

Prescribed Fire in the Nelchina Basin: A Case Study for Managing Moose Population

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Abstract

The Nelchina Basin, located west of Glenallen, AK provides important moose (*Alces alces*) habitat throughout the year. However, previous research in this area has shown that the moose populations appear to be nutritionally limited by the available forage. The Nelchina Basin was deemed an intensive management unit to increase moose populations through predator control efforts and prescribed fires to increase the amount of available forage, including the 2004 Alphabet Hills fire. We quantified the available digestible energy (DE) and digestible protein (DP) during the summer of 2018 and 2019, as well as the winter in between, and availability of forages for moose within the burn perimeter and the adjacent unburned forest during the summer of 2019. We found that total canopy cover of the primary forage species was lower in the burned areas than in the adjacent unburned forest habitats. DP concentration was not significantly different between forested and burned sites, and DE and DP content varied across the summer and winter sampling season. We also found a significant difference in DE and DP across the two sampling years. Although others have shown a positive effect of wildfire for herbivore populations, we found that some areas, including the Alphabet Hills area, may not be suitably adapted to benefit from the quick release of nutrients after fire and may not allocate more resources to biomass as previously expected. This project highlights the importance of research that quantifies both the availability of and the quantity of available food resources for herbivores.

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Introduction

Ecologists and wildlife managers generally agree that throughout the world, large-scale disturbance, such as wildfire, can be beneficial for species of large herbivores that are adapted to seral plant communities. Burned plots in states like Colorado and Nevada have been shown to increase crude protein intake for mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) in grassland and montane shrub communities (Hobbs and Spowart 1984). Higher abundances of bison (*Bison bison*) were found in recently burned watersheds within the Konza Prairie Research Natural Area in Northern Kansas (Knapp et al. 1999). In summer, these herbivores select grasses and herbaceous plants that respond rapidly to the release of post-fire nutrient deposits (Boerner 1982). In boreal forest ecosystems, post-fire stands are commonly assumed to support higher populations of moose (*Alces alces*) than adjacent unburned stands, but quantification of the impacts of fire on moose population productivity is limited. Fire, both natural and prescribed, is considered beneficial to moose because deciduous woody browses and herbaceous foods (e.g., *Chamerion angustifolium*) respond rapidly to post-fire conditions, increasing food abundance significantly (Landhausser and Wein 1993). Studies focusing on vegetation after fire show high variability with respect to both the biomass productivity and the species composition that regenerates (Rau et al. 2008, Johnstone et al. 2010).

Although there is significant evidence suggesting that browse biomass density increases after fire, there is little regarding the effect of fire on plant chemistry after fire (Bryant et al. 1983, Maier et al. 2005, Joly et al. 2016, Brown et al. 2018). Alteration of plant chemistry after fire could have dramatic effects on the overall palatability, and therefore the nutritional quality, of browse species. Globally, herbivores are limited by the availability of nitrogen, the element necessary for making protein and therefore building muscle. Nitrogen concentration in boreal plants is a limiting factor for the plants themselves and may be a limiting factor for herbivore growth and reproductive success (McArt et al. 2009, Gundale et al. 2010). Low resource environments, including the boreal forest, are dominated by plants such as evergreens that are slow growing, even when provided with an optimal supply of resources (Chapin, 1991, Gundale et al. 2010). Slow growth in these plants is attributed to an inability to quickly uptake nutrients, a higher allocation to survivorship traits such as chemical defenses, and internal constraints to growth (Chapin, 1991). Due to these growth limitations, nutrients may be leached out of a system before the species has the chance to sequester them (Chapin, 1991, Gundale et al. 2010), although fire has been found to increase nutrient availability. Deciduous species located in nutrient-limited stands have a greater proportion of secondary metabolites than in more productive ecotones, making them less usable by associated herbivores (Gundale et al. 2010). This defense strategy makes these plants less palatable to herbivores.

Nutritional carrying capacity is limited by two elements of a habitat: forage availability and forage quality. Both of which may be significantly altered after a disturbance such as fire. This potential tradeoff between higher availability of browse and potentially lower quality could affect moose productivity and movement. Hobbs and Swift (1985) showed that in high biomass areas nutrient intake is limited by the nutritional quality of the food source. If browse availability increases significantly in burned stands, but the nutritional quality declines, then moose density may increase, at the cost of per capita fitness (Hobbs and Swift 1985, 1988).

The response of moose to fire depends on browse biomass and diversity, and nutritional quality, including plant defenses (Hobbs and Swift 1985, Hobbs 2003). We measured these fundamental characteristics in a 16-year-old prescribed burn in the Nelchina Basin and in its adjacent unburned forests. The Nelchina Basin located west of Glenallen, AK, supports one of the highest moose harvests in the state (Boertje et al. 2007), drawing in hunters from throughout south-central and interior Alaska (Figure 1).

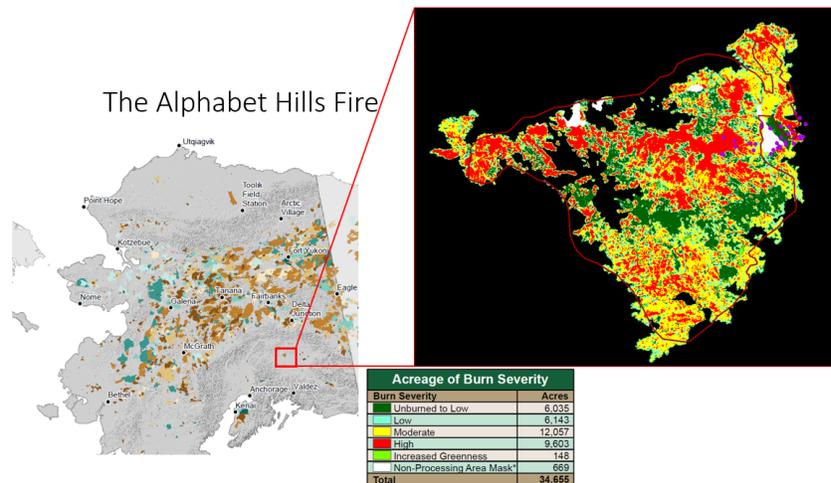


Figure 1: The Alphabet Hills fire, burned in 2004 for habitat management, is located west of Glenallen, AK. The map on the left shows the fire’s location in relation to the total fire history of Alaska while the map on the right shows the burn perimeter, the fire intensity readings (MTBS.gov), and the sampling points in purple. The legend shows the range in severity from high to low, including areas that were not processed or masked, as well as the acreage considered to be within each category.

Although moose in this area have access to large amounts of habitat, they often show indications of nutritional stress. Twinning rates and age of first parturition are significantly lower than their reproductive capacity (Testa 2004, Boertje et al. 2007). This led to an intensive management plan that includes predator controls and habitat management strategies such as prescribed burns. The Alphabet Hills, within the Nelchina Basin, was burned in 2004 as part of a management plan to increase moose habitat. The anticipated increase in moose productivity was expected to increase harvest opportunity, and to buffer losses to predation.

Stand succession, and stand quality after fire, is highly dependent on the pre-fire characteristics of the area as well as fire severity. Higher intensity fires can volatilize nitrogen that otherwise would be available to growth of forages and ultimately to the quality of moose diets (Boerner 1982, Bayley et al. 1992). The volatilization of nitrogen could be especially important in boreal regions due to the natural limitation of nitrogen in boreal soils. In addition, the response of plants to allocating carbon and nitrogen to growth vs defense is likely dependent upon browsing severity, climate and site conditions, nutrient availability, and plant competition. Taken together, it is difficult to predict the impact of natural or prescribed fire on moose populations or their productivity.

Timing since burn is itself an important factor for moose forage selection (Brown et al. 2018). Moose are considered near-obligate browsers, consuming the leaves and terminal twigs of a variety of deciduous woody trees and shrubs, particularly of the genus *Salix*. Hence, they are often associated with successional and riparian communities where such plants are abundant. In the boreal forest biome, where moose are most abundant, the climax community is typically coniferous, and in North America, dominated by black (*Picea mariana*) and white spruce (*Picea glauca*). However, early successional stages following wildfire in spruce forests are generally dominated by deciduous browses. Previous studies (Vitousek and Reiners 1975, Regelin et al. 1987, Julianus 2016) have shown that moose appear to select successional stands that are between 10 to 20 years in age post disturbance compared to stands that are less than 10 years or greater than 25 years post disturbance. For younger stands, preferred species could be small and harder to reach by moose, but, primarily, snow depth could also limit their use during the winter by burial of stems and inhibiting movement through an area (Vitousek and Reiners 1975). Deeper snow also correlates with increased selection of riparian areas and areas at lower elevations that could increase localized predation risk (Joly et al. 2016).

Stand replacement occurs between 30 and 40 years when the dominant species shift from deciduous shrubs to spruce, and competition with spruce limits the amount of forage in the area (Regelin et al. 1987, Brown et al. 2018). Studies focusing on habitat selection show that during the winter, moose did not select for areas until 10 to 25 years after a disturbance because deciduous stems were buried by the snow prior to that (Regelin et al. 1987, Joly et al. 2016).

The Alphabet Hills area of the Nelchina Basin is classified as an open spruce forest/shrub/bog or as an open and closed spruce forest (Viereck 1992, Markon and Walker 1998). These stands are typically characterized by cold, poorly drained organic soils, and overall low productivity (Landhausser and Wein 1993, Crevoisier et al. 2007). Alaskan black spruce fires typically occur every 70 to 125 years, with replacement/high severity fires that kill 75% of the upper canopy occurring in 45 to 85% of fires (Landhausser and Wein 1993, Crevoisier et al. 2007). Fire can reduce the overall organic layer thereby increasing water drainage and limiting water available to plants (Yi et al. 2009). Post-fire environmental conditions, such as increased UV exposure, water stress, and nutrient leaching/loss may place additional stresses on plant growth, which may result in an increase in secondary defense compounds such as condensed tannins. Condensed tannins are thought to have originally evolved to protect the plant from water stress, but they are also made to protect the plant from herbivores (Herms and Mattson 1992). Tannin concentration is higher in the early growth stages of browses important for moose which may be a result of induced chemical defenses of the newest, most productive tissues (Bryant and Kuropat 1980, Bryant et al. 1983, Herms and Mattson 1992, Spalinger et al. 2010). High condensed tannin concentrations in conjunction with relatively low protein concentrations in some plants can result in net negative protein gain for an herbivore due to its ability to bind both plant proteins and animal/microbial proteins endogenous to the GI tract (Spalinger et al. 2010, Tharayil et al. 2011, Adamczyk et al. 2017).

In burned habitats, defensive compounds may also increase because of environmental stresses that change the resource allocation patterns of plants. For example, increased solar radiation and more xeric soil conditions can induce water stress in summer (Herms and Mattson 1992, Gundale et al. 2010), leading to increases in oxidative stress responses, including polyphenolic concentrations (Chapin, 1991, Rau et al. 2008, Tharayil et al. 2011). Heightened solar radiation can also slow overall photosynthetic rate due to a build-up in sucrose-levels that limits the movement of carbon dioxide (Sweet and Wareing 1966). The diminished photosynthetic rate limits the productivity of the tissues which reduces the overall quality available for herbivores (Sweet and Wareing 1966). Increased tannin concentration may affect the microbiome of the rumen which ruminant species rely on to digest woody browse (Solden et al. 2017). This may result in lower nutritional quality, particularly nitrogen availability, to large herbivores, potentially limiting animal productivity (McArt et al. 2009). High concentrations of condensed tannins can also further limit nitrogen availability for plants in boreal forests by binding to amino acids and/or soil microbial exoenzymes in the soil once deposited by fire, creating a positive feedback loop (Gundale et al. 2010). This therefore limits uptake by microorganisms of both proteins, and potentially carbon as well (Gundale et al. 2010).

Development of seral vegetation following fire may attract an overabundance of moose, leading to a reduction in the overall quality of those habitats through selective removal of the most nutritional species. Fire can also redistribute moose to early seral stands, in turn leading to a reduction of the overall quality of those habitats through the removal of the most nutritional species (Collins and Schwartz 1998, Shipley 2010, Collins et al. 2011). Over browsing by moose can result in a shift in dominant species from preferred species like *Salix* spp. to the less nutritious *Betula* spp. (Christie et al. 2015). Reduction in forage diversity because of over browsing can also reduce the opportunity for the animal to balance toxin loads. Browsing by moose also has the potential to keep shrubs within browsing height, making them easily outcompeted by spruce (Pastor et al. 1988).

The objectives of this study were (1) to test the hypothesis that wildfire creates compositional and chemical changes in plants in burned habitats that are beneficial to moose and (2) to examine the potential tradeoffs between food abundance and quality on nutritional status of moose.

Materials and Methods

Study Site

To examine the impact of fire on availability and nutritional quality of browses for moose we examined the Alphabet Hills Fire (62.713906N 146.655193W), a prescribed burn intended to enhance moose habitat in the Nelchina Basin. The burn occurred in the summer of 2004 and its extent was 152 km² (Figure 1). The Nelchina Basin is dominated by black spruce forest interspersed with numerous lakes and small streams. The canopy is dominated by black spruce with white spruce dispersed intermittently. The understory is dominated by deciduous browse including diamond leaf willow (*Salix pulchra*), Grayleaf willow (*Salix glauca*), mountain alder (*Alnus crispa*), and dwarf birch (*Betula nana*). Not only does the area house a large moose population but it is also home to caribou, who use the burned area in the summer, bears, and wolves.

Field Methods

Sampling sites were randomly selected throughout both the burned and un-burned habitats within 4 km of Porkchop Lake (Figure 1). In total, 20 sites were placed in the burned habitat and 20 in the forested habitat (Figure 1). Several of the unburned sites occurred within the burn perimeter, having escaped the fire. At each sampling site plant samples were collected from all species that were considered potential browse species of moose, based on field observations of browsed plants at all the sites and previous experience from tame animal observations and browsing studies in the region. At each sampling location, three samples of the dominant browse species were collected in order to capture the spatial and individual variation in plant chemistry and nutritional quality across the burned and unburned habitats. Samples were placed into coin envelopes or zip lock bags and frozen immediately on dry ice. Sampling was done in mid-June, mid-July, and mid-August in the summer of 2018, and again in mid-June and mid-August in the summer of 2019 to capture the seasonal variation and yearly variation in nutritional quality of the plants.

During August of 2019, we also quantified canopy cover and available bites of forage at each sampling site using randomly placed point intercept transects in both habitat types. At each sample point, a point-cover transect was established to measure canopy cover of each browse species and the relative frequency of bites available to moose. Transects were 50 meters in length and oriented along a randomly selected bearing. At each meter, all species that intercepted meter marks on the tape measure were recorded, including ground cover and any overstory species (Elzinga et al. 1998). For species that could appear in a moose's diets, we also recorded the number and size of the potential bites that intercepted the point this was used to as a metric for bite frequency available in the burned/disturbed and forest sites. Interceptions of potential bites were indicated with the use of a plumb bob or a periscope.

Winter sampling was done at the same field sampling locations during March of 2019, as well as new locations accessible by helicopter. Current annual growth (CYG) of available browse species was clipped and placed into a zip lock bag and frozen immediately. We also measured the diameter at the point of browsing for each species consumed by moose in winter using Bluetooth calipers that were paired with a mobile de-vice. These measurements guided our subsequent nutritional analyses of the winter twigs (Shipley and Spalinger 1995, Shipley et al. 1999).

Lab Methods

Nutritional analyses were completed at the Alaska Department of Fish and Game (ADFG) Herbivore Nutrition Laboratory, in Palmer, AK. Digestible energy and digestible protein of all forage species were quantified using the methods outlined by Spalinger et al. (2010) and McArt et al (2006). Vegetation samples collected in the field were subsequently freeze-dried and ground in a Wiley mill over a 20-mm screen (McArt et al. 2006). Before being ground, winter twig samples were segregated into three diameter segments in order to quantify the relationship between nutritional quality and diameter of the twig. The goal was to divide the stems into three diameter classes that produced approximately equal masses with enough sample for the nutritional analyses. Regressions were then used to predict nutritional quality and bite size from diameter at point of browsing for any given species.

Nitrogen concentrations were determined using a LECO TruSpec CHN and Cos-tech CHNOS Analyzer with

NIST apple leaves used as quality control standard for every 10th sample (McArt et al. 2006). Digestible dry matter of each forage was determined from sequential fiber analysis using the ANKOM 200 fiber analysis system according to manufacturer’s recommended methods. Neutral detergent fiber (NDF) was determined with a neutral detergent solution made with sodium sulfite and an acid detergent solution was used to determine acid detergent fiber (ADF). NDF is an estimate of the ratio of insoluble fiber of the plant in the cell wall and the highly digestible cell contents while ADF is a measure of the cellulose + lignin/cutin concentration (Van Soest 1994, Spalinger et al. 2010). Samples were then extracted in 72% sulfuric acid to determine lignin + cutin concentration (Van Soest 1994, Spalinger et al. 2010). The sulfuric acid residue was then ashed at 500 for 3 hours to determine the mineral/silica concentration (Van Soest 1994, Spalinger et al. 2010, Cook et al. 2022). Because of a shift in sequential fiber values since 2012, we used a modified correction as described in Cook et al. (2022). Digestible dry matter (DDM) and energy (DE) were subsequently estimated from equations presented by Spalinger et al. (Spalinger et al. 2010).

Tannins were extracted in a 50% methanol solution under high pressure and temperature in a Dionex™ Accelerated Solvent Extractor (ASE-200) (Close et al. 2003, McArt et al. 2006). The tannin extract was then diluted with 50% methanol, mixed with bovine serum albumin (BSA) and purified with Sephadex G-25. The resulting solution was mixed with Bradford Protein Reagent and read on a UV-Vis microplate spectrometer at 595 nm to estimate protein precipitating capacity (PPC, mg DSA precipitated/mg forage DM) (McArt et al. 2006). PPC was then used to calculate the digestible protein, the percent protein reduction, and digestible energy of each sample (Robbins et al. 1987, Spalinger et al. 2010).

After freeze-drying, twigs were subdivided into 3 diameter classes for subsequent nutritional analyses, following the methods outlined above. After nutritional analyses, mass-diameter and nutrient density - diameter regressions were computed for each species. From these, estimates of nutritional quality and bite size were made for field measured browsed twigs.

Statistical Analyses

To test the hypothesis that burned habitat was of nutritionally higher quality than unburned habitats, we analyzed the nutritional quality data in a hierarchical fashion. For the analysis, we only used species that were found in both habitat treatment types. Four species that were only found in the burned habitat (fireweed, quaking aspen (*Populus tremuloides*), little tree willow (*Salix arbusculoides*), and sedges) were removed from the analysis, leaving nine different species to be included in the analysis (*Alnus crispa*, *Equisetum* spp., *Salix pulchra*, *S. glauca*, *S. pseudomyrsinites*, *S. richardsonii*, *Betula nana*, *B. glandulosa*, and *B. neoalaskana*). We first compared overall nutritional quality of habitats for all forages combined using a multivariate analysis of variance (MANOVA) with habitat type, month, and year as covariates. We tested the interaction between habitat type and month sampled using an ANOVA, with digestible energy, nitrogen concentration, percent reduction in proteins from tannins, and digestible protein as dependent variables. We also calculated the species diversity of each habitat type using the Shannon-Weiner Index (Eq. 2), where π_i is the proportion of total sample represented by species i , and H is the diversity of each study site.

$$H = -\sum (\pi_i \times \ln(\pi_i)). \quad (2)$$

Comparisons of forest versus burn for individual forage species common to both sites were done using unpaired t-tests with a Bonferroni multiple comparison adjustment. All statistical analyses were performed in R (Marsh et al. 2006), and all comparisons were considered significantly different at $p < 0.05$. Individual species that were found in both burned and unburned habitats, including diamond leaf willow, dwarf birch, and gray leaf willow, were also compared individually using unpaired t-tests with a Bonferroni multiple comparison adjustment to directly compare the two habitat treatment types.

Results

Over the 2018-2019 field seasons, we sampled the Alphabet Hills burn on six occasions, five times across the summers of 2018 and 2019 and once in the winter of 2018-2019. We collected over 500 plant samples, and measured canopy coverage of moose browses from randomly selected plots in burned ($n = 16$) and unburned

habitats ($n = 10$). We found that the total canopy cover of moose preferred browses were higher in forested sampling sites than in burned sites. There was a significant difference between browse canopy cover in the forest compared to the burn (forest % cover = 10%, SE = 0.019, burn % cover = 9%, SE = 0.01; $t = 19.18$, $p = 0.033$) (Figure 2). The burned area had higher diversity of species (burn H = 1.709, forest H = 1.509) with four species that were only found in the burned areas including fireweed, quaking aspen, little tree willow and various mushrooms (*Boletus* spp.) that are consumed by moose (Figure 2).

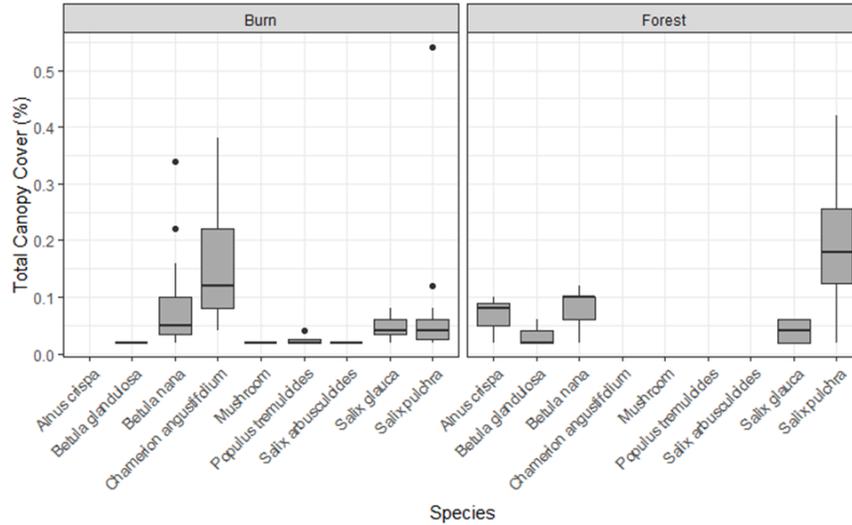


Figure 2: Total canopy cover of available browse and forbs for moose separated by the species and the habitat type.

Nutritional Quality

The digestible energy of forage overall decreased throughout summer following the browse’s phenological progression and deposition of fiber (Figure 3).

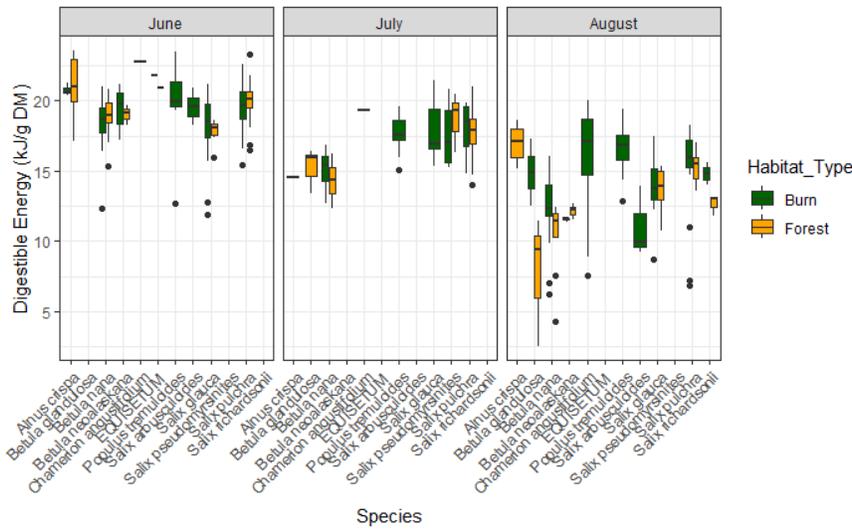


Figure 3 : Digestible Energy (kJ/g dry matter) for each preferred species for a moose during the summer

sampling periods, separated by month and by habitat type where each sample was collected.

Overall, digestible energy decreased by 50% (June mean = 19.37 kJ/g DM, SE = 1.96, August mean = 14.07 kJ/g DM, SE = 3.21, $p < 0.0001$) between June and August for the Alphabet Hills (Table 1). Average digestible energy was not significantly different between habitat types (burned mean = 14.87 kJ/g DM, SE = 4.25, forested mean = 15.42 kJ/g DM, SE = 4.32), but the interaction between habitat type and month ($F = 215.7$, $p < 0.0001$) as well as habitat type and species were both significant ($F = 2.86$, $p < 0.0001$). We also found a significant difference in year; 2018 had an average DE of 17.04 kJ/g DM (SE = 3.06) while 2019 had an average of 13.33 kJ/g DM (SE = 4.46, $p < 0.0001$).

Table 1: Comparison of average digestible energy (kJ/g DM) of species appearing in both burned and unburned sites in the Alphabet Hills, Alaska in June, August, and March

	Mean (SE)	Diff	P-value		Mean (SE)	Diff	P-value
Alphabet Hills				Alphabet Hills			
Burn	14.874 (4.245)			June	19.37 (1.958)		
Forest	15.421 (4.318)	-0.547	0.12	August	14.074 (3.212)	-5.4	
				March	10.589 (1.934)	-3.119	<0.0001***
<i>S. pulchra</i>				<i>S. pulchra</i>			
Burn	14.416 (4.268)			June	18.824 (1.441)		
Forest	15.475 (4.259)	-1.059	.053	August	15.17 (2.757)	-4.26	
				March	10.832 (1.506)	-4.338	<0.0001***
<i>B. nana</i>				<i>B. nana</i>			
Burn	13.76 (3.651)			June	18.735 (1.532)		
Forest	14.421 (4.56)	-0.661	0.33	August	11.669 (2.559)	-7.066	
				March	10.443 (2.073)	-1.226	<0.0001***
<i>S. glauca</i>				<i>S. glauca</i>			
Burn	14.651 (4.465)			June	18.112 (2.079)		
Forest	14.789 (2.936)	-0.138	0.91	August	13.933 (1.998)	-4.179	
				March	8.955 (1.961)	-4.978	<0.0001***

<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>	<p><i>Notes:</i> DM is dry matter; Diff is the difference between the two sampling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i>. Significant differences were determined with a paired t-test using a Bonferroni adjustment. Significant differences are denoted with asterisks. *p<0.05, **p<0.01, ***p<0.0001</p>
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Digestible protein is a function of nitrogen concentration and the PPC of tannins. We found that digestible protein was similarly affected by month and year, just as with nitrogen concentration and tannin effects individually (Figure 4).

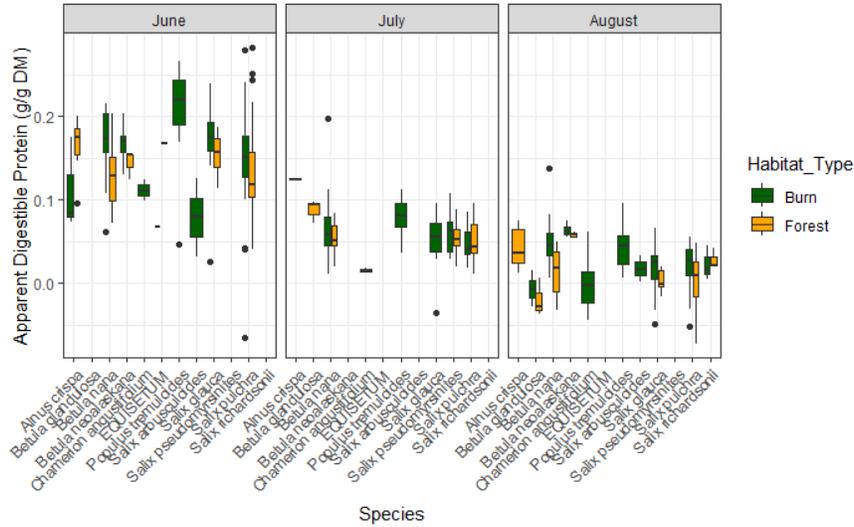


Figure 4: Apparent digestible protein (g/g DM) recorded for each species of selected for species moose for the summer sampling periods. Values are separated by the month and habitat type where each sample was collected.

For all species combined, digestible protein was significantly lower in August than in June (August = 0.023 g/g DM, SE = 0.032, June mean = 0.155 g/g DM, SE = 0.053, $p < 0.0001$) (Table 2).

Digestible protein was significantly higher in 2018 at 0.78 g/g DM (SE = 0.062) than in 2019 at 0.045 g/g DM (SE = 0.085, $p < 0.0001$). Digestible protein was not significantly different between forest and burn sites (Table 2). Nevertheless, digestible protein declined over summer at a faster rate in the burn than in the forest ($t = 4.75$, $p < 0.001$) (Figure 4). This could be due to the higher initial (June) values of digestible protein in the burn, as the values for both the burn and the forest were near or below zero by late summer (August) (Figure 4).

Table 2: Comparison of average digestible protein (kJ/g DM) of species appearing in both burned and unburned sites in the Alphabet Hills, Alaska in June, August, and March.

	Mean (SE)	Diff	P-value	P-value		Mean (SE)	Diff	P-value	P-value
Alphabet Hills					Alphabet Hills				
Burn	0.0614 (0.08)				June	0.155 (0.053)			
Forest	0.059 (0.071)	0.0024	0.677	0.677	August	0.023 (0.032)	-0.132	-0.132	
					March	-0.005 (0.025)	-0.037	-0.037	<0
S. pulchra					S. pulchra				
Burn	0.036 (0.08)				June	0.14 (0.057)			
Forest	0.045 (0.074)	-0.009	-0.009	0.35	August	0.014 (0.032)	-0.126	-0.126	
					March	-0.017 (0.022)	-0.031	-0.031	<0

B. nana Burn	0.073 (0.068)				B. nana June	0.148 (0.044)			
Forest	0.068 (0.061)	-0.005	0.66	0.66	August	0.037 (0.032)	-0.111	-0.111	<0
					March	0.018 (0.017)	-0.019	-0.019	<0
S. glauca Burn	0.072 (0.087)				S. glauca June	0.17 (0.038)			
Forest	0.06 (0.083)	-0.012	0.62	0.62	August	0.013 (0.029)	-0.157	-0.157	<0
					March	-0.012 (0.018)	-0.025	-0.025	<0

Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001	Notes: DM is dry matter; Diff is the dif- ference be- tween the two sam- pling areas, and the two plant genera are <i>Salix</i> and <i>Betula</i> . Signifi- cant differ- ences were deter- mined with a paired t-test using a Bonfer- roni adjust- ment. Signifi- cant differ- ences are de- noted with aster- isks. *p<0.05, **p<0.01, ***p<0.0001
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For winter nutritional quality, digestible energy was significantly influenced by browse species ($F = 6.01$, $p < 0.0001$) and size class ($F = 2.28$, $p = 0.02$) but not habitat type (Figure 5).

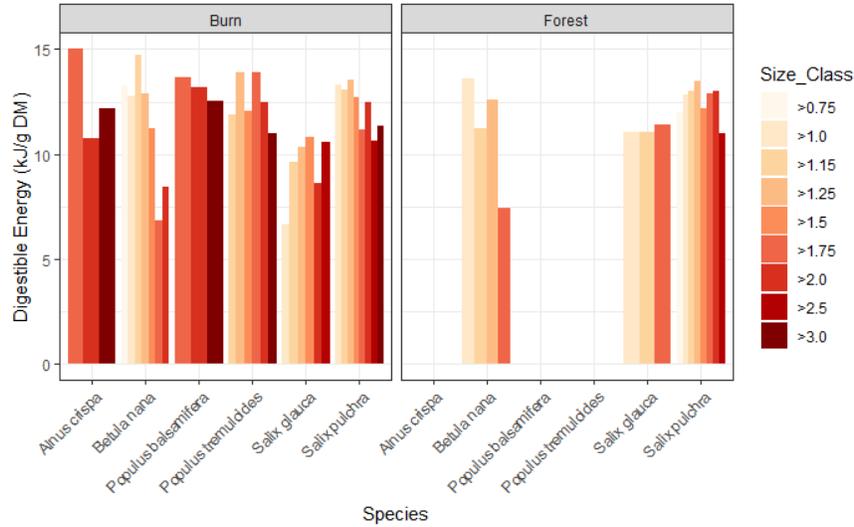


Figure 5 : Digestible Energy (kJ/ g dry matter) for each sampled species in the burned and unburned areas. Samples were collected in March 2018, and are separated by diameter class (cm).

The digestible protein was also significantly influenced by species ($F = 25.41$, $p < 0.0001$) and diameter ($F = 3.925$, $p = 0.0003$) but there was no significant difference between habitat types (Figure 6). Habitat type did have a significant influence on tannin content with the burned area having an average of 0.188 mg BSA/g DM (SE = 0.14) while the forested area had on average 0.23 mg BSA/g DM (SE = 0.14). The negative protein contribution stems from the large concentration of tannins found in those samples (Figure 6).

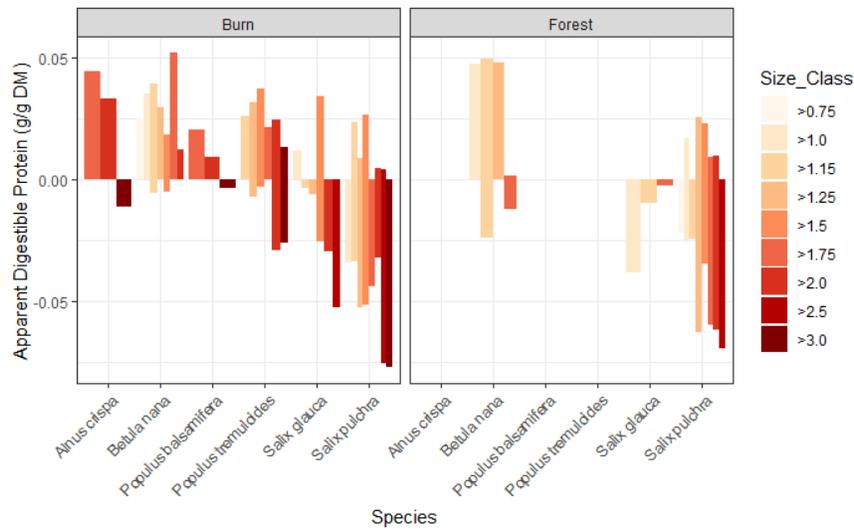


Figure 6 : Apparent digestible protein (g/g DM) recorded for each species in the burned and unburned areas. Samples were collected in March 2018, and are separated by diameter class (cm).

Discussion

We found a significant difference in the canopy cover of the browses between the burned and unburned area of the Alphabet Hills. Burned sites had a higher species diversity, which could prove to be more beneficial

to moose if forage diversity lowers the effect of toxins on digestive function, a hypothesis referred to as the detoxification limitation hypothesis (Marsh et al. 2006). This hypothesis states that reliance on a single food source with high amounts of PSMs can limit the overall detoxification system of an animal (Freeland and Janzen 1974). An overwhelming amount of PSMs can negatively affect the gut microbiome which can further limit intake and digestion (Freeland and Janzen 1974, Dearing et al. 2000, Marsh et al. 2006). Although the forest had higher canopy cover and higher bite frequency, the overall diversity of the burn plots may have more of a significant role in the tradeoff between quantity vs quality of available forage in an area.

Our findings suggest that browse availability in our study site, as measured by ground cover, was greater in the forest than in the burn, contrary to the findings of others (Hobbs and Spowart 1984, Blair 1997, Greene et al. 2012). We attribute this to several potential factors that could influence the recovery of a site after fire, including the burn severity, the site conditions prior to the fire, and that many of the unburned sites were within the total burn perimeter suggesting they were protected from the fire. The Alphabet Hills area is classified as an open spruce forest/shrub/bog or as an open and closed spruce forest (Landhausser and Wein 1993, Crevoisier et al. 2007), which are characterized by cold, poorly drained organic soils, and overall low productivity. The forest sites may have been protected from the burn due to their location of the landscape near more riparian areas or areas where moisture could accumulate due to the area's topography. Because of their potential exposure to higher moisture levels as well as retention trees, or trees that remain alive and standing after a fire (Den Herder et al. 2009), the browse in forest sites may have had higher productivity due to reduced stress. The fire history of the area, as well as the soil characteristics, could explain why there was greater average canopy cover in the forested sites over the burned sites. The burn characteristics of the Alphabet Hills fire are more aligned with the establishment stage of a younger fire which would also explain why we did not see a significant increase in browse availability in the burned sites vs the unburned sites.

One potential influence that was not included in this study is the effect of fire severity on nutritional quality and quantity. Intense, high severity fires could either promote the growth of aspen and other moose preferred browse due to their ability to bud from their roots, or they can favor lower quality species that are wind dispersed like birch (Joly et al. 2016, Wan et al. in press). Although we have relative scale of severity and how our sampling points align with the fire severity, we were unable to attribute the variation in plant chemistry to fire severity. We chose to group plots into burned and unburned to just look at the two major habitat groupings; this also groups riparian habitats and habitats with varying sun exposure that were found inside and outside the burn perimeter. Future work would need to be done to expand the number and location of sampling sites, as well as adding other characteristics that indicate changes in severity, such as soil temperatures at various depths and depth of fuel consumption, to quantify the effect fire severity has on browse species and therefore moose.

The significant decrease in digestible energy in the burn over the forest could be due to a higher desiccation rate in the burn due to the lack of cover. Shaded plants have been found to have higher levels of chlorophyll to take advantage of reduced sunlight and thinner cuticle layers which reduces the amount of indigestible material for a moose (Bø and Hjeljord 1991, Gratzner et al. 2004, Hagemeyer and Leuschner 2019). Differences in light availability will also change the distribution of nutrients and moisture in the soil, further affecting growth and allocation of resources (Bø and Hjeljord 1991, Gratzner et al. 2004). Warmer temperatures, both ambient and soil, have been shown to increase fiber deposition for browse species, lowering the quality for moose (Bø and Hjeljord 1991, Barboza et al. 2018). For immature plants with extremely low cell wall concentrations (low structural carbohydrate concentrations), we may have underestimated DDM and DE. The equations for digestibility derived in moose by Spalinger et al (2010) were based on forages of much higher structural carbohydrate concentration, and plants below approximately 20% NDF fall outside the domain of those equations (Robbins et al. 1987, McArt et al. 2006, Spalinger et al. 2010).

Moose are not immobile, although we found that the forested sites had higher abundance and quality of browse, the moose found within the Alphabet Hills and the Nelchina basin can move between habitats and in and out of the area to maintain healthy body condition, promote growth, and avoid predators. In the summer, females may choose areas that provide more cover for calving (Oehlers et al. 2011, Joly et al.

2016). In the winter, after reducing intake rates during the mating season, males may choose riskier habitat to prevent starvation (Oates et al. 2019). Habitat use is highly dependent on the season, this study chose to focus on the changes in habitat quality as summer progresses because that is a critical time for weight gain and growth of new tissues for males and females (McArt et al. 2009). Because we found an increased availability of biomass, as well as a higher quality of the browse in the forest, we may expect that moose in the area will spend a majority of their time within the forested areas (Searle et al. 2005, 2007). However, because of the increased diversity of species in the burned area, it could be a more important habitat for when the plants have the highest deposition of PSMs. For a moose, the overall dietary value of a forest stand is transient, often lasting less than 30 years, but moose need access to a wide age range in forest stands for protection from predators and available cover for their young (McMahon et al. 2000, Osko et al. 2004, Dussault et al. 2006, Joly et al. 2016). Further work is necessary to link movement of individuals throughout the area to the nutritional quality and bite frequencies throughout the year in this fire as well as other fires across the state.

Although others have shown a positive effect of wildfire for herbivore populations, we found that some areas, including the Alphabet Hills area, may not be suitably adapted to benefit from the quick release of nutrients after fire and may not allocate more resources to biomass as previously expected (Hobbs and Spowart 1984, Rea and Gillingham 2001). These findings highlight the importance of quantifying both availability and quality of food resources for herbivores, when addressing the benefits of fire. We showed that a traditional method of increasing available habitat for moose is not applicable for all habitats or areas. In the future, habitat management strategies that include wildfire should consider the history of the area and the pre-fire communities, as well as how fire can shift resource availability. Field surveys of pre-fire community characteristics such as understory community composition and individual species densities with paired surveys of plant chemistry is necessary to ensure that the fire is increasing biomass reachable by moose, while also increasing the nutritional quality. Soil characteristics, such as its water retention capacity and microbial community can also have a significant effect on post fire vegetation communities and their nutritional quality after wildfire and should be assessed before prescribing fires for habitat enhancement. Although logistically challenging, predictions of how fires may affect wildlife should be based on assessments of previously burned stands having similar physical and biological characteristics.

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