarf-shrubland</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Deciduous shrubland</td>
<td>23</td>
<td>21</td>
<td>20</td>
<td>35</td>
</tr>
<tr>
<td>Evergreen</td>
<td>18</td>
<td>18</td>
<td>31</td>
<td>9</td>
</tr>
<tr>
<td>Evergreen open tree canopy</td>
<td>17</td>
<td>8</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>Mixed</td>
<td>2</td>
<td>16</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mixed evergreen-deciduous open tree canopy</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Non-vegetated</td>
<td>7</td>
<td>3</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Perennial graminoid</td>
<td>10</td>
<td>8</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Perennial graminoid or annual</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Sparsely vegetated</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
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</table>

<table>
<thead>
<tr>
<th>% Vegetation height class</th>
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<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Sparse vegetation</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Shrub height &gt; 1.5m</td>
<td>2</td>
<td>8</td>
<td>21</td>
<td>47</td>
</tr>
<tr>
<td>Shrub height 0.5 - 1.5m</td>
<td>13</td>
<td>2</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Shrub height 0-0.5m</td>
<td>6</td>
<td>8</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Herb height &gt;0.5m</td>
<td>10</td>
<td>1</td>
<td>1</td>
<td>14</td>
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<tr>
<td>Herb height 0-0.5m</td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Forest height &gt;50m</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Forest height 5-10m</td>
<td>23</td>
<td>15</td>
<td>9</td>
<td>25</td>
</tr>
<tr>
<td>Forest height 25-50m</td>
<td>0</td>
<td>45</td>
<td>31</td>
<td>2</td>
</tr>
<tr>
<td>Forest height 10-25m</td>
<td>22</td>
<td>21</td>
<td>25</td>
<td>10</td>
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<tr>
<td>Forest height 0-5m</td>
<td>16</td>
<td>0</td>
<td>0</td>
<td>1</td>
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Appendix B. Preferred and non-preferred browse species classifications.

<table>
<thead>
<tr>
<th>Preferred browse species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Salix alaxensis</em></td>
</tr>
<tr>
<td><em>Salix pulchra</em></td>
</tr>
<tr>
<td><em>Salix arbusculoides</em></td>
</tr>
<tr>
<td><em>Salix bebbiana</em></td>
</tr>
<tr>
<td><em>Populus balsamifera</em></td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
</tr>
<tr>
<td><em>Betula neoalaskana</em> (winter only)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Non-preferred browse species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea mariana</em></td>
</tr>
<tr>
<td><em>Picea glauca</em></td>
</tr>
<tr>
<td><em>Alnus</em> spp.</td>
</tr>
<tr>
<td><em>Betula glandulosa</em></td>
</tr>
<tr>
<td><em>Betula nana</em></td>
</tr>
<tr>
<td><em>Populus tremuloides</em>(^a)</td>
</tr>
<tr>
<td><em>Populus balsamifera</em>(^a)</td>
</tr>
<tr>
<td><em>Betula neoalaskana</em>(^a)</td>
</tr>
</tbody>
</table>

\(^a\) mature individual (>3 m tall)
Appendix C. Winter browse survey sampling effort by burn stratum, 2013-2014.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>$n$ Plots</th>
<th>$n$ Plants</th>
<th>$n$ Twigs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unburned</td>
<td>8</td>
<td>37</td>
<td>372</td>
</tr>
<tr>
<td>F-72</td>
<td>9</td>
<td>39</td>
<td>386</td>
</tr>
<tr>
<td>F-90</td>
<td>11</td>
<td>76</td>
<td>747</td>
</tr>
<tr>
<td>F-05</td>
<td>9</td>
<td>43</td>
<td>430</td>
</tr>
<tr>
<td>Total</td>
<td>37</td>
<td>195</td>
<td>1935</td>
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</table>
CONCLUSION

The results of this study indicate the following: 1) while 11-30 year old stands remain important for moose on Kanuti NWR, older stands serve as important habitat as well, and 2) moose are not taking advantage of the browse resources in recently burned areas in proportion to their abundance. These results suggest that moose are responding to other factors in addition to simply vegetative succession as a function of stand age. Here, I explore these factors and the roles they play. Specifically, I discuss the impacts of a changing fire regime on moose habitat.

I observed selective feeding patterns on Kanuti NWR, as moose did not use seasonal biomass in proportion to its availability in F-05. In fact, seasonal browse use was lowest in this stratum despite this burn having comparatively high browse biomass. The majority of the woody biomass in this burn was composed of birch, which is less preferred compared to species such as aspen and willow. This preference was clearly demonstrated in this study, as I did not observe browsing on birch in either summer or winter.

Nutrition plays an important role in food selection and feeding patterns of moose. Foraging theory suggests that moose seek to maximize quality food intake while minimizing the time it takes to process that food (Franzmann and Schwartz 2007). Moose are highly selective when forage quality and quantity are high (Sæther and Andersen 1990). They feed only on certain species, take smaller bites, and often take fewer bites per plant, thereby maximizing digestibility (Hjeljord et al. 1982, Vivas and Sæther 1987). By contrast, they will more fully utilize available resources when forage is limited. The smaller bite size observed on browse in F-05 is consistent with these ideas.

Additionally, I observed selective habitat use patterns. For example, collared moose demonstrated avoidance of recently burned areas, despite high browse biomass in these areas. Avoidance of recent burns was most pronounced in winter. Collared moose generally favored
older successional stands, and cows preferred unburned stands during calving. These data suggest that large scale habitat selection is not dictated solely by food resources. Rather, habitat selection at this scale may be a function more of the need for adequate cover and predator avoidance.

Area wildlife managers have identified predation as the primary factor limiting population growth on Kanuti NWR (Stout 2010). Calf and yearling cohorts are often subject to particularly high predation rates, resulting in low adult recruitment. Whereas habitat on the Refuge likely has the capacity to support higher densities of moose, local densities remain moderate. Given this, it is not surprising that moose are exhibiting selective feeding behaviors. Competition for food is likely nonexistent, and, with nutrition needs satisfied, individuals are able to make habitat use decisions that reduce predation risk.

These observations are particularly interesting in light of climate change. There is conclusive evidence that the fire regime in interior Alaska is changing. Wildfire frequency and severity are increasing, and large fires are occurring more frequently (Kasischke et al. 2010). Successional processes and vegetation patterns are changing as a result of these landscape-scale changes. Whereas boreal forest uplands formerly underwent self-replacement after disturbances such as fire, studies have shown that relay floristics is becoming more dominant as a successional pathway under this new fire regime, particularly as high fire severity becomes more common (Dyrness et al. 1986, Johnstone et al. 2010). When fire severity is high, exposure of mineral soil enables wind-dispersed species such as aspen, willows, and birch to colonize sites that would otherwise be dominated by ericaceous species and ultimately, black spruce (Chapin et al. 2008). Under relay floristics, establishment of black spruce and other species may be delayed
or permanently converted to a deciduous stand or open meadow (Kasischke et al. 2010, Shenoy et al. 2011).

The changing fire regime is generally predicted to be beneficial to moose both through the expansion of shrub habitats in arctic and alpine regions, and the increase of deciduous species on the landscape (Tape et al. 2016, Franzmann and Schwartz 2007). However, the type of deciduous species that reestablish in recent burns is important in determining the characteristics and quality of these areas as moose habitat. Higher fire severity may be advantageous to wind-dispersed species such as birch, but may hinder the ability of willows and other shrubs to re-sprout from surviving plants post-fire. Moose habitat will change considerably if birch does indeed become the dominant deciduous species to colonize upland areas after wildfire. Moose populations such as the Kanuti moose may be restricted in their ability to be highly selective simply because the presence of high quality habitat declines. While it is unclear whether this will negatively impact the health of individual moose or local population dynamics, careful study of these changes in individual burns such as the 2005 burn will be important for informing both wildlife and land management.
References


