Fire-mediated patterns of habitat use by male moose (*Alces alces*) in Alaska

C.L. Brown, K. Kielland, E.S. Euskirchen, T.J. Brinkman, R.W. Ruess, and K.A. Kellie

Abstract: Fire severity is an important control over regeneration of deciduous species and can influence the overall quality of habitat for herbivores, such as moose (*Alces alces* (Linnaeus, 1758)), but the relationships between availability and duration of biomass production and moose habitat use are largely unknown. We evaluate the relative influence of a regenerating burn, paying particular attention to fire severity, on winter forage production and duration, offtake, nutritional quality, and seasonal moose habitat use. We used data from 14 GPS collared male moose in the 20-year-old Hajdukovich Creek Burn (HCB) in interior Alaska, USA, to generate seasonal dynamic Brownian bridge movement models. Within HCB, moose selected for low-severity sites more than high- and moderate-severity sites during the winter. Over the past decade, willow (species of the genus *Salix* L.) biomass production in low-severity sites has doubled and is likely influencing winter habitat selection patterns. In summer, moose selected for high-severity sites where there is a more abundant understory layer (e.g., stem densities) providing both forage and cover. The initial pulse of biomass production in high-severity sites, as well as the delay in growth and maturation of vegetation in low-severity sites, indicate that differing distributions of wildfire severity can create a dynamic mosaic of habitat patches that may extend the value of burns over time for moose.

Key words: biomass, space use, landscape heterogeneity, fire severity, nutritional quality, moose, *Alces alces*.

Résumé : Si l'intensité des incendies est un important facteur de contrôle de la régénération des espèces à feuilles caduques et peut influencer la qualité globale des habitats d'herbivores, comme l'orignal (*Alces alces* (Linnaeus, 1758)), les relations entre la disponibilité et la durée de la production de biomasse et l'utilisation d'habitats par les orignaux demeurent méconnues. Nous évaluons l'influence relative d'un brûlage de régénération en portant une attention particulière à l'intensité du brûlage, à la production et la durée de la nourriture hivernale, au retrait, à la qualité nutritive et à l'utilisation saisonnière d'habitats par les orignaux. Nous avons utilisé des données provenant de 14 orignaux mâles dotés de colliers GPS dans le brûlis de Hajdukovich Creek (HCB), dans l'intérieur de l'Alaska (États-Unis), pour produire des modèles de dynamique saisonnière des déplacements par ponts browniens. Dans le HCB, les orignaux préféraient les sites de faible intensité aux sites d'intensité élevée ou modérée durant l'hiver. Au cours de la dernière décennie, la production de biomasse de saules (espèces du genre *Salix* L.) dans les sites de faible intensité a doublé et influence vraisemblablement les motifs de sélection d'habitats hivernaux. L'été, les orignaux choisissaient des sites de forte intensité où la couche du sous-étage est plus abondante (p. ex. densité de tiges), offrant à la fois nourriture et couvert. La pointe initiale de production de biomasse dans les sites de forte intensité et la croissance et la maturation retardées de la végétation dans les sites de faible intensité indiquent que différentes répartitions de l'intensité des feux d'origine naturelle peuvent créer une mosaïque dynamique de parcelles d'habitat qui peut faire en sorte que la valeur des brûlages pour les orignaux se prolonge dans le temps. [Traduit par la Rédaction]

Mots-clés : biomasse, utilisation de l'espace, hétérogénéité du paysage, intensité du feu, qualité nutritive, orignal, *Alces alces*.

Introduction

Wildfire is the most common ecological disturbance and source of large-scale spatial heterogeneity in the Alaskan boreal forest, burning, on average, 1–2 million acres per year (Chapin et al. 2008). Spatial heterogeneity of landscapes can have important effects on wildlife by influencing patch size and shape, as well as the composition and distribution of habitat types (Turner 1989; Li and Reynolds 1994). These changing habitat characteristics can influence predator–prey interactions (Pierce et al. 2000; Kauffman et al. 2007), population dynamics (Dempster and Pollard 1986), community structure (Pacala and Roughgarden 1982), and animal movement and distribution (Kie et al. 2002; Boyce et al. 2003). In forest-dominated landscapes, disturbances such as fire produce spatial heterogeneity by creating new patches of early successional habitat within the forest matrix (McCarthy 2001). A fire-mediated shift to deciduous-dominated species could affect a broad suite of ecosystem processes, including the production of important forage and cover species that are known to influence habitat-use patterns for boreal herbivores such as moose (*Alces alces* (Linnaeus, 1758)).

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) forests are the most common forest type in interior Alaska. These forests typically follow a post-fire successional trajectory of self-replacement where the dominant pre-fire stand replaces itself within the first two decades after low-severity fires (Van Cleve and Viereck 1981). However, recent studies in interior Alaska and Canada have shown that fire severity, in particular, is an important

driver for post-fire succession in boreal forests (Johnstone et al. 2010, 2011). High-severity fires (i.e., those that burn through the organic soil layer exposing the mineral soil) are favorable for seeding deciduous shrubs and trees (Johnstone and Chapin 2006; Brown et al. 2015). Additionally, the recruitment and establishment of deciduous species in high-severity patches persists for several decades post fire shifting the composition from black spruce to hardwood-dominated forests (Shenoy et al. 2011). Fire severity is also linked to an increase in fire extent across Alaska (Duffy et al. 2007). Thus, fire severity can alter the spatial heterogeneity within boreal forests by influencing the composition, age structure, and size of habitat patches.

The effects of fire severity on spatial heterogeneity manifested in the distribution of forest cover and vegetation in early successional patches may be a key variable influencing habitat use by moose (Lord and Kielland 2015). Throughout the year, moose must balance the costs and benefits associated with accessing forage and finding cover against predation and weather conditions (Dussault et al. 2005). The effects of fire severity on woody biomass production are especially important during winter when moose maintain a neutral to negative energy balance (Schwartz et al. 1988). For example, past biomass surveys in our study area found that an increase in winter forage production in high-severity sites was accompanied by a 49% proportional offtake rate (Lord and Kielland 2015). Therefore, burned areas could represent habitat mosaics of productive forage patches dispersed within areas of continuous cover. It remains unknown, however, whether moose select for high-severity habitat patches in relation to low- or moderate-severity patches or other unburned features (e.g., riparian habitat) that may occur within their range.

Despite recent research on the effects of fire severity on forest recruitment (Johnstone and Kasischke 2005; Shenoy et al. 2011), the duration of post-fire browse availability for moose is less understood. Additionally, browse quality of selected diets by ungulates may also differ between habitats that are burned and unburned (Hobbs and Spowart 1984; Blair 1997; Van de Vijver et al. 1999). However, the effects of fire severity on within-species nutritional quality are unknown. Low-severity sites have been characterized by cool (~8 °C), moist soils that are generally less productive, whereas high-severity sites have warmer (~10 °C), dry soils that are more productive (Shenoy et al. 2013). Nitrogen, in particular, is a limiting nutrient to plant growth in boreal regions (Bryant et al. 1983) and dietary nitrogen can act as a nutritional constraint for moose in these environments (McArt et al. 2009). If wildfire severity does have significant impacts on forage quality, then these differences will be important during the winter when forage quality is at its lowest point and moose are typically in a negative energy or protein balance (Oldemeyer et al. 1977).

The objective of this research was to evaluate the influence of a regenerating burn compared with other habitat features on seasonal (winter and summer) male moose habitat use. Additionally, we examined if fire severity influenced the use of habitat patches within individual winter core use areas (i.e., 40% use area), and performed winter browse assessment surveys to assess forage production, offtake, and nutritional quality (e.g., protein precipitation capacity (PPC), digestible protein (DP), acid detergent fiber (ADF), and neutral detergent fiber (NDF)) at high- and low-severity sites within a regenerating burn. We used GPS telemetry data from 14 male moose to examine how the regenerating burn affected habitat-use patterns. To examine the difference in biomass production and offtake overtime, we compared our estimates with previous research that used the same sites and methods.

Materials and methods

Study area

Research was conducted approximately 40 km southeast of Delta Junction, Alaska, USA (63°50′N, 145°40′W), in game management unit (GMU) 20D. We defined the study-area boundary by mapping the winter locations from 14 GPS-collared male moose over 2 years (2013–2014) and created a minimum convex polygon. The study area is characterized by deciduous and needle-leaf canopy forest, agricultural fields near Delta Junction, and subalpine shrub communities. Within the study area, the 1994 Hajdukovich Creek Burn (HCB) affected 89 km² of black spruce forest in a flat glacial outwash plain north of the Alaska Range. Soils in the HCB consist predominantly of silt loam overlying sand and gravel deposits, with some areas having a layer of stream-deposited cobble on top of the silt (Johnstone and Kasischke 2005). The climate is continental and mean annual precipitation is approximately 28.6 cm, most of which is received as rain during May to September. Winter temperatures during our study ranged from –10 to –42 °C (daily mean (±SE) = –14.5 ± 1.3 °C), whereas summer temperatures ranged from 0 to 30 °C (daily mean (±SE) = 12.3 ± 2.1 °C) (C.L., Brown, unpublished data, 2014). Mean (±SE) snow depth during winter months was 0.43 ± 0.01 m and did not differ significantly between stands with different fire severities (p = 0.97; C.L. Brown, unpublished data). Predators in the study area included wolves (Canis lupus Linnaeus, 1758), brown bears (Ursus arctos Linnaeus, 1758), and black bears (Ursus americanus Pallas, 1780). Proximity to human development, habitat manipulation (e.g., agriculture), and accessible road and trails for trapping and hunting in the region limits local predator densities (Boertje et al. 2010) and the role of predation is likely less important compared with other areas in the state that have low-density moose populations (Gasaway et al. 1992).

Fire severity and habitat classification

During June–September 1994, the fire burned approximately 8900 ha of predominantly mature black spruce stands with few mixed stands of quaking aspen (Populus tremuloides Michx.) (Michalek et al. 2000; Johnstone and Kasischke 2005). Vegetation composition in high-severity patches is dominated by deciduous trees and shrubs, such as willows (Scouler's willow (Salix scouleriana Barratt ex Hook.), gray willow (Salix bebbiana Sarg.), grayleaf willow (Salix glauca L.)), quaking aspen, or Alaska birch (Betula neoalaskana Sarg.), whereas low-severity patches are primarily composed of black spruce, willows, and few quaking aspen and Alaska birch (Shenoy et al. 2011). In 1996, fire-severity classes were determined using post-fire satellite imagery and later validated with field measurements of soil organic matter combustion (Michalek et al. 2000). In total, 61% of the HCB burn was classified as low severity, 6% as moderate severity, and 33% as high severity (Fig. 1).

We merged 2001 National Land Cover Data (NLCD) with the HCB perimeter (Michalek et al. 2000) to produce a map of relevant habitat types for the study area. We reclassified habitat types into seven primary habitat classes: evergreen forest, deciduous forest, shrubs, mixed forest, open water, agriculture, and burn. The burn class represented areas within the HCB perimeter, whereas the evergreen forest, deciduous forest, shrubs, mixed forest, open water, and agriculture classes were all unburned habitat types outside of the HCB. We validated our reclassified NLCD layer with 243 point locations that were ground-truthed outside the HCB within the GMU 20D (Salcha-Delta Soil and Water Conservation District 2012, 2014). We found that 88% of the ground-truthed locations outside the HCB were classified accurately by our NLCD habitat layer.

In addition, we used a recent habitat layer to examine the dominant forest types found within the HCB. This layer was ground-truthed in 2013 using 88 point locations. We reclassified

Fig. 1. Fire severity map of the Hajdukovich Creek Burn (HCB) in interior Alaska, USA, with 2013 winter core areas. The HCB is located 40 km southeast of Delta Junction, Alaska. Individual winter core areas (colored pixels in the online version; gray pixels in print) from 2013 were overlaid on the fire severity map (Michalek et al. 2000) to characterize space use. There were some areas within the fire perimeter that did not burn, as depicted by the white areas on the map.
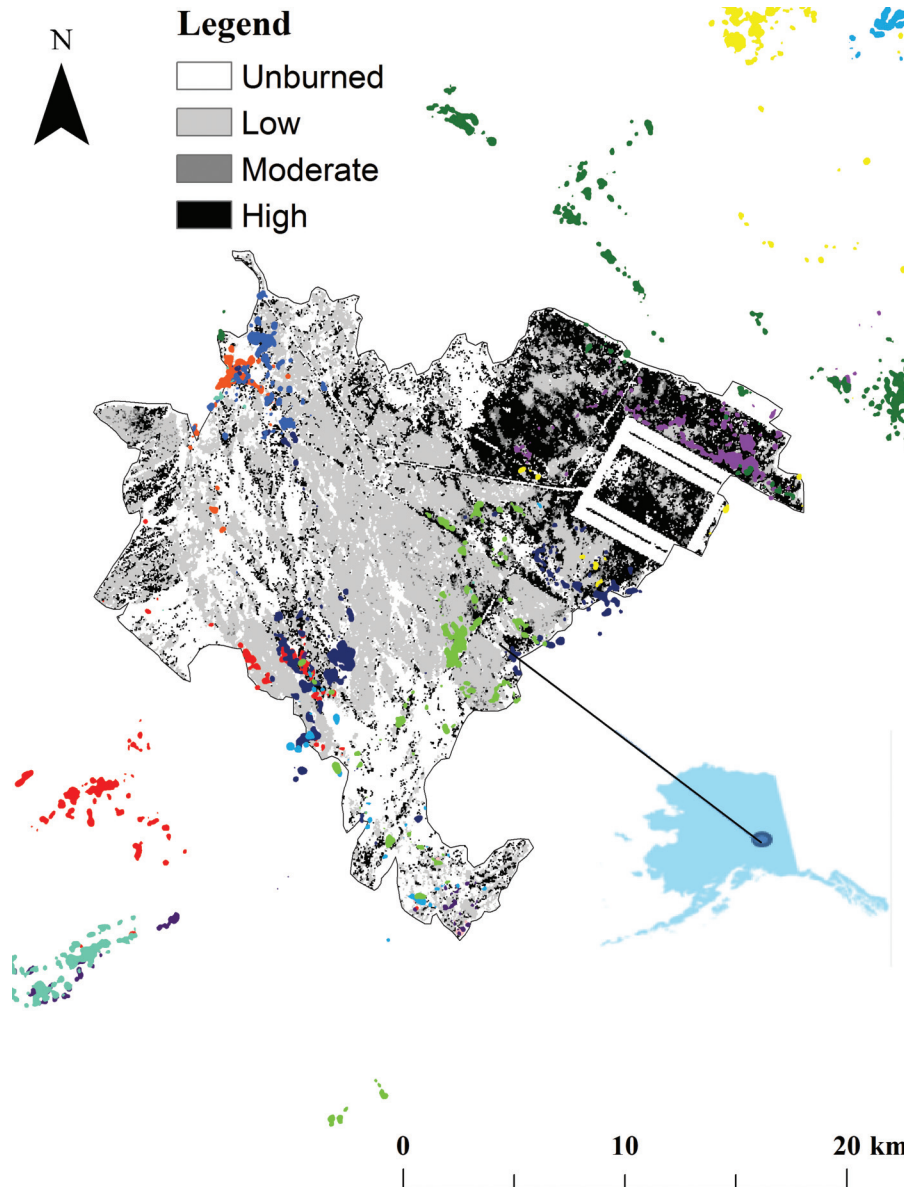

vegetation types to consist of black spruce – willows, coniferous (black spruce and white spruce (*Picea glauca* (Moench) Voss)), deciduous (quaking aspen, Alaska birch, willows), shrub (low-lying willows and dwarf birch (*Betula nana* L.)), agriculture, mixed (deciduous and coniferous species), and open water. We found that 86% of the ground-truthed locations within the HCB were classified accurately. We intersected these habitat layers in Geospatial Modeling Environment (Beyer 2012) to calculate the proportion of vegetation types within each fire-severity class (Fig. 2).

Biomass production and quality

To estimate forage composition within fire-severity classes, we used 16 pre-established sites (Johnstone and Kasischke 2005; Lord 2008; Shenoy et al. 2011) (low: *n* = 6; high: *n* = 10) for browse assessment surveys. The sites were distributed along the trail system within the burn scar and accessed via snowmobile in March 2013. We did not include data from moderate-severity sites due to low sample size (*n* = 3) and the fact that a small percentage of the

burn was classified as moderate severity (4%). At each site, we established one 30 m diameter circular plot and randomly selected three plants of each forage species within each plot. We defined forage species as willows, quaking aspen, or Alaska birch that were of foraging height for moose (0.5–3 m; Peek et al. 1976; Risenhoover 1989). Whereas willows were identified to species in the field, they were grouped into *Salix* spp. (or willows) for the final analysis. For each plant, we recorded species and height and visually estimated percent dead of woody stems by volume and architecture class. Plant-architecture classes were categorized as the percentage of the current growth by volume of the plant arising from lateral branching that was due to moose herbivory, defined as unbrowsed (no evidence of browsing prior to the current year), browsed (<50% of current annual growth (CAG) stems arose from lateral stems that were produced as a result of past browsing), and broomed (<50% of CAG twigs arose as lateral stems produced as a result of past browsing) (Seaton et al. 2011). Stem

Fig. 2. Map of spatially reclassified habitat types in the Hajdukovich Creek Burn (HCB) in interior Alaska, USA: agriculture, black spruce (*Picea mariana*) – willows (*Salix* spp.), coniferous (black spruce – white spruce (*Picea glauca*)), deciduous (quaking aspen (*Populus tremuloides*), Alaska birch (*Betula neoalaskana*), willows), mixed (coniferous and deciduous species), open water, shrub (low-lying willows and dwarf birch (*Betula nana*)), and tundra.
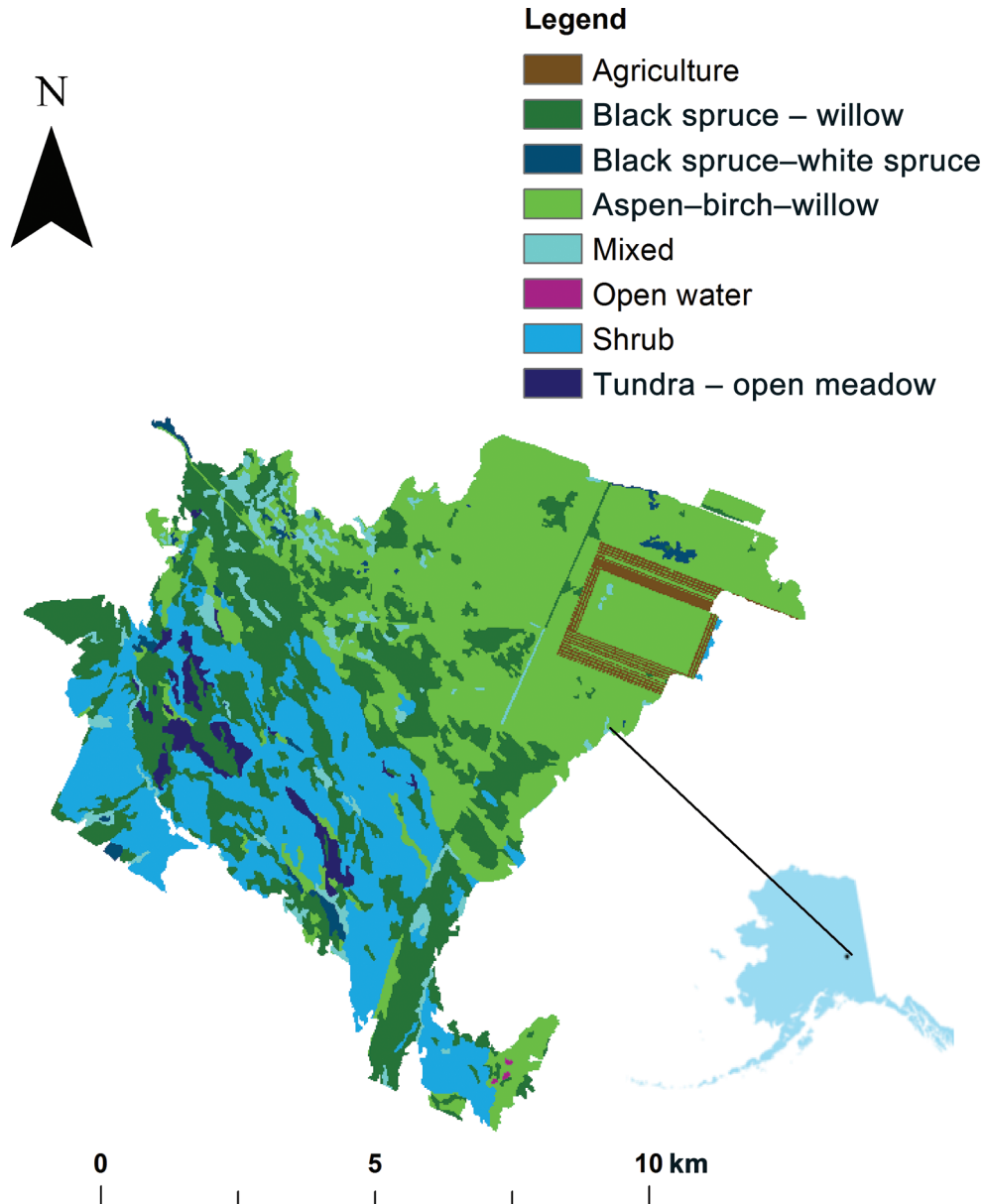
densities can be used to estimate the abundance of forage species and to estimate cover for moose (i.e., depending on age class and degree of browsing, high numbers of stems·m^{-2} is equivalent to thicker cover; Dussault et al. 2005). To estimate stem densities (m^2), we divided 30 m diameter plots into quadrants, counted the number of stems of all forage species and nonforage species above 0.5 m in each quadrant, summed the total number of forage and nonforage species per plot, and divided this sum by the area of the plot.

Additionally, we estimated biomass production and browse offtake at each site following techniques from Seaton et al. (2011). We measured production and offtake from the same three plants that were used to assess percent dead by volume and plant architecture. For each plant, we recorded the diameter of the base of CAG for 10 twigs per plant, as well as the diameter at the point of browsing (DPB) if twigs were browsed. When necessary, more

than three plants were sampled until 30 twigs per species or all of the twigs available in the plot were measured. Total twig densities were then estimated for each plant sampled.

Biomass was calculated using the estimated dry mass from mass–diameter regression equations. The formula used for estimating biomass production and offtake was

$$(1) \qquad \hat{B}_k = \Sigma \frac{M_{jk}}{m_{jk}} \Sigma \frac{N_{ijk}}{n_{ijk}} \Sigma Z_{hijk}$$

where B is the site estimate of offtake or production biomass in grams. Twigs are denoted by h, plants by i, species by j, and the sites by k. M and m are the total and sampled plants in each plot, respectively, whereas N and n are the total and sampled twigs, respectively. Individual twig biomass is represented by z (Seaton

et al. 2011). We used a program developed in R version 2.14.1 (R Core Team 2016) by the Alaska Department of Fish and Game using plot counts, twig diameters, diameter–biomass pairs, and dry mass conversions to estimate production and offtake (kg·ha^{-1}·year^{-1}) (Paragi et al. 2008). Proportional removal was calculated by dividing the estimated offtake by moose by the biomass produced at each site. All models were checked to ensure that they met basic assumptions of normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test). To test differences between high- and low-severity sites among stem densities, biomass, and offtake estimates, we used Tukey's adjustment for pairwise comparisons. To examine the duration of biomass production in high- and low-severity sites, we compared our results (2013) to a previous study that used the same browse survey methods (Lord 2008) and used the same sites to estimate biomass production and offtake. To test for differences between years (2007, 2013), we used Wilcoxon signed rank tests. Values are reported as mean ± SE.

Additionally, at 4 of the 16 pre-established sites, we randomly sampled twigs from 4 to 5 individual plants of the following species: gray willow, quaking aspen, and Alaska birch. All twig samples were within the defined foraging height for moose. Samples were kept frozen until they were freeze-dried in the laboratory. Freeze-dried twig samples were ground in a Wiley mill over a 20 mesh (1 mm) screen and stored in airtight containers prior to chemical analysis. Nitrogen concentrations (N) were analyzed on a Truspec C-N Analyzer. Tannin–PPC was determined with bovine serum albumin using the method of Martin and Martin (1983). Sequential fiber analysis was conducted on all forages according to the methods of Van Soest et al. (1991) yielding NDF and ADF. All results are reported on a dry matter basis. Finally, digestible protein concentration was calculated using the equation of Robbins et al. (1987):

$$(2) \qquad DP = -3.97 + 0.9283 \times CP - 11.82 \times PPC$$

where DP is digestible protein as a percentage of dry matter, CP is crude protein as a percentage of dry matter (6.25 × N concentration), and PPC is protein precipitation capacity (mg·g^{-1}). We analyzed our data with a linear mixed model in the lme4 package in R version 2.14.1 (R Core Team 2016) with plant species (gray willow, quaking aspen, Alaska birch), fire-severity category (high vs. low), and plant species × severity as explanatory variables. We added site ID as a random factor to account for within-site dependency among the observations. The dependent variables were PPC, DP, ADF, and NDF. We fit models with Gaussian error distribution and the significance of effects were assessed by Wald tests (α = 0.05).

Estimating core use areas

In October 2012, 15 adult male moose were captured in the HCB by darting from helicopter. All moose captures were carried out with approval from the Alaska Department of Fish and Game Institutional Animal Care Use and Committee (No. 2012-033). We fitted the captured moose with GPS radio collars (TDW-4780, Telonics, Mesa, Arizona, USA) equipped with ARGOS connectivity. Collars were programmed to collect one location every hour from 16 August to 15 October, and once every 2 h for the rest of the year. The increased rate of GPS fixes during late summer was for an additional research question not addressed here. Location data (n = 220 000) were downloaded weekly from October 2012 to November 2014. One moose died in December 2012 and was excluded from all analyses. Two additional mortalities occurred in spring 2013 and these two moose were only included in the winter 2012 analysis. Prior to data analysis, GPS locations were screened to ensure all erroneous locations were removed.

We used dynamic Brownian bridge movement models (dBBMM; Kranstauber et al. 2012) to estimate the utilization distribution (UD) for each individual moose based on movement data collected from the GPS collars (Fig. 3). The UD is a probability density function that quantifies an individual's relative use of space (Kernohan et al. 2001). The UDs were calculated for the winter (1 November – 1 April) and summer (1 May – 1 September) seasons. These dates correspond with observed weather and habitat conditions (e.g., snow, temperatures, annual leaf out) associated with seasonal behavioral states (Hjeljord et al. 1990; Ball et al. 2001; van Beest et al. 2012). Brownian bridge movement models (BBMM) are continuous-time stochastic movement models that predict the probability of occurrence by incorporating the distance and elapsed time between consecutive locations, the location error, and an estimate of the animal's mobility, referred to as the Brownian motion variance (σ_m^2; Horne et al. 2007). The BBMM assumes a constant σ_m^2 along the entire movement path. However, animal movement is often composed of a series of behaviorally unique movements that change over time (e.g., diurnal versus nocturnal movement patterns). Moose movement, in particular, can change daily from foraging, bedded, or traveling behaviors (Moen et al. 1996) and seasonally during rut (Miquelle 1990). Therefore, we used the dBBMM, which allows σ_m^2 to vary along a path corresponding to changes in the animal's behavior over time (Kranstauber et al. 2012). The σ_m^2 is essentially a mean of multiple σ_m^2 for each time step executed via a sliding window. Thus, the dBBMM allows for a more precise estimate of the UD by introducing changing behavioral states into the estimate of the σ_m^2. Walter et al. (2015) found that home-range estimators that incorporate a temporal component (e.g., BBMM and dBBMM) into model estimation typically perform better than traditional first- and second-generation estimators (e.g., fixed kernel home range and local convex hull).

We calculated UDs using the Brownian.bridge.dyn function (move package) in R. Core use areas were defined by isopleths (i.e., contours of equal probability) that divided intensively used areas from peripheral home-range areas (Vander Wal and Rodgers 2012). To calculate core use areas, we fit an exponential regression to a plot of UD area against UD volume (i.e., isopleth value) and determined the point at which the slope of the line fitted was equal to 1 (Vander Wal and Rodgers 2012; Feierabend and Kielland 2014). This point represents a limit where the home-range area begins to increase at a greater rate than the probability of use and the corresponding UD volume defines the boundary of the core area. Core use isopleths ranged between winter (31%–47%, 40% ± 4%) and summer (61%–67%, 64% ± 2%) seasons.

Habitat use

Each pixel within the core use areas was assigned a UD value denoting the probability that the individual was located within that pixel during a given period relative to all other pixels within the core use area. The sum of these probabilities associated with occurrence in one of the seven types of habitat classified was equal to the total probability of occurrence within that habitat type (Marzluff et al. 2004). Habitat consisted of unburned types (evergreen forest, deciduous forest, shrubs, mixed forest, open water, agriculture) and burn habitat. We define availability as the proportion of habitat types within moose core use areas. To estimate selection for a particular habitat type, we divided the total probability of occurrence by its availability for each individual, referred to as "concentration of use" (Neatherlin and Marzluff 2004; Bjørneraas et al. 2012). Concentration of use is an index measuring habitat use relative to its availability. This index is similar to other use and availability selection coefficients (e.g., Manly et al. 2002). However, this approach incorporates variation of use within habitat types instead of assigning space "used" versus "unused" (Neatherlin and Marzluff 2004). We then divided the sum of all UD values associated with a particular habitat by the availability. We scaled the concentration of use index to a value between 0 and 1 within each individual core area (Bjørneraas et al. 2012).

Fig. 3. Concentration of use values and proportional availability for habitat types in the Hajdukovich Creek Burn (HCB) in interior Alaska, USA. Concentration of use values for (*a*) winter core areas and (*b*) summer cores areas. Here, we show mean (±95% confidence interval (CI)) concentration of use for each habitat type within seasonal moose (*Alces alces*) core use areas (winter: *n* = 26; summer: *n* = 24). Concentration of use is the ratio of an individual's total likelihood of occurrence in a particular habitat type (volume of utilization distribution associated with the habitat classification) divided by the total occurrence of that habitat class (availability) in the core area. Because availability can impact habitat selection, we also present the proportion of habitat types within (*c*) winter 40% utilization distribution (UD) and (*d*) summer 64% UD. The BURN class denotes area within the boundary of the 1994 HCB. Values are means ± 95% CI.
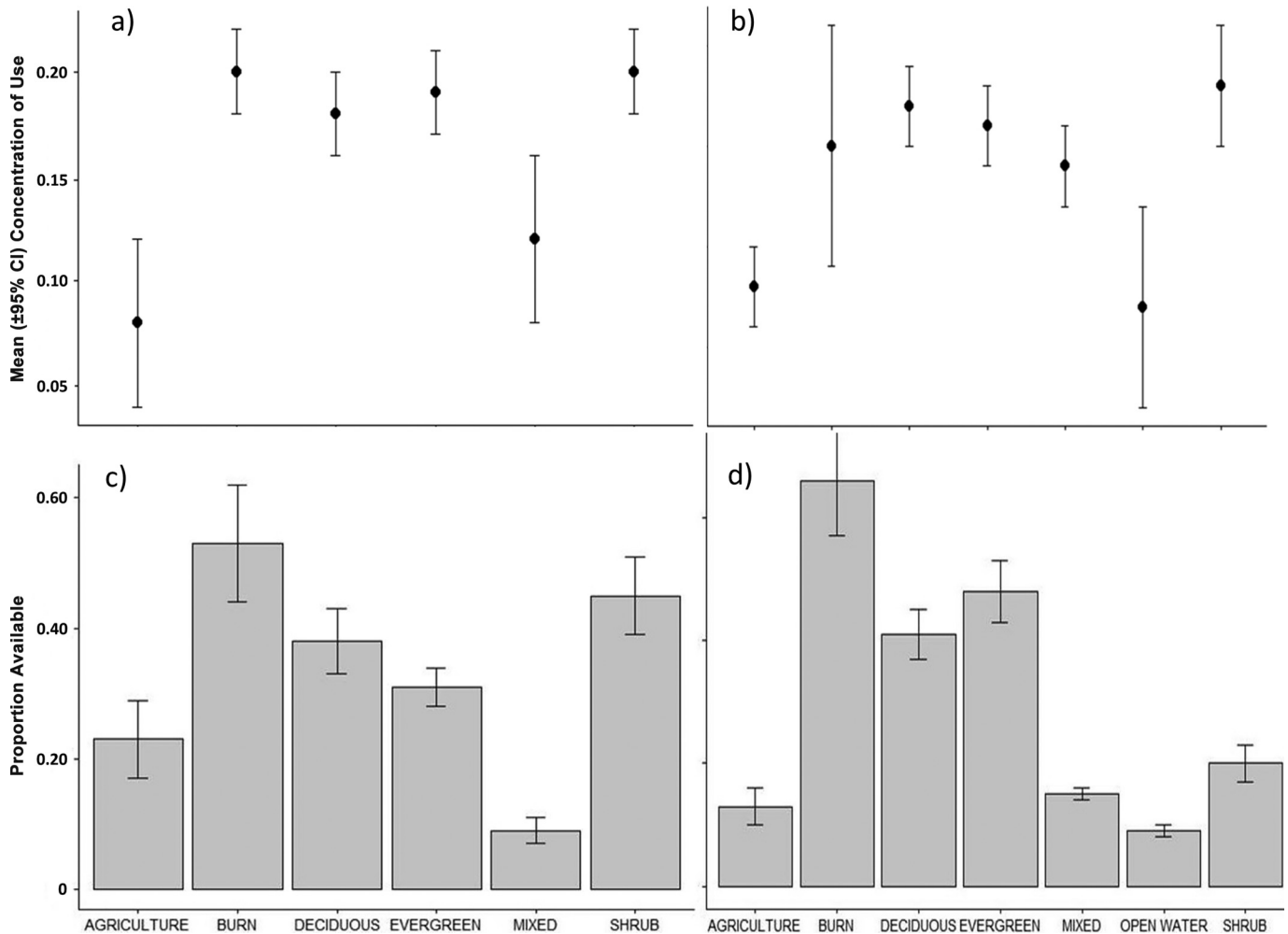
We compared use of the HCB relative to other habitat types (see below) across seasonal core use areas by defining availability as the proportion of habitat types inside the 40% (winter) and 64% (summer) isopleth boundaries. To test whether moose selected certain habitats, we compared the concentration of use across all habitat types among individual core use areas using a linear mixed model in the lme4 package in R version 2.14.1 (R Core Team 2016). We added moose ID as a random factor to account for within-site dependency among the observations. We fit models with a binomial distribution and the significance of effects were assessed by Wald tests (α = 0.05). Concentration of use values for all habitat and burn classes were used as the response variables. We added individual moose as a random factor to account for within-individual dependency among the observations. Differences among means were based on mean separations using Tukey's honestly significant difference. Statistical significance was assessed at α = 0.05. Additionally, we compared the concentration of use within the HCB across all fire-severity types among seasonal individual core use areas. Fire-severity types consisted of high, moderate, and low severities. We used Michalek et al.'s (2000) fire-severity classifications for this analysis. Although only
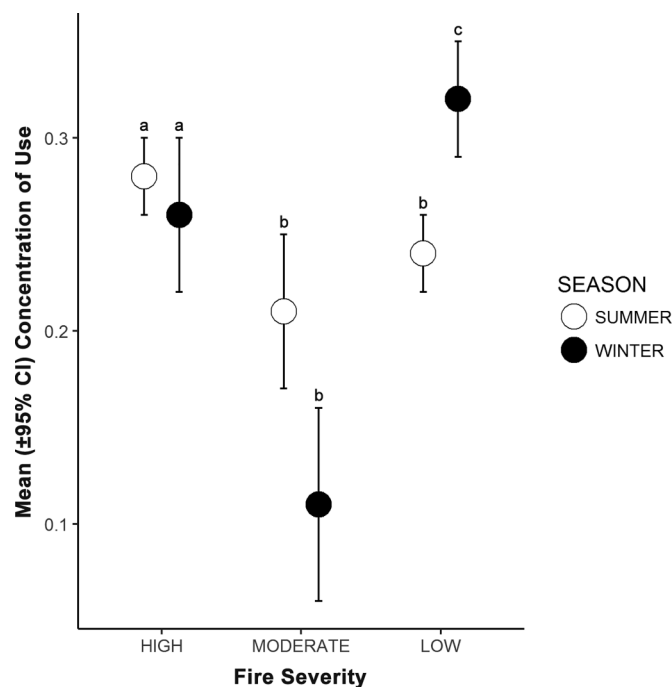
4% of the burn was classified as moderate severity, we included this classification into the analysis to avoid gaps in concentration of use values.

Results

Spatial reclassification of dominant vegetation types indicates that high-severity patches were heavily dominated by the deciduous (71%) class (Fig. 2). Moderate-severity patches were also composed of the deciduous class (75%); however, these areas had a moderate coniferous (15%) component as well. Low-severity patches were predominately composed of black spruce – willows (40%) and shrub (29%) classes.

We estimated 50 UDs across 2 years (26 winter, 24 summer) from radio-collared moose throughout our study. During the winter season, core area size was 1.2 ± 0.10 km². In the summer months, core area size was 6.3 ± 0.40 km². We found no significant difference in seasonal core area size among years (winter: $F_{[1,25]}$ = 0.43, *p* = 0.52; summer: $F_{[1,23]}$ = 1.7, *p* = 0.20), so data were pooled across years to analyze seasonal habitat use. Burn habitat was most abundant during both winter (53% ± 0.08%) and summer

Fig. 4. Seasonal concentration of use values for fire severities. Here, we show mean (±95% confidence interval (CI)) concentration of use for each fire-severity type within seasonal moose (*Alces alces*) core use areas (winter: *n* = 26; summer: *n* = 24). Fire-severity classes were first determined by post-fire satellite imagery and ground-truthed with field-based comparisons of the degree of soil organic matter (Michalek et al. 2000). The NONBURN variable refers to areas within the burn perimeter that were not consumed by fire. Lowercase letters represent statistically significant differences among fire severities for the winter and summer seasons.

Table 1. Comparisons of estimates of biomass production and biomass offtake from 2007 browse assessment surveys (Lord 2008) and 2013 browse assessment surveys in the Hajdukovich Creek Burn in interior Alaska, USA.

	Biomass production (kg·ha⁻¹·year⁻¹)		Biomass offtake (kg·ha⁻¹·year⁻¹)	
	2007	2013	2007	2013
High-severity sites				
BENA	4±3	11±6**	1±0.3	4±2*
POTR	77±12	132±38	45±7	26±9
SASP	157±21	126±25	76±10	52±13**
Total	238±36	269±69	122±17.3	82±18
Low-severity sites				
BENA	1±0.1	5±3*	0.08±0.02	2±1
POTR	41±25	20±15	6±1	7±4
SASP	55±13	138±65**	10±2	15±5
Total	97±38.1	163±83	17±3.02	24±10

Note: BENA represents Alaska birch (*Betula neoalaskana*), POTR represents quaking aspen (*Populus tremuloides*), and SASP represents all willow species (e.g., Scouler's willow (*Salix scouleriana*), gray willow (*Salix bebbiana*), grayleaf willow (*Salix glauca*), littletree willow (*Salix arbusculoides* Andersson)). Values are reported as mean ± SE. The significance of the Wilcoxon signed rank test is indicated by asterisks: *, $p < 0.10$; **, $p < 0.05$.

production by species, we found that high-severity sites produced more quaking aspen (132 ± 38 kg·ha⁻¹·year⁻¹; $F_{[1,15]} = 2.9$, $p = 0.08$) than low-severity sites (29 ± 15 kg·ha⁻¹·year⁻¹).

From 2007 and 2013, in low-severity sites, biomass production of willows increased more than twofold ($p = 0.05$; Table 1). We also found a significant increase in biomass production ($p = 0.01$; Table 1) and a borderline significant increase in offtake ($p = 0.07$; Table 1) of Alaska birch in high-severity sites. Willow offtake has significantly decreased in high-severity sites since 2007 ($p = 0.01$; Table 1). The mean proportional removal across all sites declined from 36% in 2007 (Lord and Kielland 2015) to 24% in 2013. This decline is especially apparent in high-severity sites where proportional removal has declined ~50% between 2007 and 2013.

We analyzed indices of plant nutritional quality (PPC, DP, ADF, and NDF), and although there were differences among species, we found no effects of fire severity. We did find a significant severity × species interaction for PPC ($F_{[1,2]} = 6.29$, $p = 0.02$). Additionally, we found that differences were for digestible protein in aspen relative to other browse species due to very low protein precipitation capacity (Table 2).

Discussion

Our results indicate that a large regenerating burn (HCB) with varying distributions of wildfire severity can create a dynamic mosaic of seasonal habitat patches that were broadly used by male moose 20+ years post burn. We found that the HCB was the most abundant habitat class across seasonal core use areas. Moreover, male moose respond to changes in vegetation composition related to differences in burn severity. During winter, moose selected core use areas within the burn perimeter that had high availability of willow biomass (i.e., low-severity sites) rather than for habitats that had the most total available woody browse biomass (i.e., high-severity sites). In summer, however, moose selected for habitat in high-severity patches more than low-severity patches. The increase in selection for high-severity patches in summer may be due to cover provided by deciduous tree and shrub species (as discussed below), as well as greater availability of forage in the form of foliage. Despite an abundance of burned habitats in seasonal core areas, concentrations of use for the burn were not significantly greater than unburned shrub, deciduous, and evergreen forest classes outside the burn perimeter, suggesting that male moose need resources from a variety of different habitat attributes and that habitats still have value even if it is

(66% ± 0.09%) seasons across individual home ranges, followed by the unburned evergreen and deciduous forest types (Figs. 3*c*, 3*d*).

Within winter core areas, moose concentrated their use in shrub habitats and burn habitat (Fig. 3*a*). However, selection for burn habitat was insignificant when compared with deciduous ($F_{[1,25]} = 0.05$, $p = 0.81$), evergreen ($F_{[1,25]} = 0.04$, $p = 0.83$), and shrub ($F_{[1,25]} = 0.02$, $p = 0.87$). Concentration of use (i.e., probability of occurrence of a particular habitat type relative to the availability) within the burn was significantly greater during the winter for low-severity patches than moderate-severity patches ($F_{[1,25]} = 32$, $p \leq 0.001$; Fig. 4) and high-severity patches ($F_{[1,25]} = 3.9$, $p = 0.05$). Within summer core areas, moose showed a slight preference for shrub and deciduous habitat within core areas (Fig. 3*a*). Moose also selected high-severity patches significantly more than low-severity patches ($F_{[1,23]} = 4.4$, $p = 0.04$; Fig. 4) and moderate-severity patches ($F_{[1,23]} = 5.3$, $p = 0.02$).

The total stem density of deciduous browse (willows, quaking aspen, and Alaska birch) was significantly greater ($F_{[1,15]} = 7.75$, $p = 0.02$) in high-severity sites than in low-severity sites (1.2 ± 0.18 vs. 0.40 ± 0.09 stems·m⁻², respectively). High-severity sites also had a slightly higher, but insignificant ($F_{[1,15]} = 0.59$, $p = 0.45$), percentage of brooming (54% ± 4%) compared with low-severity sites (38% ± 7%). Additionally, high-severity sites had a significantly higher ($F_{[1,15]} = 4.84$, $p = 0.04$) proportion of dead stems by volume (41% ± 0.05%) compared with low-severity sites (15% ± 0.03%).

In 2013, 186 ± 5.7 kg·ha⁻¹·year⁻¹ of browse biomass was produced across all sites within the burn. High-severity sites produced 252 ± 51 kg·ha⁻¹·year⁻¹, whereas low-severity sites produced 141 ± 33 kg·ha⁻¹·year⁻¹, but this difference was on the borderline of significant ($F_{[1,15]} = 3.2$, $p = 0.07$; Table 1). When examining biomass

Table 2. Comparison of protein-precipitating capacity of tannins of winter woody browse species and concentrations (percent dry matter (% DM)) of digestible protein, acid detergent fiber (ADF), and neutral detergent fiber (NDF) for all forage species in high- and low-severity sites in the Hajdukovich Creek Burn (HCB) in interior Alaska, USA.

	Protein-precipitation capacity (mg·g⁻¹)	Concentration (% DM)		
		Digestible protein	ADF	NDF
Fire severity				
High	38±6a	2.0±0.30a	35±0.91a	49±0.96a
Low	30±7a	1.8±0.32a	34±1.1a	47±1.1a
Forage species				
Gray willow, *Salix bebbiana*	100±0.003a	0.71±0.23a	39±0.85a	53±1.04a
Quaking aspen, *Populus tremuloides*	0.00±0.00b	3.1±0.22b	32±0.77b	45±0.93b
Alaska birch, *Betula neoalaskana*	51±4c	1.4±0.29c	34±1.0b	47±1.3b

Note: Additionally, we compared differences among species (gray willow, quaking aspen, and Alaska birch) within the HCB. Within a group of factors, rows with different lowercase letters are significantly different from each other (Wald χ^2 tests, $p < 0.05$). Values are reported as least squares means ± SE.

used in proportion to its availability. Others have found that moose may select a full range of habitat types depending on seasonal nutritional demands (White et al. 2014) and thermoregulatory behavior (van Beest et al. 2012; Street et al. 2015).

Although we did not detect significant differences in biomass production estimates across fire severities, recent trends suggest that low-severity sites, in particular, have been slower to regenerate since time of the fire (Shenoy et al. 2013). We found that willow biomass production has more than doubled in low-severity burns, now surpassing willow biomass production in high-severity patches compared with what it was 10 years ago. Additionally, our re-classified habitat layer showed that low-severity sites were predominately composed of willows and black spruce, and male moose seem to be responding to changing successional conditions by increased use of these low-severity sites during the winter. High-severity sites have experienced a slight increase in total biomass production; however, these sites also have high levels of plant mortality and brooming, which likely results in the reduction of browse consumption. Additionally, recent research in the HCB found that aspen in high-severity sites have showed abrupt growth releases in tree rings (20+ years post burn) and are now, on average, above moose browse height (>3 m; Conway and Johnstone 2017). We speculate that forage availability has started to decline in high-severity sites in the 20+ years after the fire, whereas production of preferred browse is still increasing in low-severity sites, as indicated by the large increases in willow production. However, low statistical power from small sample sizes makes our conclusions conservative. Our findings suggest that low-severity patches may extend male moose use of burns due to slow regeneration rates of woody deciduous browse, whereas, high-severity sites are important for moose in the first few decades following a fire event due to a pulse of rapid deciduous growth (Lord and Kielland 2015).

Although we had expected to find higher browse quality in browse species in high-severity sites due to the warmer, more productive soils, we did not find significant differences between severity classes. The lack of significance could be due to several factors including the age of the HCB, past browsing history, plant physiological mechanisms, and a spatially limited sample size. For example, the increased growth of the deciduous forest canopy in high-severity sites (Conway and Johnstone 2017) is likely affecting the amount of light reaching the forest floor influencing photosynthesis and decomposition rates. Additionally, the effects of past herbivory on plant chemical responses, especially in high-severity sites, could explain the high concentration of tannins (Bryant and Kuropat 1980), which reduces the digestion of protein (Spalinger et al 2010). There could also be seasonal differences in plant nutritional quality across high- and low-severity sites.

Vartanian (2011) found that wildfires created heterogeneity in forage and diet quality, but only during the summer months. We focused our biomass and nutritional survey efforts during the winter months, when moose survival is dependent on maintaining a near-neutral energy balance. Therefore, in the future, we recommend quality measurements in high- and low-severity sites throughout the year and as a burn regenerates overtime. Although high-severity sites produced more aspen, male moose were still selecting low-severity sites characterized by willows, which had the lowest digestible protein.

The seasonal shift of habitat-use patterns within the burn also suggests that patches of different fire severity can offer distinct resources depending on the time of year. During summer, male moose select for high-severity sites over low-severity sites. Despite the high rates of brooming and plant mortality, these sites exhibit a more abundant understory layer (e.g., stem densities) providing both summer forage and shade. During summer months, ambient air temperatures above 14 °C can be stressful for moose, and as a result, moose may seek out vegetative cover during hot days (Dussault et al. 2004). In winter, our study area experiences strong wind events and prevailing southeasterly winds. Because wind can exacerbate heat loss by increasing thermal conduction rates (Blix 2016), moose may seek vegetative cover and avoid open areas.

Other factors could also influence the use of burned areas by moose in Alaska. For instance, pre-fire population densities may also impact dispersal rates into burned areas, as moose appear to only use burns that overlap with their pre-fire home ranges (Gasaway and Dubois 1985). A density-driven mismatch in timing of colonization could allow woody shrubs to grow out of browsing height and reduce the duration of forage availability. Lastly, females relative to males may exhibit different habitat-use patterns within a burned area. For example, females with calves will often avoid habitat in open areas to minimize predation risk (Dussault et al. 2005; Bjørneraas et al. 2011). Thus, females may avoid low-severity patches and select edge habitat that offers more cover. Additionally, the increase in biomass production can have important implications on female moose nutrition and associated survivorship and fecundity. Future work should investigate the role of fire severity on female moose habitat use and nutrition.

Combining habitat assessment surveys with dBBMMs has allowed us to effectively monitor habitat conditions and subsequent habitat use by moose in a post-disturbance landscape. Our research shows that a mosaic of burn severities within a wildfire parameter created patches of habitat that moose select for at different times (seasons and years) following a wildfire. Given the increase in wildfire frequency in Alaska, moose management may benefit by accounting for the spatial and temporal effects of wildfire severity on biomass availability, which is commonly used to

inform moose population objectives and harvest rates. Moose constitute the largest terrestrial subsistence and recreational hunting resource in interior Alaska (Nelson et al. 2008), making fire-related habitat shifts especially important given that stable populations are a critical food resource to many communities. Effects of fire severity on moose habitat use and browse availability may inform male population models and help to optimize harvest strategies. Our research also highlights the utility of long-term monitoring of biomass production within burns to assess the trajectory, peak, and longevity of wildlife habitat quality.

Acknowledgements

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