AVAILABILITY AND USE OF MOOSE BROWSE IN RESPONSE TO POST-FIRE SUCCESSION ON KANUTI NATIONAL WILDLIFE REFUGE, ALASKA

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ABSTRACT: Wildfire is a prominent landscape-level disturbance in interior Alaska and associated vegetation changes affect quantity and quality of moose (*Alces alces*) habitat. These changes are important to land and wildlife managers responsible for managing habitat and ensuring sustained yield of game species such as moose. Considering the changing fire regime related to climate change, we explored post-fire dynamics of moose habitat to broaden understanding of local habitat characteristics associated with wildfire on the Kanuti National Wildlife Refuge in interior Alaska. We studied 34 sites in different aged stands (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, and revisited each site the following March to estimate winter browse availability and offtake. We also used location data from 51 radio-collared moose to quantify use of burns on the Kanuti National Wildlife Refuge. We found that summer density and biomass of preferred browse was highest at sites in the 1990 burn, although use of burns varied seasonally. Despite high biomass in the most recent 2005 burn, radio-collared moose avoided burns <11 years old in summer and had preference for older stands (>30 years old). Winter browse offtake was highest in the 1990 and 1972 burns despite relatively high biomass available in the 2005 burn. The disparate use of burns, particularly low use of the 2005 burn, likely reflected a combination of influences including species composition and preference, predator avoidance strategies, a low density moose population, and historic moose distribution patterns.

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The fire regime in interior Alaska is changing as a result of climate change. This shift is characterized by shorter fire intervals and an increase in late-season fires, frequency of large (>1000 km^2) fires, and higher-severity fires (Kasischke and Turetsky 2006, Kasischke et al. 2010) that influence post-fire vegetation patterns at local and landscape scales. Specifically, higher-severity fires result in deeper burning of the surface organic layer that increases establishment of deciduous species while negatively impacting recruitment of black spruce (*Picea mariana*) (Johnstone 2006). Increased prevalence of high-severity fires could cause a major vegetative shift from coniferous black spruce communities to those dominated by deciduous species (Johnstone et al. 2010b). Such

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landscape-scale changes can impact wildlife habitat and, consequently, wildlife populations either in a positive or negative direction depending on species-specific habitat requirements. Therefore, vegetation changes associated with a changing fire regime are essential to consider when developing future habitat management objectives.

Predicted change in the boreal fire regime is anticipated to be generally beneficial to moose (*Alces alces*) because it is hypothesized that deciduous species will increase in and/or dominate certain plant communities (Chapin et al. 2008, Johnstone et al. 2010a). Moose commonly consume willow (*Salix* spp.), birch (*Betula neoalaskana)*, and aspen (*Populus tremuloides*) regrowth maintained by natural disturbances such as wildfire. Maier et al. (2005) found that in November moose preferentially use forest stands where fire occurred 11–30 years ago, and quantity and quality of browse is highest (Oldemeyer 1974, Oldemeyer et al. 1977, MacCracken and Viereck 1990, Lord and Kielland 2015). Additionally, the physical structure of these stands provides moose year-round access to browse, whereas shorter vegetation in early seral stands (<11 years old) is often unavailable due to snow depth. Likewise, mature birch and Bebb's willow (*S. bebbiana)* in late seral stands are often inaccessible given their height >3.0 m (Wolff and Zasada 1979, Danell and Ericson 1986). Moose populations respond to disturbance and vegetative succession in a number of ways; for example, individuals actively immigrate into recently disturbed areas (Peek 1974b) and moose density changes through time in response to habitat (Loranger et al. 1991).

Wildfire and flooding are the primary natural disturbance agents on the Kanuti National Wildlife Refuge (Refuge). The varied fire history on the Refuge has created many forest stands of diverse size and age, although it is dominated currently by black spruce communities highly susceptible to conversion to deciduous communities after severe wildfire. In addition, moose populations in the upper Koyukuk River drainage, including the Refuge, are primarily regulated by predation (Stout 2010). The role of wildfire in areas with dense moose populations is well studied in Alaska, specifically due to management concerns regarding habitat degradation and carrying capacity (Boertje et al. 2000, 2009, Lord and Kielland 2015). Conversely, habitat use is less explored in regions with lower density populations regulated by predation.

Although habitat is not believed to regulate the Refuge moose population, it is important to understand the influence of a changing fire regime on the interactions between habitat dynamics and moose distribution and habitat use. We sought to examine habitat characteristics in stands at various stages of post-fire succession on the Refuge to provide insight about these interactions. Specifically, we evaluated browse availability and use in summer and late winter in multiple-aged burn scars within the Refuge. We also used location data from radio-collared moose to explore their use of burns. We predicted that summer and winter browse availability and use would be highest in 11–30 year-old stands, and that moose would exhibit a preference for these stands in winter.

STUDY AREA

The study took place on the Refuge which consists of ~3.2 million roadless ha (1.3 million acres) located between 65° 59' to 66° 53' N and 150° 58' to 152° 58' W in interior Alaska (Fig. 1). It is representative of the boreal forest biome characterized by plant diversity and vegetation patterns dictated by climate, hydrology, and wildfire. The climate is cold and continental, with

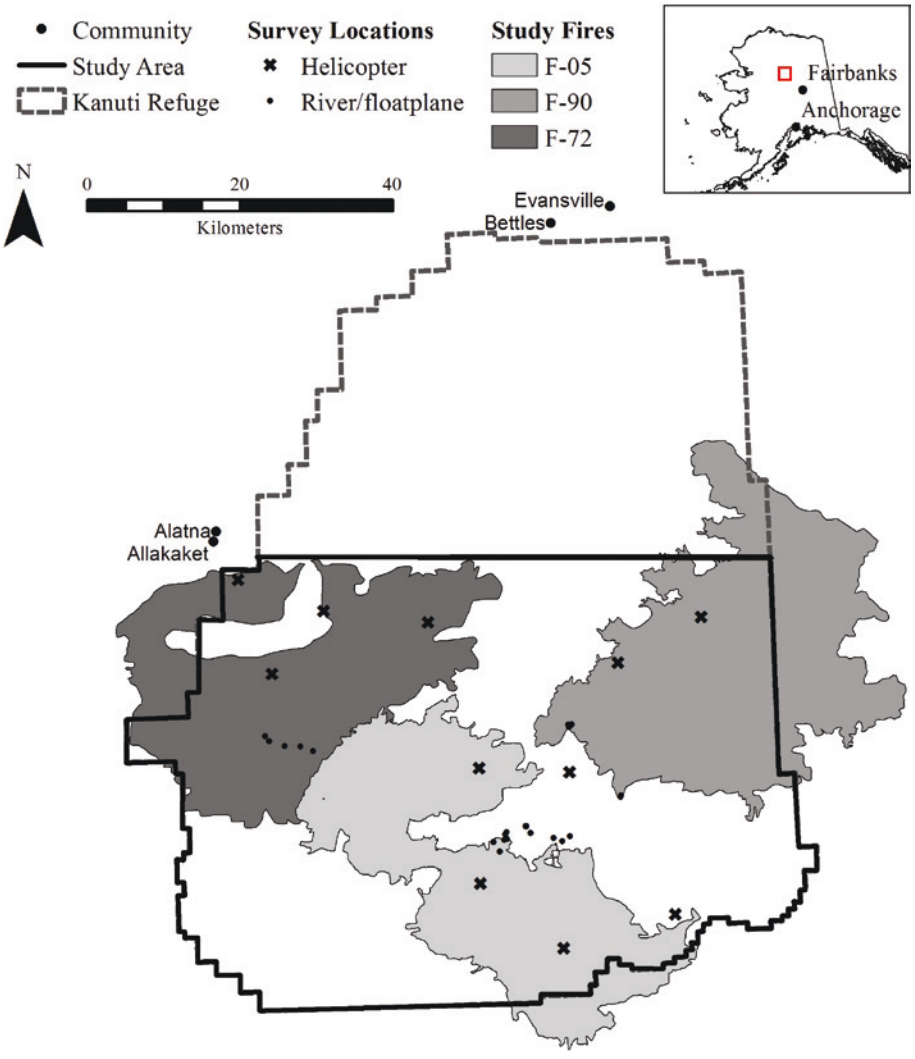

Fig. 1. Sample site locations and age of fire scars studied in the Kanuti National Wildlife Refuge, Alaska, USA (2012–2013).

short hot summers and long cold winters. Mean monthly temperature ranges from ~ −28°C in January to 20°C in July (Western Region Climate Center 2014; http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak0761). The growing season is short, generally beginning in late May and ending in August.

The Refuge occupies the broad lowland flats between the Koyukuk and Kanuti Rivers. The Kanuti basin is characterized by poor drainage and riparian wetlands created and maintained by seasonal flooding and the presence or absence of permafrost. Vegetation patterns 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 density ranges from 0.07 to 0.18 moose/km^2, with the Kanuti population fluctuating between 551 and 759 moose since 1993 (Julianus and Longson 2018). The most recent Refuge estimate was 1311 ± 252 (90% CI) in 2017 (Julianus and Longson 2018). Hunting pressure is light and localized near villages and along navigable rivers. Moose are considered large and healthy with high twinning rates (35–60%) indicative of good nutrition (Franzmann and Schwartz 1985, Stout 2010) in the Game Management Unit that includes the Refuge. 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) and purportedly due to high calf and yearling mortality from predation (Saperstein et al. 2009, Craig and Stout 2011). The characteristics of adequate production yet low adult recruitment have been documented in other low density moose populations in Alaska (Bertram and Vivion 2002, Lake et al. 2013).

METHODS

Site description

We established 4 burn age strata across fire scars on the Refuge based on seasonal landscape use patterns by moose (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 3 different 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); unburned sites were visited to identify sites for burn stratum 4.

We characterized abiotic factors across each burn stratum (F-05, F-90, F-72, and Unburned). We used a digital elevation model (DEM) to determine the mean, minimum, and maximum elevations, and ArcMap 10.1 (Esri, Redlands, California, USA) 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°).

The Alaska LANDFIRE vegetation map (2008) was used to quantify vegetation types and stand height classes in each burn strata. Because much of the Refuge is dominated by black spruce communities considered low quality moose habitat, we excluded these during site selection. Instead, we selected vegetation types that were more likely used by moose within each burn stratum (Appendix A). We isolated vegetation types with >3 adjacent pixel groups (areas >30 m^2) and generated different lists for randomly derived boat/float plane or helicopter accessible sites. In 2012, field work was restricted to areas accessible by boat/float plane from the Kanuti River; in 2013, a helicopter was used to access more remote areas within a burn. For the boat/float plane accessible sites, a 200 m buffer was created around the Kanuti River and Tachlodaten Lake (a lake ~12 miles north of the Kanuti River) and random points were generated within 300 m outside the buffer. If necessary, a <200 m buffer was implemented to avoid sampling in the floodplain which was subject to flood disturbance dynamics. In total, 34 sites were sampled (8 in Unburned, 9 in F-72, 8 in F-90, and 9 in F-05): 11 boat/float plane sites in summer 2012 and spring 2013, and 23 helicopter sites in summer 2013 and spring 2014 (Fig. 1). Because the digital vegetation classification pre-dated F-05 and post-burn vegetation class information was lacking, we selected 6 of the 9 F-05 sites *post-hoc* while conducting fieldwork. We classified vegetation at these sites

using the scheme developed by Viereck et al. (1992).

Summer field work and analyses

A 30 m diameter plot was established at each site and flagged to facilitate relocation for winter browse surveys. The following were measured at each plot: vegetation community type, slope (°), aspect, elevation, average tree canopy height (m), and shrub height (m). Additionally, we used photos to evaluate and classify fire severity at each plot as low, moderate, or high (Kasischke et al. 2008). Vascular and nonvascular plant species were inventoried and classified relative to moose browsing preference of deciduous trees and shrubs described in the literature (Oldemeyer et al. 1977, Wolff and Zasada 1979, Bryant and Kuropat 1980; Appendix A). We did not consider birch as preferred summer browse.

Two 30 m transect lines were established in each plot. We counted individual preferred plants within 1 m of the line (both sides or 120 m^2) to estimate browse species density (individuals/ha) and evidence of past browsing (individuals browsed/ha) in the 120 m^2 transect area. Evidence of browsing by moose, snowshoe hare (*Lepus americanus*), and other species was noted. Browsing was identified from leaf stripping and the presence of dead stems. We counted stems at the general foraging height of moose between 0.5 and 3.0 m above ground level (Wolff 1978, Danell and Ericson 1986). The extent of browsing was not described during summer, but architecture classes (unbrowsed, browsed, or broomed) were assigned to individual plants during winter field work (see *Winter field work and analyses*).

Stems within 10 cm of each other were defined as one plant. At the center of the 30 m plot, we also established a second plot to measure browse biomass. The size of this sub-plot varied depending on browse plant density and vegetative homogeneity. Within this sub-plot, the current annual growth (CAG) of stems on preferred browse species was removed and oven dried at 110°C for 48 h. Stem and leaf material were weighed separately, and leaf material was used to estimate summer biomass (kg/ha).

We evaluated normality for all data sets prior to analysis; however, data were not normally distributed or 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 evaluated biomass availability and use of winter woody browse in the 4 burn strata (Unburned, F-72, F-90, and F-05) following the methods of Paragi et al. (2008) and Seaton et al. (2011). 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 not considered preferred in summer, we classified birch as a preferred winter browse species (unpublished data, 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 species, 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 (707 m^2).

In each plot we randomly selected 3 plants of each preferred browse species, or if <3 plants, all available specimens. We recorded the species, plant height, number of CAG stems (0.5–3.0 m above ground level), and classified each plant as having 0%, <50%, or >50% dead CAG stems. An architecture class was also assigned to each plant: unbrowsed (no evidence of browse), browsed (<50% of CAG stems were from lateral stems produced from browsing), or 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, and if a twig was browsed, the diameter at point of browsing (DPB). The winter sampling effort (stems/plot measured) is provided in Appendix B.

Data were entered into a Microsoft Access database and processed using software written in R (Microsoft Corporation, Redmond, Washington, USA; R Project for Statistical Computing, <http://www.r-project.org> [accessed February 2015]). Mass:diameter regression relationships for each browse species were previously developed (Paragi et al. 2008) from sample twigs gathered on the Refuge in 2007 and provided by the Alaska Department of Fish and Game (ADFG) (T. Paragi, ADFG, personal communication). We calculated winter browse biomass availability and removal using these mass:diameter relationships, and our estimates of plant density (individuals/ha) and CAG twigs/plant with the following formula:

$$\hat{\mathrm{B}} = \Sigma_j \frac{M_{jk}}{m_{jk}} \Sigma_i \frac{N_{ijk}}{n_{ijk}} \Sigma_h z_{hijk}$$

where $\hat{\mathrm{B}}$ denotes estimated plot biomass, twigs are denoted by *h,* plants *i*, species *j*, and sites *k*. *M* denotes total plants in each plot, *m* sampled plants, and *N* and *n* total and sampled twigs, respectively; *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 rates (%) based on browse production and consumption for each area (kg/ha) per year.

Habitat use

In 2008 the ADFG, U.S. Fish and Wildlife Service (USFWS), National Park Service (NPS), and Bureau of Land Management (BLM) initiated a radio-telemetry study of moose in Game Management Unit 24 which includes the Refuge (Joly et al. 2015). Of the 120 moose, 51 (48 adult cows, 3 adult bulls) ranged at least partially within the Refuge; the study targeted adult cows (97 of 123 captured animals). Radio-collared moose were located monthly or as weather allowed during telemetry flights from 2008 to 2013. The average number of relocations per animal was 45, ranging from 31 to 56 per animal.

Radio-collared moose were observed when possible to, in part, document the vegetation type within which they were observed. Capture efforts occurred throughout the Refuge and were not confined to specific habitat types (e.g., burns); 25 moose were captured in Unburned areas, 6 in >30 year-old burns, and 10 in both 11–30 and >11 year-old burns. We used their location data to evaluate use of the burn strata and assumed independence between locations (Dunn and Gipson 1977).

The VHF data set was characterized by small (<50 locations) sample sizes for each marked animal. Because appropriate methods for analyzing habitat use with these sample sizes are limited, we used methods described by Neu et al. (1974) to examine general use of burn strata. Habitat use by

individual moose was difficult to assess due to sample size; therefore, we combined all locations within the Refuge for analysis.

We used a chi-square goodness-of-fit test to determine whether moose exhibited seasonal patterns of habitat use that deviated from proportional habitat availability. We first determined proportional availability of burn strata by dividing the number of ha within each burn class by the total Refuge area. We designated 2 seasons – "winter" (October–April) and "summer" (May–September) – and also a separate "calving" season (May 28–June 23; Joly et al. 2015). We compared the observed number of seasonal locations in each stratum to the expected number based on each stratum's proportional availability. If $P < 0.05$, we concluded that seasonal use did not occur in proportion to availability.

Where use of burn strata was not in proportion to availability ($P < 0.05$), we examined whether moose demonstrated 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 equaled:

$$\overline{p}_i - z_{(1-\alpha/2k)}\sqrt{\frac{\overline{p}_i\left(1-\overline{p}_i\right)}{n}} \le \overline{p}_i \le \overline{p}_i + z_{(1-\alpha/2k)}\sqrt{\frac{\overline{p}_i\left(1-\overline{p}_i\right)}{n}}$$

where $\overline{p}_i$ is the proportion of moose locations in the ith 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 lower bound of the confidence interval was greater than the proportion of available habitat, we concluded preference was exhibited; alternatively, if the upper bound was less than the proportion of available habitat, we concluded that avoidance was exhibited.

RESULTS

Site description

Each burn used in this study was >80,000 ha and F-90 and F-05 occurred during 2 of the biggest fire seasons on record. Abiotic characteristics of the 4 burn sites are summarized in Appendix C. The F-72 burn perimeter contained both flat wetlands and uplands with gentle (<10°) south-facing slopes, with an elevation of 213 m. F-90 was also characterized by gentle slopes, although much of the burn scar was >300 m in elevation and dominated by upland vegetation types. The southern perimeter of F-05 abutted the foothills of the Ray Mountains with most of the burn consisting of wetlands and permafrost-rich soils; fire severity was classified as moderate-high based on multiple site assessments within the fire scar (Appendix D).

Based on LANDFIRE (Appendix E), F-72 was dominated by deciduous vegetation types, and F-90 consisted mostly of deciduous and tall shrub vegetation types (38% and 20% respectively). Post-burn LANDFIRE data for F-05 were unavailable; however, prior to burning, F-05 was mostly deciduous (25%) and shrub vegetation types (35%). The Unburned stratum contained a wide variety of vegetation types and was without a dominant cover type. Vegetation types were further documented during site visits (Table 1): the F-72 fire scar

Table 1. Vegetation types studied in 4 burn strata in the Kanuti National Wildlife Refuge, Alaska, USA. Using the Alaska Vegetation Classification (Viereck et al. 1992), types are ranked based on their frequency in each stratum.

Stratum	Vegetation code	Vegetation type	# Plots
Unburned	I.A	Needleleaf forest	3
	II.C	Low shrub	3
	I.B	Deciduous forest	1
	I.C	Mixed forest	1
F-72	I.A	Needleleaf forest	3
	I.B	Deciduous forest	2
	I.C	Mixed forest	2
	II.D	Dwarf shrub	2
	II.C	Low shrub	1
F-90	II.C	Low shrub	3
	I.B	Deciduous forest	1
	I.C	Mixed forest	1
	II.B	Tall shrub	1
	II.D	Dwarf shrub	1
	III.A	Graminoid herbaceous	1
F-05	II.C	Low shrub	5
	II.D	Dwarf shrub	2
	I.B	Deciduous forest	1
	III.A	Graminoid herbaceous	1

was ~67% forest and 33% shrub; the F-90 fire scar was ~25% forest, 63% shrub, and 12% herbaceous; the F-05 fire scar was ~11% forest, 78% shrub, and 11% herbaceous; and the Unburned stratum was ~63% forest and 37% shrub.

Canopy height varied considerably among burn strata (Appendix C). In F-72 the height of >80% of vegetation was >10 m, and 65% was >5 m in F-90; conversely, 33% of vegetation in F-90 and 18% in F-72 was classified as shrubs 0.5–1.5 m in height, and 50% in F-05 was classified as shrubs >1.5 m. Vegetation >5 m tall was mostly concentrated in riparian areas. In the Unburned, only 45% of trees were >5 m; heights <5 m reflected the preponderance of old growth black spruce stands throughout.

Availability and use of browse during summer

We documented 3 preferred browse species in Unburned and F-72, and 5 in F-90 and F-05 (Table 2); the range was 1–5 species at a given site. Density of summer browse (excluding birch) ranged from ~500 to 18,000 individuals/ha across the burn strata; the Kruskal–Wallis test indicated that the median (mdn) values were different. Pairwise comparisons (Mann–Whitney test) among strata indicated that browse density in F-90 and F-05 (mdn = 10,084 and 6833 individuals/ha, respectively) was greater than that in F-72 (2000 individuals/ha) and Unburned (5666 individuals/ha) (U = 6–31, P = 0.01–0.04; Fig. 2). No differences were found in plant density between Unburned and F-72 ($P > 0.05$) or F-90 and F-05 ($P > 0.05$).

Relative abundance (based on the number of individuals) of browse species and birch in summer varied among burn strata (Fig. 3). Of the 6 species identified, 2 (*Salix arbusculoides* and *Populus tremuloides)* contributed little to overall abundance (0% Unburned, 0% F-72, 0% F-90, and 12% F-05). Willow species (*S. pulchra, S. glauca,* and *S. bebbiana*) dominated Unburned (87%), F-72 (99%), and F-90 (98%). Of note, *Betula neoalaska* was 48% of the relative abundance in F-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. 2). The proportion of browsed individuals with evidence of browsing did not differ among Unburned, F-72, and F-05 ($P > 0.05$). The proportion of individuals with evidence of browsing did not differ among F-72 and F-90 ($P > 0.05$); however, F-90 had a significantly higher proportion of browsing than Unburned and F-05 (U = 9, P = 0.03 and

Table 2. Preferred browse species (trees and shrubs) documented in 4 burn strata in the Kanuti National Wildlife Refuge, Alaska, USA. Genera are *Betula* (*B.*), *Salix* (*S.*), *Populus* (*Pop.*), *Picea* (*P.*), *Alnus* (*A.*), and *Rosa* (*R.*).

Unburned	F-72	F-90	F-05
Preferred			
B. neoalaskana[1]	*B. neoalaskana*[1]	*B. neoalaskana*[1]	*B. neoalaskana*[1]
S. bebbiana	*S. bebbiana*	*S. arbusculoides*	*S. arbusculoides*
S. glauca	*S. glauca*	*S. bebbiana*	*S. bebbiana*
S. pulchra	*S. pulchra*	*S. glauca*	*S. glauca*
		S. pulchra	*S. pulchra*
		Pop. tremuloides	*S. scouleriana*
			Pop. tremuloides
Non-preferred			
A. crispa	*A. crispa*	*A. crispa*	*A. crispa*
A. tenufolia	*B. glandulosa*	*B. glandulosa*	*B. glandulosa*
B. glandulosa	*B. nana*	*B. nana*	*B. nana*
B. nana	*B. neoalaskana*[2]	*B. neoalaskana*[2]	*B. neoalaskana*[2]
B. neoalaskana[2]	*P. balsamifera*[2]	*P. balsamifera*[2]	*P. mariana*
S. bebbiana[2]	*S. bebbiana*[2]	*S. bebbiana*[2]	*Pop. tremuloides*
P. glauca	*P. glauca*	*Pop. tremuloides*[2]	*R. acicularis*
P. mariana	*P. mariana*	*P. glauca*	*S. beauverdiana*
		P. mariana	

[1]Considered as browse species in winter only; [2]mature individuals (>3 m height).

$U = 10$, $P = 0.02$ respectively), and was similar to that in F-72 and F-90 ($P > 0.05$). Leaf biomass (excluding birch) in summer ranged from ~40 to >400 kg/ha (Fig. 4). Biomass in F-90 and F-05 (mdn = 143 and mdn = 189 kg/ha, respectively) was higher than in Unburned and F-72 (mdn = 16 and mdn = 9 kg/ha, respectively; $U = 10–20$, $P = 0.001–0.03$), a pattern consistent with browse density measurements.

Availability and use of browse during winter

Available winter biomass ranged from ~2 to 30 kg/ha across study sites (Fig. 5), and 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, whereas willow was predominant in the other burn strata; e.g., willow was 61% of available biomass in F-90 and only 10% in F-05 (Fig. 6).

The relative offtake of woody biomass across all burn strata was 5.4% (95% CI = 3.9–6.9%; Fig. 5). The highest offtake was 6% in F-72 and the lowest 4.5% in Unburned and F-05. Use (2.2 kg/ha) was higher in F-72 and F-90 than in Unburned and F-05 ($P = 0.001$). Moose generally took larger bites of willow in F-90 and Unburned (both willow-dominated) and smaller bites in F-05 (birch-dominated) (Fig. 7); broomed plants were not observed (data not presented). These burns were dominated by willow, whereas F-05 was dominated by birch. Browsing on birch was not observed despite its high availability as potential winter browse in F-90 and F-05 (Fig. 5 and 7).

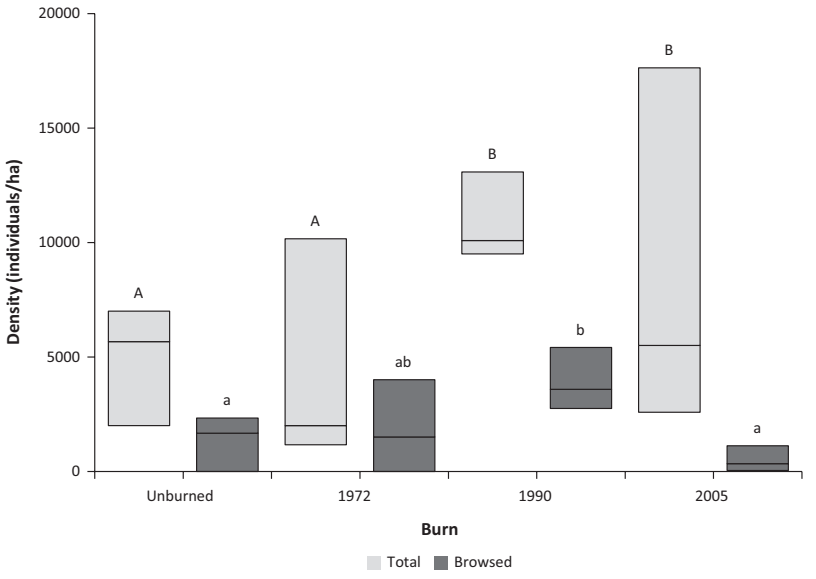

Fig. 2. Density of total available and browsed plants (individuals/ha) for preferred browse during summer (excluding *Betula neoalaskana*) on the Kanuti National Wildlife Refuge, Alaska, USA. The lower bound represents the 1st (25%) quartile, center lines indicate median values, and the upper bound represents the 3rd (75%) quartile. Letters denote significantly different groups based on Kruskal–Wallis analysis of variance and Mann–Whitney U *post-hoc* pairwise comparisons.

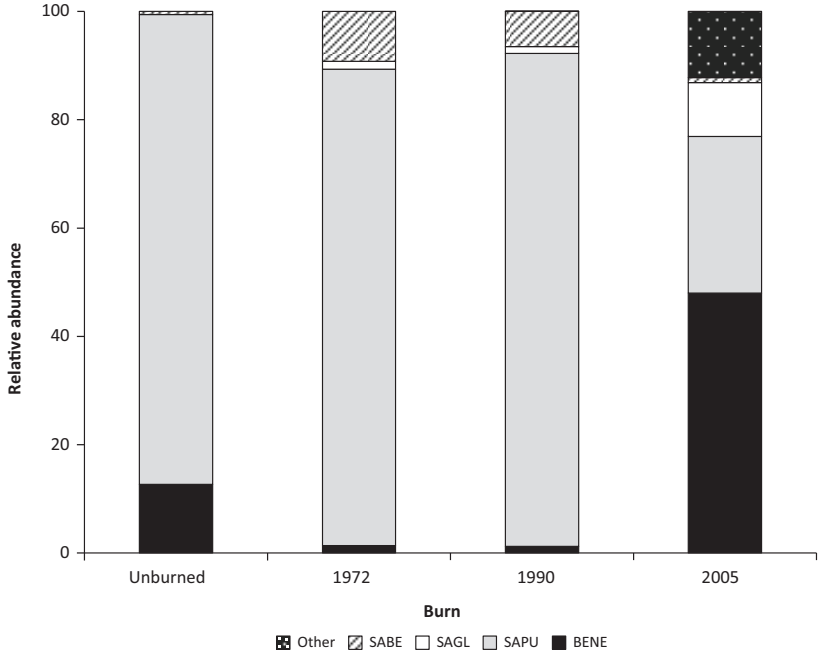

Fig. 3. Composition (based on number of individuals) of preferred browse species and birch during summer on the Kanuti National Wildlife Refuge, Alaska, USA. BENE denotes *Betula neoalaskana*, SAPU denotes *Salix pulchra,* SAGL denotes *S. glauca,* and SABE denotes *S. bebbiana.* "Other" denotes *Populus tremuloides* and *Picea balsamifera.*

Fig. 4. Total leaf biomass (kg/ha) of preferred summer browse by burn strata on the Kanuti National Wildlife Refuge, Alaska, USA. The lower bound represents the 1st (25%) quartile, center lines indicate median values, and the 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.

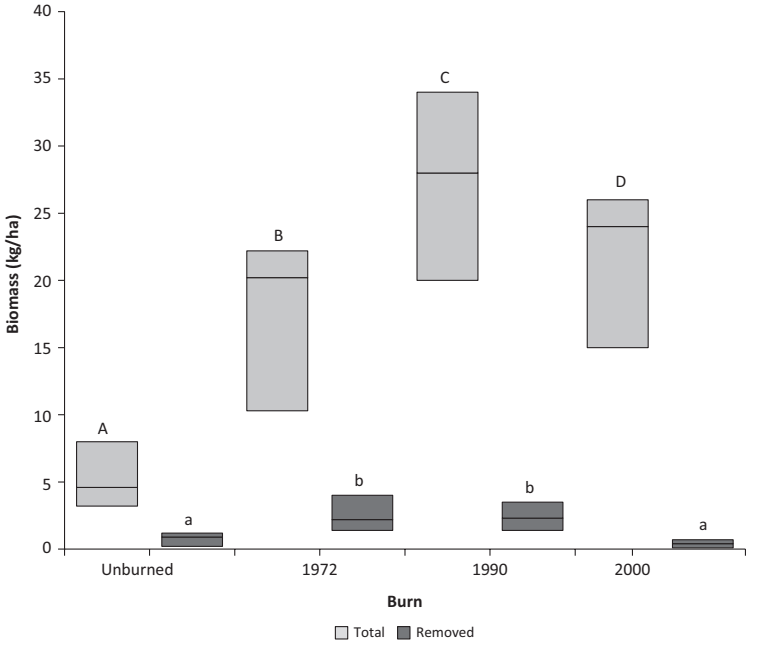

Fig. 5. Winter biomass and removal (kg/ha) of preferred browse by burn strata on the Kanuti National Wildlife Refuge, Alaska, USA. The lower bound represents the 1st (25%) quartile, center lines indicate median values, and the upper bound represents the 3rd (75%) quartile. Letters denote significantly different groups based on Kruskal–Wallis analysis of variance and Mann–Whitney U *post-hoc* pairwise comparisons. Values of removed biomass represent *Salix* spp. exclusively; *Betula neoalaskana* was not browsed.

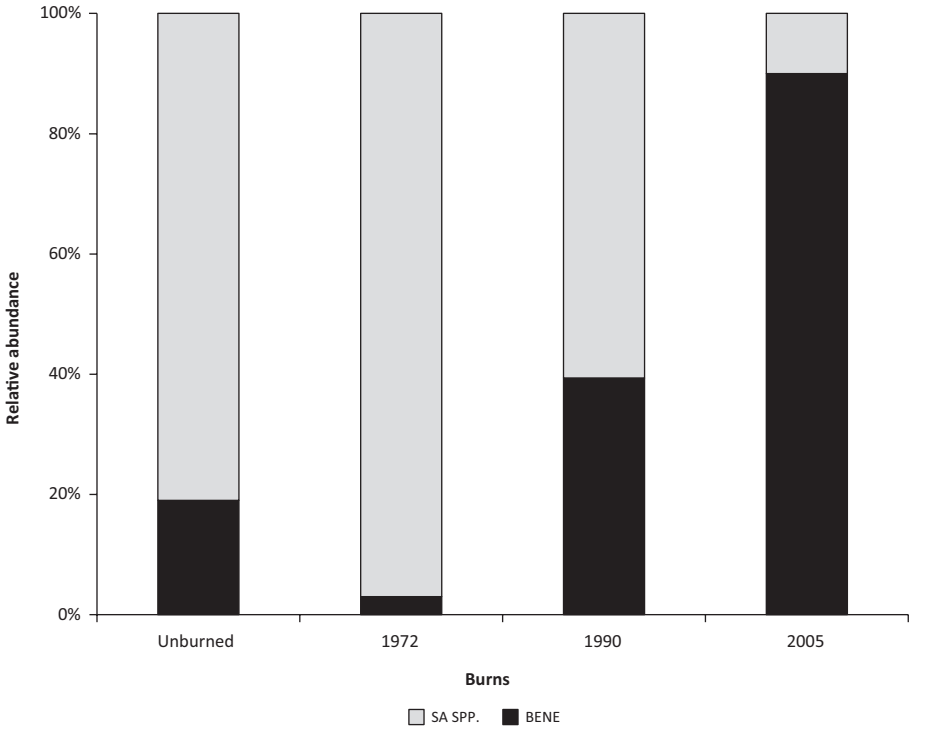

Fig. 6. Relative abundance (biomass) of winter browse in 4 burn strata on the Kanuti National Wildlife Refuge, Alaska, USA. SA SPP. denotes *Salix* spp. and BENE denotes *Betula neoalaskana*.

Habitat use

Capture locations of radio-collared moose did not appear to influence or relate to habitat use because the relatively large number of moose (25) captured in Unburned did not demonstrate exclusive preference for this habitat. Further, only 6 animals were captured in burns >30 years old, yet moose demonstrated preference for this stratum in both summer and winter. As such, preference or avoidance was likely not an artifact of capture location.

During the "summer" season, moose exhibited preferential use of burns >30 years old and avoidance of burns <11 years old ($\chi^2 = 17.675$, $P < 0.001$; Fig. 8). Moose did not appear to actively select or avoid Unburned or 11–30 year-old burns ($P > 0.05$). Cows (n = 120) preferred Unburned stands ($\chi^2 = 11.766$, df = 3, $P = 0.01$) during calving (28 May–23 June; Fig. 8). In winter, 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. 8). Winter use of unburned areas and stands >30 years old was proportional to availability.

DISCUSSION

Overall, our results are consistent with the general understanding that moose habitat quality peaks at 11–30 years post-fire (Maier et al. 2005). We found that density and biomass of summer browse were highest in F-90, and that browse removal was highest in F-90 and F-72. Although browse density and biomass in F-05 were also high, use in summer was low. Similarly, marked moose avoided <11 year-old stands and preferred >30 year-old stands in summer suggesting

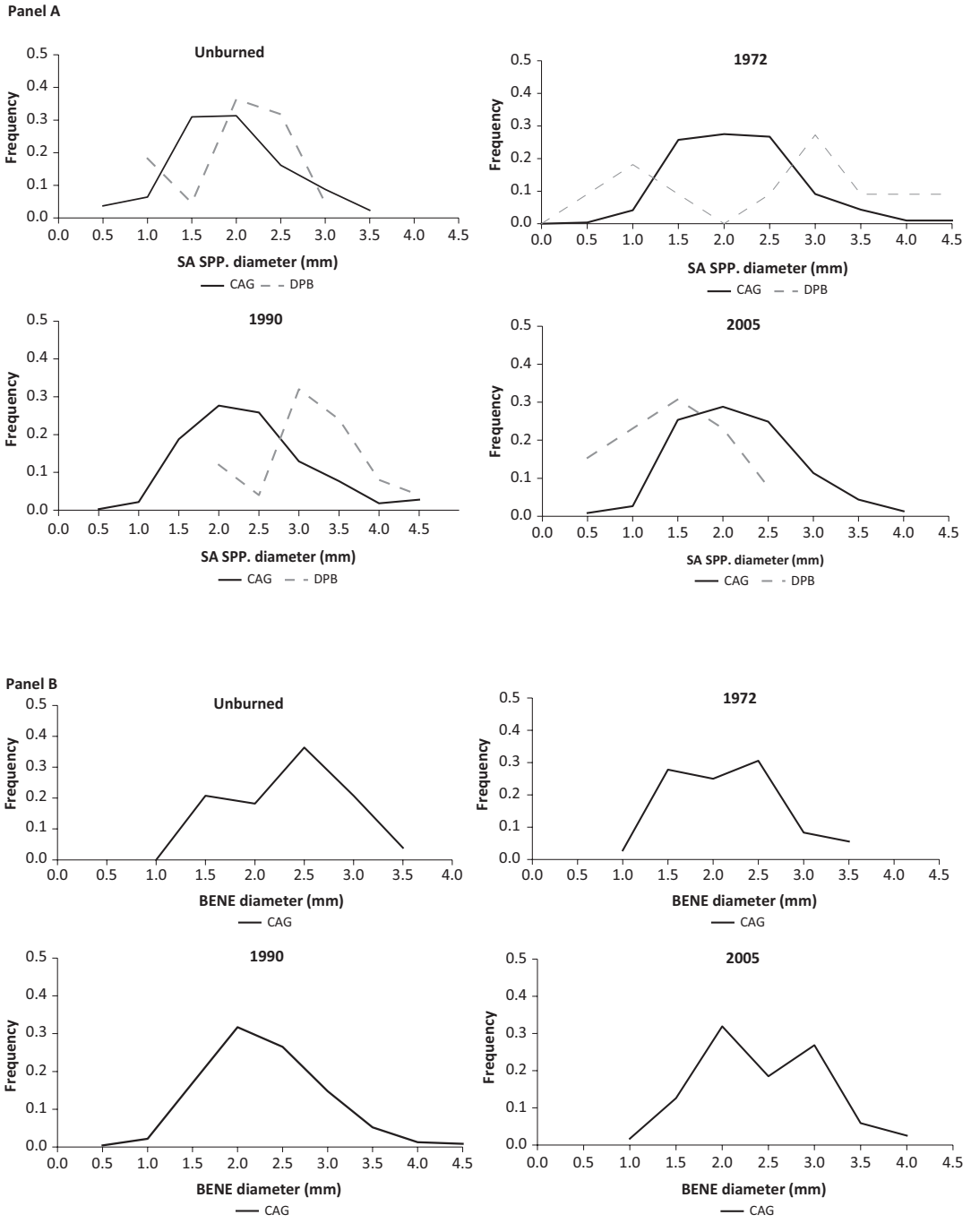

Fig. 7. Panel A: frequency distributions of CAG (current annual growth) and DPB (diameter at point of browsing) of willow in 4 burn strata on the Kanuti National Wildlife Refuge, Alaska, USA. Panel B: frequency distribution of CAG (current annual growth) of *Betula neoalaskana* in each burn stratum; browsing of birch was not observed.

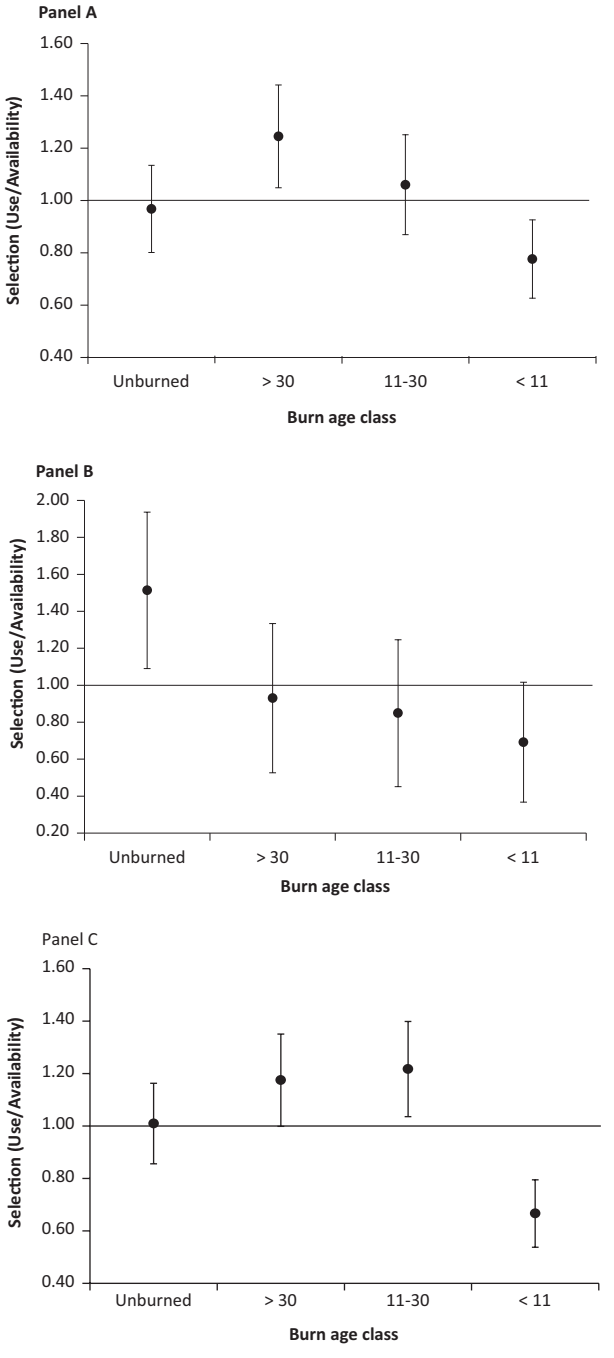

Fig. 8. Panel A: selection (use/availability) of burn age classes by radio-collared moose in summer (May–September), Kanuti National Wildlife Refuge, Alaska, 2008–2013. Panel B: selection of burn age classes by radio-collared cow moose during calving (28 May–23 June), Kanuti National Wildlife Refuge, Alaska, 2008–2013. Panel C: selection of burn age classes by radio-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.

that moose were not using plentiful forage available in young burns; rather, use was focused in burns >11 years old.

Available winter browse ranged from < 1 to ~26 kg/ha across the burn strata. While consistent with a 2007 browse survey (22 kg/ha) on the Refuge, these values are low compared to other areas in interior Alaska. For example, estimates from similar ecological regions in interior Alaska frequently average >200 kg/ha, with local estimates >400 kg/ha (Paragi et al. 2008). While browse use in these regions vary, they are typically much higher than the <5% use that we measured; for example, use was >20% and as high as 49% in areas where biomass abundance was >200 kg/ha (Paragi et al. 2008). But importantly, low use and consistently high twinning rates in our study area suggest that individually, moose are not negatively impacted by low browse availability (Craig and Stout 2014).

Available winter browse and summer biomass were highest in F-90 which supports our original hypothesis that this burn (11- 30 years post-fire) likely provides the best overall habitat of the 4 burn strata. In further support of this hypothesis was that winter offtake was highest in F-90 and F-72, and while considerable food resources (primarily birch) were available in F-05, the majority of winter browsing occurred in older stands. These results were corroborated by habitat use of the marked moose in summer and winter.

Selective feeding on higher quality forage is evident across all results. 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 low (<0.5 kg/ha). We also observed that the relative abundance of birch to willow in F-05 was much higher than in other burns. Despite its predominance in F-05, use was not observed, suggesting that although accessible and relatively plentiful in this burn, moose did not measurably use birch as winter forage. Rather, they preferentially used willow species that are nutritionally superior to birch (Hjeljord et al. 1982). We also found that the DPB of willow twigs was smaller in F-05 than the other burns (data not presented), suggesting that moose maximized browse consumption in older stands by taking larger bites, but possibly at the expense of nutritive value because digestibility declines as twig diameter increases.

While the results generally support our hypothesis that 11–30 year-old burns would have high biomass, browse use did not occur strictly in proportion to availability. Areas <11 years old had relatively high biomass, but browse use was minimal in these areas, and marked moose spent little time in recent burns. It is likely that vegetation/browse composition contributed to the patterns we observed, but historic moose distribution patterns (Craig and Stout 2011), the spatial distribution of collaring efforts (G. Stout, ADF&G, personal communication), and predation and predator avoidance strategies (Ballard and Van Ballenberghe 1998) also influence relative habitat use.

We found that moose in the Refuge exhibited selective feeding behavior by consuming a higher relative proportion of willow than birch. They appeared to forego birch even in winter when available food resources were restricted to a few species of deciduous trees and shrubs, and avoided recent burns despite measurable food resources that were available in these areas. When they did feed in recent burns, they took smaller bites. These patterns in foraging behavior were likely a consequence of interactions between population density and habitat availability. In our study area, moose densities were moderate (Craig and Stout 2014), and as such, browsing pressure and competition for habitat and resources were

low, and browse pressure on food resources was minimal. Thus, moose could afford to be selective not only as they foraged, but as they used the wide array of habitat types within their home range.

Our data indicate that moose were not using areas burned in the last decade, despite readily available food resources. Gasaway et al. (1989) found that immigration rates are low in low to moderate density populations, 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 populations limited by predation. High density populations have undergone local density changes in as little as 2 years post-fire (Peek 1974a), but moose density in F-05 has remained low (Craig and Stout 2014). We hypothesize that this delayed population response will persist because moose in the Refuge are less pressured to occupy recently burned areas because they are not habitat or forage-limited. Assuming that forage availability is relatively unconstrained, on a relative scale it may be that behaviors that reduce predation risk or offspring establishing home ranges overlapping or adjacent to the cow's home range (Gasaway et al. 1985, Ballard et al. 1991) are more influential on habitat use/selection.

These results are particularly interesting in light of evidence suggesting a changing fire regime with larger, and more severe and frequent fires in interior Alaska (Kasischke et al. 2010). We found no differences in browse use in the fire severity categories in F-05 (unpublished data), although sample size was limited (n = 7). However, if a higher proportion of landscape shifted to "younger" successional stages, habitat use and preference may shift considerably; albeit, calculated preferences in habitat and forage use are often a quantitative function of relative availability and not biological importance. Regardless, the effects of fire severity on post-fire vegetation will become an increasingly important factor in areas of moderate moose density. The relative effects of high-severity fires on browse quality, and how moose respond to such, are dependent on the species that regenerate/recolonize post-burn as illustrated by our disparate consumption data of willow and birch.

Predation on calves and yearlings in the upper Koyukuk River drainage is high. Calf mortality is estimated as 74% from spring parturition to population surveys in November, with 22% annual predation of yearlings, mostly by wolves (*Canis lupus*) (ADFG 2012). Previous studies indicate that moose, particularly cows with calves, preferentially inhabit forest stands dominated by conifers that provide more protection from wolves and other predators (Mech 1966, Peterson 1977, Poole et al. 2007). Similarly, the marked cows showed preference for unburned stands during the calving season and >30 year-old stands throughout summer. Vegetation in F-05 was characterized by homogeneous stands of early seral vegetation, and avoidance of burns <11 years old was presumably due to lack of vegetative cover and increased predation risk.

Although the characteristics of vegetation in F-05 will change considerably in the coming years, given the population characteristics of moose in the region, it may be a number of years before moose regularly use and establish core home ranges within F-05 and other recent burns. Semi-annual moose surveys will continue on the Refuge to quantify temporal changes in population and distribution. These surveys will help land and wildlife managers understand the nuances of reestablishment in recent burns, and to document changes in moose population dynamics and address broader management issues.

Continued study of habitat and population change through time is particularly relevant in light of climate change. As deciduous forest succession becomes dominant in uplands of interior Alaska, implications for moose and other species must continue to be explored. While research suggests that increase in deciduous species will benefit moose, the nutritive value of deciduous trees and shrubs varies, and other factors also influence habitat use. It is necessary to study successional change at both the landscape and individual burn scales, specifically as it relates to moose distribution and habitat use, to improve our understanding of habitat dynamics under a changing fire regime.

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Appendix A. Preferred and non-preferred browse species classifications (based on literature review) established *a priori* in 4 burn strata on the Kanuti National Wildlife Refuge, Alaska, USA.

Preferred browse species
Salix alaxensis
Salix pulchra
Salix arbusculoides
Salix bebbiana
Populus. balsamifera
Populus tremuloides
Betula neoalaskana (winter only)
Non-preferred browse species
Picea mariana
Picea glauca
Alnus spp.
Betula glandulosa
Betula nana
Populus tremuloides[1]
Populus balsamifera[1]
Betula neoalaskana[1]

[1]Mature individuals (>3 m tall).

Appendix B. Sampling effort on winter browse surveys in 4 burn strata on the Kanuti National Wildlife Refuge, Alaska, USA, 2013–2014.

Stratum	# Plots	# Plants	# Twigs
Unburned	8	37	372
F-72	9	39	386
F-90	11	76	747
F-05	9	43	430
Total	37	195	1935

Appendix C. Elevation, slope, dominant aspect, and vegetation characteristics based on a digital elevation model (DEM) and LANDFIRE data in 4 burn strata on the Kanuti National Wildlife Refuge, Alaska, USA.

		Stratum			
		Unburned	F-72	F-90	F-05
Elevation (m)	Mean	224	213	332	261
	Min	121	116	160	151
	Max	1068	459	809	889
Slope (°)	Mean	2.06	2	4	3
Slope class (%)[1]	Flat	12	31	16	46
	Gentle (<10°)	24	66	76	46
	Medium (10–30°)	32	2	8	9
	Steep (>30°)	32	0	0	0
Dominant aspect		Southeast	South	Southwest	South
Canopy height (m)	Mean	9	8	3	1
Tree height (m)	Max	12	10	5	4

[1]% of burn in each slope c.

Appendix D. Fire severity classification in the F-05 burn stratum, Kanuti National Wildlife Refuge, Alaska, USA. Classification was determined from photographs.

Site	Severity
F-05 – 1	Low
F-05 – 2	Low
F-05 – 3	Moderate/High
F-05 – 4	Moderate/Low
F-05 – 5	High
F-05 – 6	Moderate
F-05 – 7	High
F-05 – 8	Moderate

Appendix E. LANDFIRE classification of vegetation types in 4 burn strata on the Kanuti National Wildlife Refuge, Alaska, USA. Note that vegetation types for F-05 reflect composition prior to burning.

	% Class			
	Unburned	F-72	F-90	F-05
Closed tree canopy	28	50	55	15
Dwarf shrubland	3	2	1	3
Herbaceous – grassland	11	9	5	14
Non-vegetated	7	2	2	4
Open tree canopy	21	13	4	10
Shrubland	30	23	34	53
Sparse tree canopy	0	0	0	0
Sparsely vegetated	1	0	0	1
	% Sub-class			
Aquatic	2	1	0	1
Deciduous	16	19	38	25
Deciduous dwarf-shrubland	1	2	0	2
Deciduous shrubland	23	21	20	35
Evergreen	18	18	31	9
Evergreen open tree canopy	17	8	3	7
Mixed	2	16	0	0
Mixed evergreen-deciduous open tree canopy	3	5	1	3
Non-vegetated	7	3	2	4
Perennial graminoid	10	8	5	11
Perennial graminoid or annual	0	0	0	2
Sparsely vegetated	1	1	0	1
	% height class			
Sparse	1	0	0	0
Shrub > 1.5 m	2	8	21	47
Shrub 0.5–1.5 m	13	2	8	0
Shrub 0–0.5 m	6	8	4	0
Herb >0.5 m	10	1	1	14
Herb 0–0.5 m	1	0	0	0
Forest >50 m	0	0	0	0
Forest 5–10 m	23	15	9	25
Forest 25–50 m	0	45	31	2
Forest 10–25 m	22	21	25	10
Forest 0–5 m	16	0	0	1