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Research article

Prescribed fire in the Nelchina Basin: a case study for managing moose population

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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, but only by 1%. Summer DP was significantly impacted by burn/unburn, caused by a 6% difference between the burn (avg = 2.58%) and the forest (avg = 2.43%). 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 the Alphabet Hills fire may not have made as much of a positive impact as in other systems. This project highlights the importance of research that quantifies both the availability of and the quantity of available food resources for herbivores.

Keywords: Alaska, forage resources, moose, nutrition, nutritional ecology, population management

Introduction

Ecologists and wildlife managers generally agree that in many ecosystems of 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



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shrub communities (Hobbs and Spowart 1984). 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 (Maier et al. 2005, Mack et al. 2008, Nelson et al. 2008, Johnstone et al. 2010), but quantification of the impacts of fire on moose population productivity is limited (Weixelman et al. 1998, Boertje et al. 2019). 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).

Although there is significant evidence suggesting that browse biomass density increases after fire (Sousa 1984, Maier et al. 2005, Brown et al. 2018), there is little regarding the effect of fire on plant chemistry after fire (Weixelman et al. 1998). Alterations of plant chemistry after fire could have dramatic effects on the overall palatability, and therefore the nutritional quality, of browse species. 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 (Bryant et al. 1992). This defense strategy makes these plants less palatable to herbivores by diluting the available nutrients (e.g. tannins ability to bind to nitrogen) (Dearing et al. 2005, Iason and Villalba 2006). Plant secondary metabolites can either be toxic to herbivores, causing detrimental effects independent of dosage; or they can be quantitative defenses, reducing the quality of the plant or plant part but requiring high doses to deter large herbivores (Mangione et al. 2001, Marsh et al. 2006).

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. 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). 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 gastrointestinal tract (Spalinger et al. 2010, Tharayil et al. 2011,

Adamczyk 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).

Timing since burn is itself an important factor for moose forage and habitat selection (Fisher and Wilkinson 2005, Nelson et al. 2008). 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* (Shipley 2010). 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 et al. 2019) 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). 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).

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). Therefore, 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 nutritional quality.

Material and methods

Study site

We measured cover and nutritional quality of browse species found in a 16-year-old prescribed burn, the Alphabet Hills (62°42'50.0616"N, 146°39'18.6948"W), 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 (Fig. 1). 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 and covered 152 km² (Fig. 1). The anticipated increase in moose productivity was expected to increase harvest opportunity, and to buffer losses to predation. Not only does the area house a large moose population, but it is also home to caribou *Rangifer tarandus*, who use the burned area in the summer, as well as brown bears *Ursus arctos* and wolves *Canis lupus*.

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 (Vioreck 1992, Walker 1999). These stands are

typically characterized by cold, poorly drained organic soils, and overall low productivity (Landhauser and Wein 1993, Crevoisier et al. 2007). Alaskan black spruce fires typically occur every 70–125 years, with replacement/high severity fires that kill 75% of the upper canopy occurring in 45–85% of fires (Landhauser and Wein 1993, Crevoisier et al. 2007). The canopy is dominated by black spruce with white spruce dispersed intermittently. The understory is dominated by mosses and the middle canopy consists of deciduous browse species including diamond leaf willow *Salix pulchra*, Grayleaf willow *Salix glauca*, mountain alder *Alnus crispa* and dwarf birch *Betula nana*.

Field methods

We randomly selected sampling sites using random GPS points that were mapped in ArcMap throughout both the burned and un-burned habitats within 4 km of Porkchop Lake (Fig. 1). In total, 20 sites were placed in the burned habitat and 20 in the forested habitat. Several of the unburned sites occurred within the burn perimeter, having escaped the fire. We chose to focus on all species that were considered potential browse species of moose, based on field observations of browsed plants, previous experience from tame animal observations, and browsing studies in the region, to ensure we were examining what was most important for a moose in the area. At each sampling location, we collected three samples of the dominant and preferred browse species to capture the spatial and individual variation in plant chemistry and

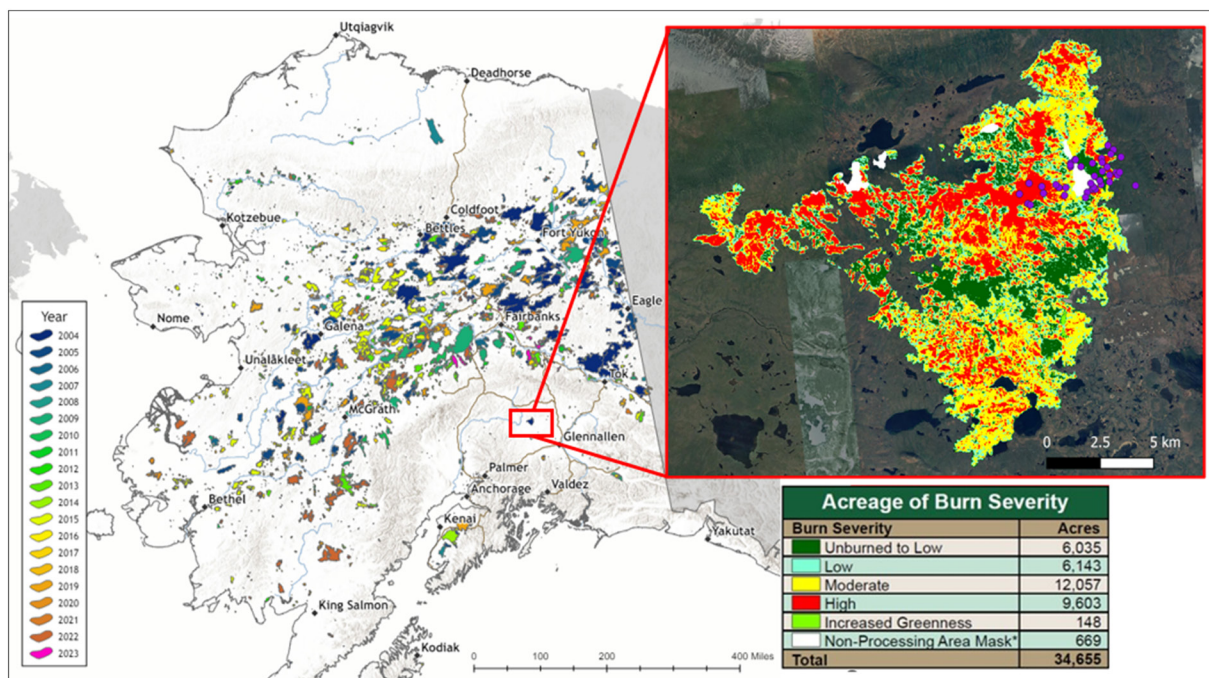


Figure 1. The Alphabet Hills fire, burned in 2004 for habitat management, is located west of Glenallen, AK. The map on the left shows the fire's location in relation to the total fire history (www.akfreinfo.com) of Alaska whereas the map on the right shows the burn perimeter, the fire severity readings (www.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.

nutritional quality across the burned and unburned habitats. Preferred species included species in the *Salix*, *Betula*, *Populus* and *Alnus* genus, as well as forbs (i.e. fireweed, mushrooms (*Boletus* spp.), *Equisetum* spp.) that have been shown to be selected for by moose (Spalinger and Hobbs 1992, Weixelman et al. 1998, Shipley 2010). Samples of the preferred species consisted of leaves and the new shoots, in order to collect the tissues that would most likely be selected for by a moose (Shipley et al. 1999). Samples were then placed into coin envelopes or zip lock bags and frozen immediately on dry ice. We sampled 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 in both the burn and unburned areas. At each sample point, a randomly oriented point-cover transect was established to measure canopy cover of each browse species available to moose. Transects were 50 m in length and oriented along a randomly selected bearing. At each meter, we recorded all species that intercepted meter marks on the tape measure, including ground cover and any overstory species (Elzinga et al. 1998).

Winter sampling was done at the same field sampling locations during March of 2019, as well as new locations accessible by helicopter. The current year's growth 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 device. These measurements guided the 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 McArt et al. (2006) and Spalinger et al. (2010). 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.

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°C for 3 h 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. (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 three 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 habitats were nutritionally higher in 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 using a multivariate analysis of variance (MANOVA) with burn/unburn, month, year, and the interaction between month and year as covariates. We tested the interaction between burn/unburn 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 burn/unburn using the Shannon–Weiner Index (Eq. 1).

$$H = \sum[(p_i) \times \ln(p_i)]. \quad (1)$$

Where p_i is the proportion of total sample represented by species i , and H is the diversity of each study site. 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 $p < 0.05$.

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 was higher in forested sampling sites than in burned sites. The forest percent cover was 10% ($SE=0.019$) while the burn had a percent cover of 9% ($SE=0.01$; $t=19.18$, $p=0.033$) (Fig. 2). The burnt 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 that are consumed by moose (Fig. 2).

Nutritional quality

From the MANOVA of the summer samples, we found that month, year, and the interaction between month and year all had significant impacts on the digestible energy of forage sampled. The digestible energy of forage overall decreased throughout summer following the browse's phenological

progression and deposition of fiber ($F=431.64$, $p < 0.0001$) (Fig. 3). Overall, digestible energy decreased by 42% (June mean = $19.42 \text{ kJ g}^{-1} \text{ DM}$, $SE=5.11$, August mean = $14.04 \text{ kJ g}^{-1} \text{ DM}$, $SE=3.13$) between June and August for the Alphabet Hills.

Digestible energy, on average, decreased between the two years sampled; 2018 had an average DE of $17.01 \text{ kJ g}^{-1} \text{ DM}$ ($SE=3.11$) while 2019 had an average of $13.34 \text{ kJ g}^{-1} \text{ DM}$ ($SE=4.46$, $F=25.91$, $p < 0.0001$). Digestible energy was also significantly different among the sampled species ($F=4.46$, $p < 0.0001$). Average digestible energy was not significantly different between burn/unburns (burned mean = $14.9 \text{ kJ g}^{-1} \text{ DM}$, $SE=4.26$, forested mean = $15.38 \text{ kJ g}^{-1} \text{ DM}$, $SE=4.34$).

Nitrogen concentration and tannin were similarly influenced by month (nitrogen $F=22.45$, $p < 0.0001$, BSA $F=13.37$, $p=0.0002$). Nitrogen concentration was also significantly higher in the burnt areas than the unburned (burn mean = 2.6 , burn $SE=1.1$, unburned mean = 2.4 , unburned $SE=0.88$, $F=6.55$, $p=0.011$) and the interaction between month and year ($F=27.32$, $p < 0.0001$) (Fig. 4). Tannin concentration was significantly higher in 2018 than 2019. On average 2018 had 0.22 mg BSA/g DM ($SE=0.11$) while 2019 had on average $0.169 \text{ mg BSA g}^{-1} \text{ DM}$ ($SE=0.09$) ($F=9.9$, $p=0.0018$).

We found that digestible protein was similarly affected by burn/unburn, month, and the interaction between month and year (Fig. 5). For the summer samples, digestible protein was significantly lower in August than in June (August = 3.29 g/g DM , $SE=3.13$, June mean = $15.95 \text{ g g}^{-1} \text{ DM}$, $SE=5.11$, $F=92.73$, $p < 0.0001$). Digestible protein was higher in 2018 at $8.56 \text{ g g}^{-1} \text{ DM}$ ($SE=5.94$) than in 2019 at $5.34 \text{ g g}^{-1} \text{ DM}$ ($SE=8.18$) but not significantly. Much like digestible energy, the interaction between month and year was significant ($F=334.24$, $p < 0.0001$). Digestible protein was not significantly different between forest and burn sites.

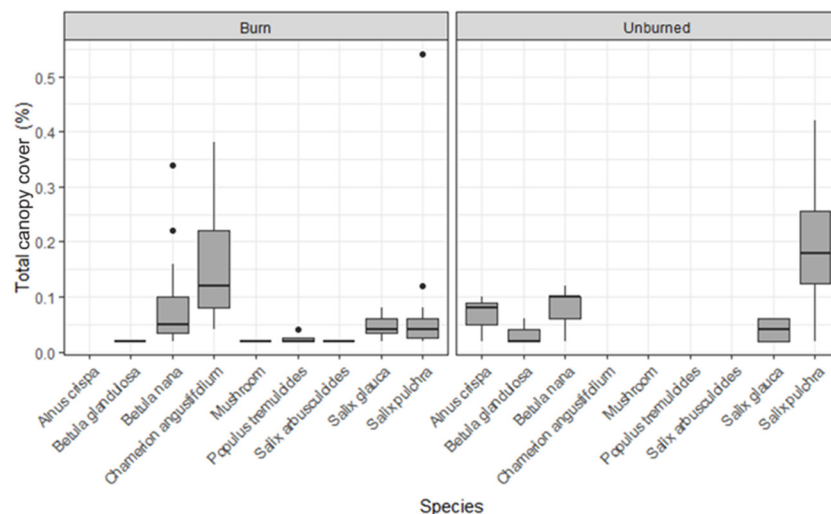


Figure 2. Total canopy cover of available preferred browse and forb species for moose found in the Alphabet Hills region of the Nelchina Basin, AK. Separated by the species and the burn/unburn.

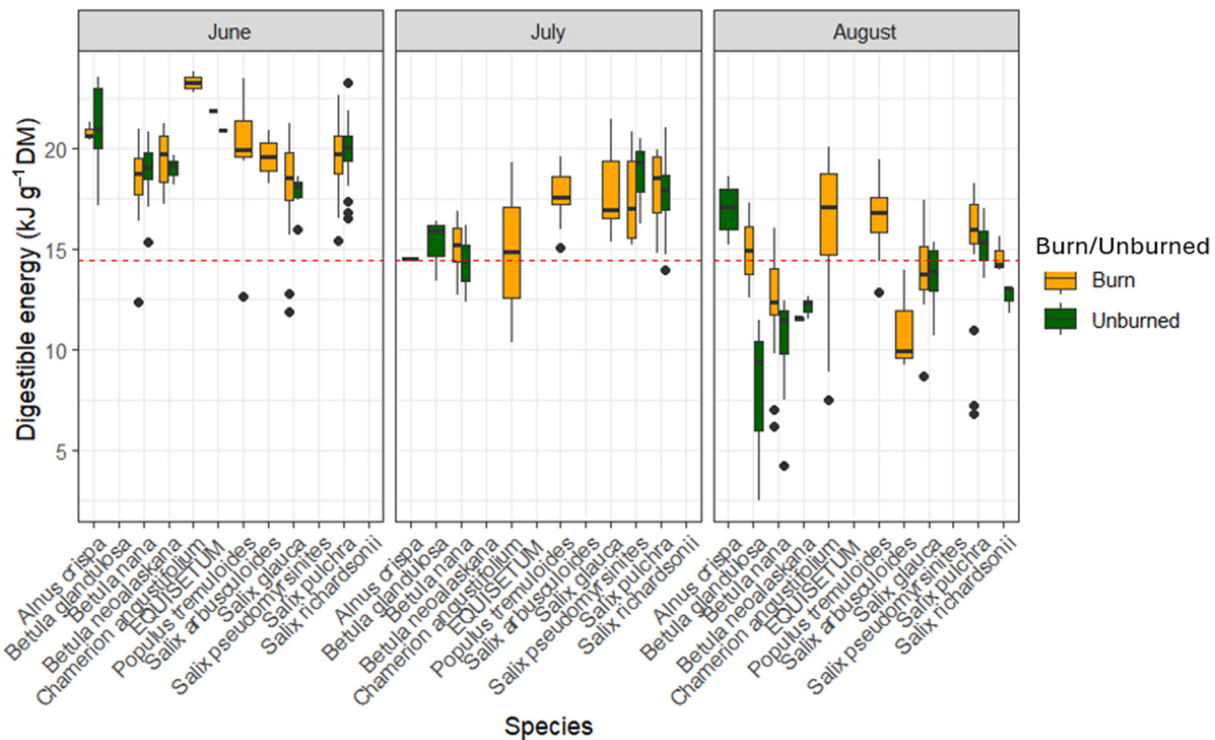


Figure 3. Digestible energy (kJ g⁻¹ dry matter) for each preferred species for a moose during the summer sampling periods, separated by month and by burn/unburn where each sample was collected. Red dashed line indicates minimum energy (kJ g⁻¹ day⁻¹) required for lactation, calculated using the equations published by [Reese and Robbins \(1994\)](#), [National Research Council \(2007\)](#) and [White et al. \(2014\)](#).

For winter nutritional quality, the MANOVA showed that digestible energy was significantly different among browse species ($F = 5.09$, $p = 0.0002$) and size class ($F = 2.04$, $p = 0.04$) but not burn/unburn ([Fig. 6](#)).

The digestible protein was also significantly influenced by species ($F = 23.73$, $p < 0.0001$) and diameter ($F = 4.14$, $p = 0.0001$) but there was no significant difference between the burn and unburned areas. Tannin concentration was significantly higher in the burnt area having an average of $0.188 \text{ mg BSA g}^{-1} \text{ DM}$ ($\text{SE} = 0.14$) while the unburned area had on average $0.23 \text{ mg BSA g}^{-1} \text{ DM}$ ($\text{SE} = 0.14$, $F = 7.01$, $p = 0.009$) ([Fig. 8](#)). Species had a significant impact on tannin content ($F = 30.17$, $p < 0.0001$), and the species ($F = 5.59$, $p < 0.0001$) as well as size class ($F = 6.31$, $p < 0.0001$) had a significant impact on nitrogen concentration ([Fig. 7](#)). The negative protein contribution stems from the large concentration of tannins found in those samples ([Fig. 8](#)).

Discussion

We found a statistically significant difference in the canopy cover of the browse species between the burned and unburned area of the Alphabet Hills, contrary to the findings of others ([Hobbs and Spowart 1984](#), [Blair 1997](#), [Greene et al. 2012](#)), but the difference may not be biologically significant. Burned sites did have 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 overwhelming amount of plant secondary metabolites (PSMs) can negatively affect the individual and its gut microbiome, limiting intake and digestion ([Freeland and Janzen 1974](#), [Dearing et al. 2000](#), [Marsh et al. 2006](#)). The overall higher species diversity of the burnt plots may have more of a significant role in the tradeoff between quantity versus quality of available forage in an area.

We attribute the observed differences 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 located in riparian areas which may have been protected from the effects of 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 proximity to riparian areas or areas where moisture could accumulate due to the area's topography ([Den Herder et al. 2009](#)). However, there were also several burned sites that were found in more mesic areas, suggesting that the prescribed fire produced a variable mosaic of conditions. This could increase the diversity of species in the entire area, making it a more important and selected for habitat by moose when the plants have the highest deposition of PSMs ([Villalba et al. 2017](#)).

Because we found minimal consistent differences between the burn/unburned areas, the moose in this area may be selecting habitat based on other characteristics such as ease of transport, distance to water, or predation risk (Maier et al. 2005, Oehlers et al. 2011, Street et al. 2015). Moose found within the Alphabet Hills and the Nelchina basin will move between habitats and in and out of the area to maintain healthy body condition, promote growth, and avoid predators. The heterogeneous nature of the fire creates habitat heterogeneity, and thus provides more opportunities for moose to select a more diverse diet, limiting toxin overloads or meeting nutritional needs, especially at key times of year (e.g. lactation). The

Stand succession, and stand quality after fire, is highly dependent on the pre-fire characteristics of the area as well as

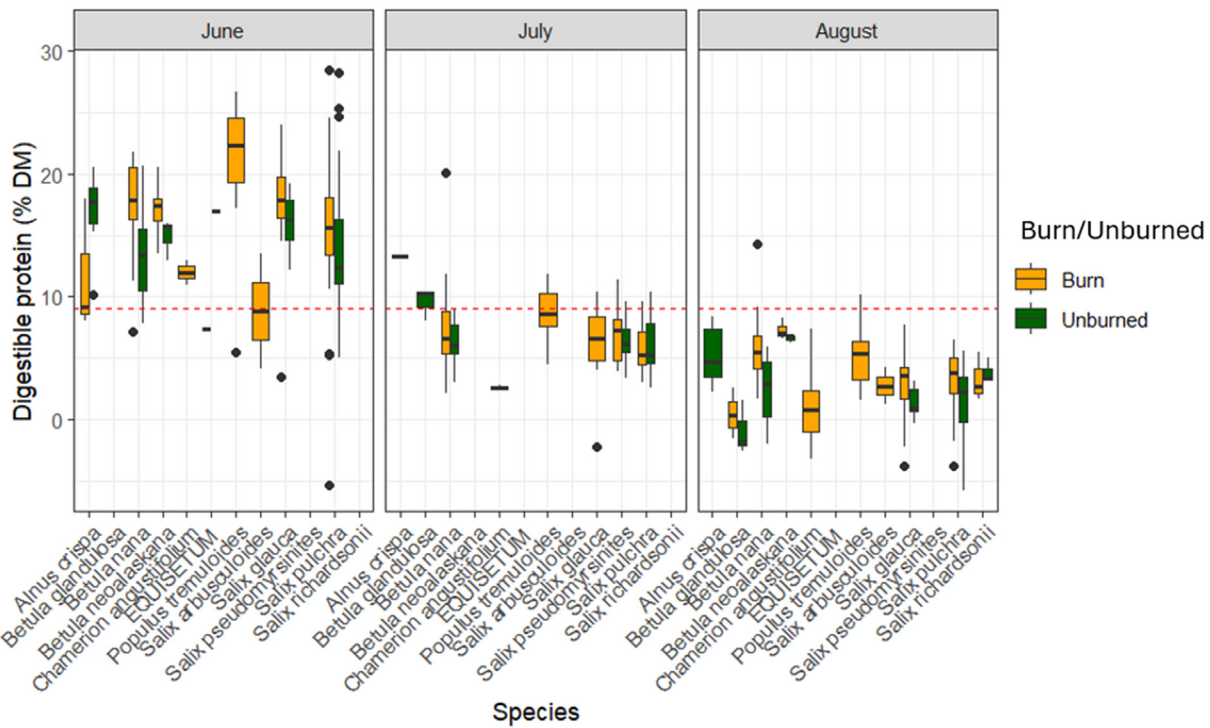


Figure 5. Digestible protein (%) recorded for each species of selected for species moose for the summer sampling periods. Values are separated by the month and burn/unburn where each sample was collected. The red dashed line indicates the minimum protein (% DM day⁻¹) required for lactation, calculated using the equations published by [McArt et al. \(2009\)](#) and Reese and Robbins (1994).

fire severity. 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 such as grasses and promote monocultures ([Wan et al. 2001](#), [Joly et al. 2016](#)). Higher intensity fires can also 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 deficiency of nitrogen in boreal soils ([Sponseller et al. 2016](#)). 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

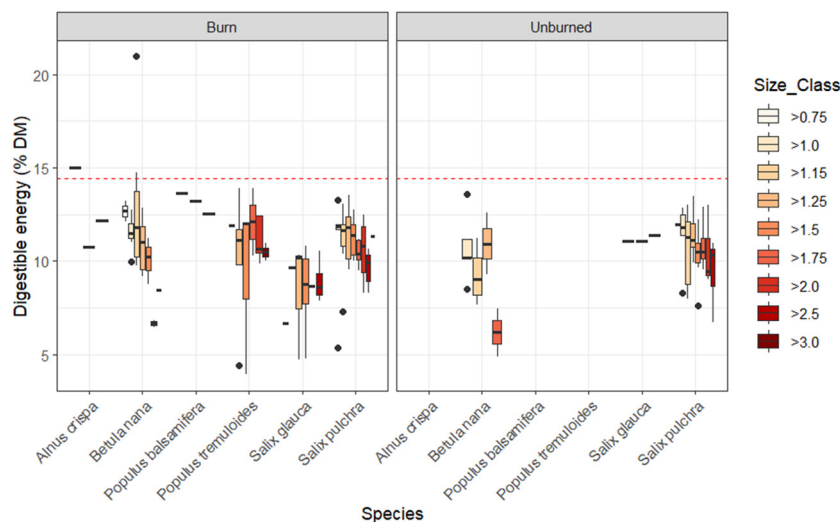


Figure 6. Digestible energy (kJ g⁻¹ dry matter) for each sampled species in the burned and unburned areas. Samples were collected in March 2018, and are separated by diameter class (cm), due to the differences in quality with increasing woody material. Red dashed line indicates minimum energy (kJ g⁻¹ day) required for lactation, calculated using the equations published by Reese and Robbins (1994), National Research Council (2007) and White et al. (2014).

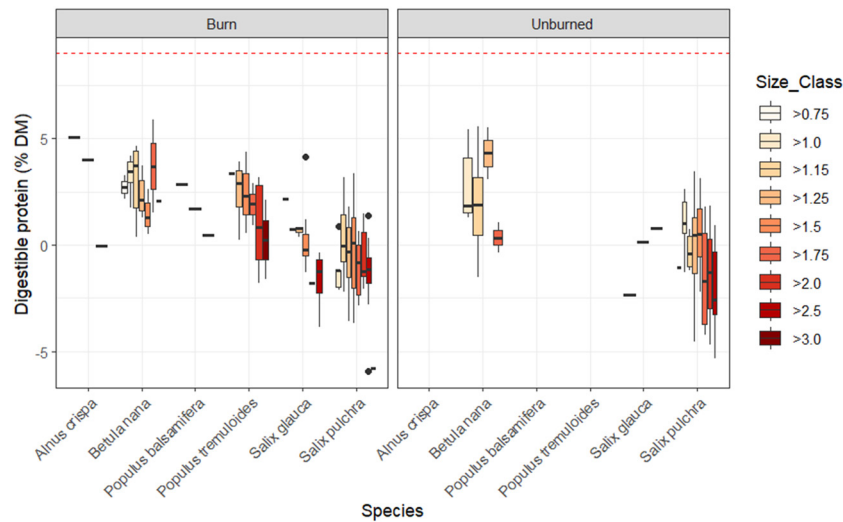


Figure 7. Digestible protein (%) recorded for each species in the burned and unburned areas. Samples were collected in March 2018, and are separated by diameter class (cm). Digestible protein levels can fall under zero due to the nitrogen binding capability of condensed tannins in the samples. The red dashed line indicates the minimum protein (% DM day⁻¹) required for lactation, calculated using the equations published by [McArt et al. \(2009\)](#) and [Reese and Robbins \(1994\)](#).

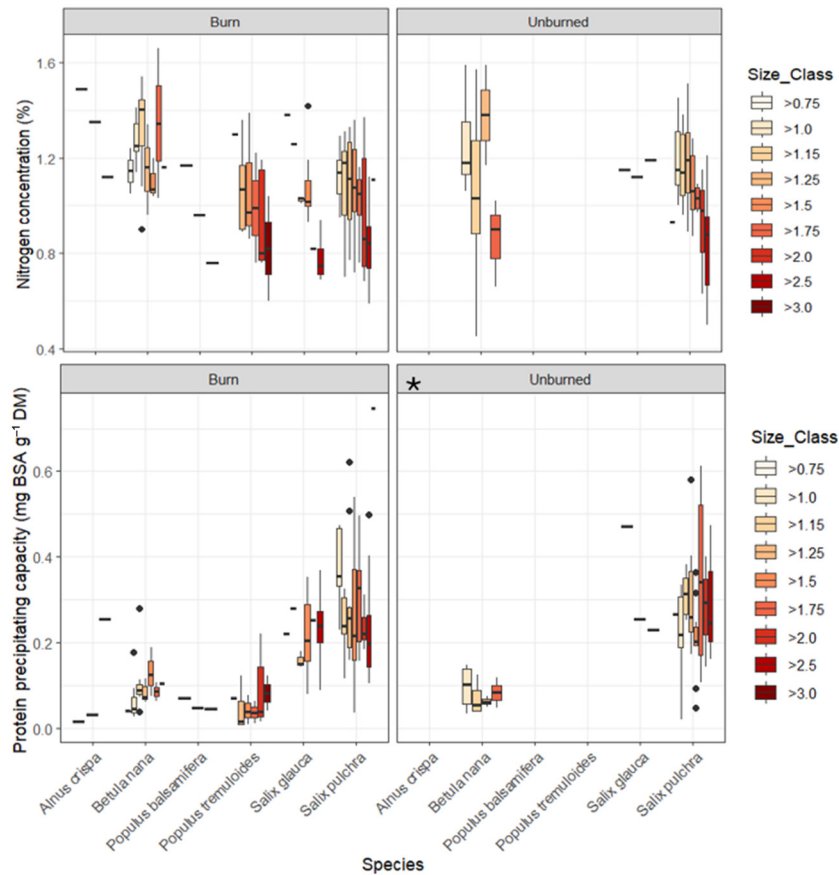


Figure 8. Nitrogen concentration (%), (A) and protein precipitating capacity (mg BSA g⁻¹ DM), (B) recorded for each species of selected for species moose for the summer sampling periods. These values are then used to calculate digestible protein. Values are separated habitat type and size class. Asterisk denotes a significant difference in protein precipitating capacity between the samples collected in the burnt and unburned areas.

(Collins and Schwartz 1998, Shipley 2010, Collins et al. 2011). Over browsing by moose could possibly result in a shift in dominant species and reduced richness, ultimately promoting high light demanding species (Ramirez et al. 2009, De Vriendt et al. 2021). Reduction in forage diversity because of over browsing can also reduce the opportunity for the animal to balance toxin loads. Lastly, browsing by moose also has the potential to keep shrubs within browsing height, making them easily outcompeted by spruce (Pastor et al. 1988). 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 (Fig. 1).

Future work should also add other characteristics that indicate effects of severity, such as soil temperatures at various depths of fuel consumption, to quantify the effect fire severity has on browse species and therefore moose. Because prescribed fires are only set when conditions are cool and controllable, which results in more heterogeneity as well as inclusions, future work should compare these results with a natural fire in a similar area. In addition, the response of plants to allocating carbon and nitrogen to growth versus defense is likely dependent upon browsing severity, climate and site conditions, nutrient availability and plant competition (Herms and Mattson 1992). Taken together, it is difficult to predict the impact of natural or prescribed fire on moose populations or their productivity.

Although the sampled area is limited, the Alphabet Hills fire is within the post disturbance window that is traditionally believed to be the best for moose. However, we did not find a significant increase in biomass or cover in the burnt area, nor did we find a major difference in nutritional quality of the available browse. Describing an area's nutritional quality separated by burned or unburned is not comprehensive enough to quantify the effects of large-scale habitat disturbance. This study shows that there are many characteristics of major disturbances, especially fires, that can impact how moose and other herbivores will interact with the new environment that can influence movement and population dynamics. 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 to ensure that fire will create the desired results.

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 composition can also have a significant effect on post fire vegetation communities due to their role in nutrient cycling, and their nutritional quality after wildfire and should be assessed before prescribing fires for habitat enhancement. Another alternative for assessing habitat quality, that would link more strongly to how an animal perceives quality, would be assessing fecal nitrogen. This non-invasive sampling technique has been used to accurately assess dietary nitrogen

in herbivore species such as bighorn sheep and elk *Cervus canadensis* (Irwin et al. 1993, Cook et al. 1994). Although logistically challenging, predictions of how fires may affect wildlife should be based on assessments of the targeted area, as well as how animals in the area already interact with their environment, instead of the expectation of burn success on the availability and quality of browse for all herbivore species.

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Author contributions

Katie L. Anderson: Conceptualization (supporting); Formal analysis (lead); Supervision (supporting); Validation-Equal, Visualization (lead); Writing – original draft (lead). **Donald E. Spalinger:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Writing – review and editing (equal). **William B. Collins:** Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available at: <https://github.com/MooseKate/AlphabetHills> (Anderson et al. 2024).

References

- Adamczyk, B., Simon, J., Kitunen, V., Adamczyk, S. and Smolander, A. 2017. Tannins and their complex interaction with different organic nitrogen compounds and enzymes: old paradigms versus recent advances. – *ChemistryOpen* 6: 610–614.
- Anderson, K. L., Spalinger, D. E. and Collins, W. B. 2024. Data from: Prescribed fire in the Nelchina Basin: A case study for managing moose populations. – Data available at, <https://github.com/MooseKate/AlphabetHills>.
- Bayley, S. E., Schindler, D. W., Beaty, K. G., Parker, B. R. and Stainton, M. P. 1992. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. – *Can. J. Fish. Aquat. Sci.* 49: 584–596.
- Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. – *Ecology* 78: 2359–2368.
- Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. – *BioScience* 32: 187–192.
- Boertje, R. D., Kellie, K. A., Seaton, C. T., Keech, M. A., Young, D. D., Dale, B. W., Adams, L. G. and Aderman, A. R. 2007.

- Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. – *J. Wildl. Manage.* 71: 1494–1506.
- Boertje, R. D., Frye, G. G. and Young, D. D. 2019. Lifetime, known-age moose reproduction in a nutritionally stressed population. – *J. Wildl. Manage.* 83: 610–626.
- Brown, C. L., Kielland, K., Euskirchen, E. S., Brinkman, T. J., Ruess, R. W. and Kellie, K. A. 2018. Fire-mediated patterns of habitat use by male moose (*Alces alces*) in Alaska. – *Can. J. Zool.* 96: 183–192.
- Bryant, J. P. and Kuropat, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. – *Annu. Rev. Ecol. Syst.* 11: 261–285.
- Bryant, J. P., Chapin, F. S. and Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. – *Oikos* 40: 357–368.
- Bryant, J. P., Reichardt, P. B. and Clausen, T. P. 1992. Chemically mediated interactions between woody plants and browsing mammals. – *J. Range Manage.* 45: 18.
- Chapin, F. S. 1991. Integrated responses of plants to stress. – *BioScience* 41: 29–36.
- Close, D., McArthur, C., Paterson, S., Fitzgerald, H., Walsh, A. and Kincade, T. 2003. Photoinhibition: a link between effects of the environment on *Eucalyptus* leaf chemistry and herbivory. – *Ecology* 84: 2952–2966.
- Collins, W. B. and Schwartz, C. C. 1998. Logging in Alaska's boreal forest: creation of grasslands or enhancement of moose habitat. – *Alces* 34: 355–374.
- Collins, W. B., Dale, B. W., Adams, L. G., McElwain, D. E. and Joly, K. 2011. Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska's taiga. – *J. Wildl. Manage.* 75: 369–377.
- Cook, J. G., Irwin, L. L., Bryant, L. D. and Thomas, J. W. 1994. Fecal nitrogen and dietary quality relationships in juvenile elk. – *J. Wildl. Manage.* 58: 46–53.
- Cook, R. C., Shipley, L. A., Cook, J. G., Camp, M. J., Monzingo, D. S., Robatcek, S. L., Berry, S. L., Hull, I. T., Myers, W. L., Denryter, K. and Long, R. A. 2022. Sequential detergent fiber assay results used for nutritional ecology research: evidence of bias since 2012. – *Wildl. Soc. Bull.* 46: e1348.
- Crevoisier, C., Shevliakova, E., Gloor, M., Wirth, C. and Pacala, S. 2007. Drivers of fire in the boreal forests: data constrained design of a prognostic model of burned area for use in dynamic global vegetation models. – *J. Geophys. Res.* 112: 2006JD008372.
- De Vriendt, L., Lavoie, S., Barrette, M. and Tremblay, J.-P. 2021. From delayed succession to alternative successional trajectory: how different moose browsing pressures contribute to forest dynamics following clear-cutting. – *J. Veg. Sci.* 32: e12945.
- Dearing, M. D., Mangione, A. M. and Karasov, W. H. 2000. Diet breadth of mammalian herbivores: nutrient versus detoxification constraints. – *Oecologia* 123: 397–405.
- Dearing, M. D., Foley, W. J. and McLean, S. 2005. The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. – *Annu. Rev. Ecol. Syst.* 36: 169–189.
- Den Herder, M., Kouki, J. and Ruusila, V. 2009. The effects of timber harvest, forest fire, and herbivores on regeneration of deciduous trees in boreal pine-dominated forests. – *Can. J. For. Res.* 39: 712–722.
- Dussault, C., Courtois, R. and Ouellet, J.-P. 2006. A habitat suitability index model to assess moose habitat selection at multiple spatial scales. – *Can. J. For. Res.* 36: 1097–1107.
- Elzinga, C. L., Salzer, D. W. and Willoughby, J. W. – Bureau of Land Management Measuring & Monitoring Plant Populations 1998 BLM/RS/ST-98/005+1730, p. 15–492.
- Fisher, J. T. and Wilkinson, L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. – *Mamm. Rev.* 35: 51–81.
- Freeland, W. J. and Janzen, D. H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. – *Am. Nat.* 108: 269–289.
- Greene, L., Hebblewhite, M. and Stephenson, T. R. 2012. Short-term vegetation response to wildfire in the eastern Sierra Nevada: implications for recovering an endangered ungulate. – *J. Arid Environ.* 87: 118–128.
- Gundale, M. J., Sverker, J., Albrechtsen, B. R., Nilsson, M.-C. and Wardle, D. A. 2010. Variation in protein complexation capacity among and within six plant species across a boreal forest chronosequence. – *Plant Ecol.* 211: 253–266.
- Harms, D. A. and Mattson, W. J. 1992. The Dilemma of plants: to grow or defend. – *Q. Rev. Biol.* 67: 283–335.
- Hobbs, N. T. and Spowart, R. A. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. – *J. Wildl. Manage.* 48: 551.
- Hobbs, N. T. and Swift, D. M. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. – *J. Wildl. Manage.* 49: 814.
- Hobbs, N. T. and Swift, D. M. 1988. Grazing in herds: when are nutritional benefits realized? – *Am. Nat.* 131: 760–764.
- Iason, G. R. and Villalba, J. J. 2006. Behavioral strategies of mammal herbivores against plant secondary metabolites: the avoidance-tolerance continuum. – *J. Chem. Ecol.* 32: 1115–1132.
- Irwin, L. L., Cook, J. G., McWhirter, D. E., Smith, S. G. and Arnett, E. B. 1993. Assessing winter dietary quality in bighorn sheep via fecal nitrogen. – *J. Wildl. Manage.* 57: 413–421.
- Johnstone, J. F., Hollingsworth, T. N., Chapin, F. S. and Mack, M. C. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. – *Global Change Biol.* 16: 1281–1295.
- Joly, K., Sorum, M. S., Craig, T. and Julianus, E. L. 2016. The effects of sex, terrain, wildfire, winter severity, and maternal status on habitat selection by moose in north-central Alaska. – *Alces* 52: 15.
- Julianus, E., Hollingsworth, T. N., McGuire, A. D. and Kielland, K. 2019. Availability and use of moose browse in response to post-fire succession on Kanuti National Wildlife Refuge, Alaska. – *Alces* 55: 24.
- Landhausser, S. M. and Wein, R. W. 1993. Postfire vegetation recovery and tree establishment at the arctic treeline: climate-change-vegetation-response hypotheses. – *J. Ecol.* 81: 665.
- Mack, M. C., Treseder, K. K., Manies, K. L., Harden, J. W., Schuur, E. A. G., Vogel, J. G., Randerson, J. T. and Chapin, F. S. 2008. Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. – *Ecosystems* 11: 209–225.
- Maier, J. A., Ver Hoef, J. M., McGuire, A. D., Bowyer, R. T., Saperstein, L. and Maier, H. A. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. – *Can. J. For. Res.* 35: 2233–2243.
- Mangione, A. M., Dearing, D. and Karasov, W. 2001. Detoxification in relation to toxin tolerance in desert woodrats eating creosote bush. – *J. Chem. Ecol.* 27: 2559–2578.
- Marsh, K. J., Wallis, I. R., Andrew, R. L. and Foley, W. J. 2006. The detoxification limitation hypothesis: where did it

- come from and where is it going? – *J. Chem. Ecol.* 32: 1247–1266.
- McArt, S. H., Spalinger, D. E., Kennish, J. M. and Collins, W. B. 2006. A modified method for determining tannin–protein precipitation capacity using accelerated solvent extraction (ASE) and microplate gel filtration. – *J. Chem. Ecol.* 32: 1367–1377.
- McArt, S. H., Spalinger, D. E., Collins, W. B., Schoen, E. R., Stevenson, T. and Bucho, M. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. – *Ecology* 90: 1400–1411.
- National Research Council 2007. Nutrient requirements of small ruminants: sheep, goats, cervids, and New World camelids. – National Acad. Press.
- Nelson, J. L., Zavaleta, E. S. and Chapin, F. S. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. – *Ecosystems* 11: 156–171.
- Oehlers, S. A., Bowyer, R. T., Huettmann, F., Person, D. K. and Kessler, W. B. 2011. Sex and scale: implications for habitat selection by Alaskan moose *Alces alces* gigas. – *Wildl. Biol.* 17: 67–84.
- Osko, T. J., Hiltz, M. N., Hudson, R. J. and Wasel, S. M. 2004. Moose habitat preferences in response to changing availability. – *J. Wildl. Manage.* 68: 576–584.
- Pastor, J., Naiman, R. J., Dewey, B. and McInnes, P. 1988. Moose, microbes and the boreal forest. – *BioScience* 38: 770–777.
- Ramirez, I., Volcke, E. I. P., Rajinikanth, R. and Steyer, J.-P. 2009. Modeling microbial diversity in anaerobic digestion through an extended ADM1 model. – *Water Res.* 43: 2787–2800.
- Rau, B. M., Chambers, J. C., Blank, R. R. and Johnson, D. W. 2008. Prescribed fire, soil, and plants: burn effects and interactions in the central Great Basin. – *Rangeland Ecol. Manage.* 61: 169–181.
- Reese, E. O. and Robbins, C. T. 1994. Characteristics of moose lactation and neonatal growth. – *Can. J. Zool.* 72: 953–957.
- Regelin, W. L., Hubbert, M. E., Schwartz, C. C. and Reed, D. J. 1987. Field test of a moose carrying capacity model. – *Alces* 23: 243–284.
- Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C. and Mautz, W. W. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. – *Ecology* 68: 98–107.
- Shipley, L. A. 2010. Fifty years of food and foraging in moose: lessons in ecology from a model herbivore. – *Alces* 46: 13.
- Shipley, L. A. and Spalinger, D. E. 1995. Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. – *Oecologia* 104: 112–121.
- Shipley, L. A., Illius, A. W., Danell, K., Hobbs, N. T. and Spalinger, D. E. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. – *Oikos* 84: 55.
- Sousa, W. P. 1984. The role of disturbance in natural communities. – *Annu. Rev. Ecol. Syst.* 15: 353–391.
- Spalinger, D. E. and Hobbs, N. T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. – *Am. Nat.* 140: 325–348.
- Spalinger, D. E., Collins, W. B., Hanley, T. A., Cassara, N. E. and Carnahan, A. M. 2010. The impact of tannins on protein, dry matter, and energy digestion in moose (*Alces alces*). – *Can. J. Zool.* 88: 977–987.
- Sponseller, R. A., Gundale, M. J., Fitter, M., Ring, E., Nordin, A., Näsholm, T. and Laudon, H. 2016. Nitrogen dynamics in managed boreal forests: recent advances and future research directions. – *Ambio* 45: 175–187.
- Street, G. M., Vander Vennen, L. M., Avgar, T., Mosser, A., Anderson, M. L., Rodgers, A. R. and Fryxell, J. M. 2015. Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). – *Can. J. Zool.* 93: 813–821.
- Testa, J. W. 2004. Population dynamics and life history tradeoffs of moose (*Alces alces*) in south-central Alaska. – *Ecology* 85: 1439–1452.
- Tharayil, N., Suseela, V., Triebwasser, D. J., Preston, C. M., Gerard, P. D. and Dukes, J. S. 2011. Changes in the structural composition and reactivity of *Acer rubrum* leaf litter tannins exposed to warming and altered precipitation: climatic stress-induced tannins are more reactive. – *New Phytol.* 191: 132–145.
- Van Soest, P. 1994. Nutritional ecology of the ruminant. – Cornell Univ. Press.
- Viereck, L. A. 1992. The Alaska vegetation classification. – US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Villalba, J. J., Costes-Thiré, M. and Ginane, C. 2017. Phytochemicals in animal health: diet selection and trade-offs between costs and benefits. – *Proc. Nutr. Soc.* 76: 113–121.
- Vitousek, P. M. and Reiners, W. A. 1975. Ecosystem succession and nutrient retention: a hypothesis. – *BioScience* 25: 376–381.
- Walker, D. A. 1999. An integrated vegetation mapping approach for northern Alaska (1:4 M scale). – *Int. J. Remote Sens.* 20: 2895–2920.
- Wan, S., Hui, D. and Luo, Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. – *Ecol. Appl.* 11: 1349–1368.
- Weixelman, D. A., Bowyer, R. T. and Ballenbergh, V. V. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. – *Alces* 34: 213–238.
- White, R. G., Russell, D. E. and Daniel, C. J. 2014. Simulation of maintenance, growth and reproduction of caribou and reindeer as influenced by ecological aspects of nutrition, climate change and industrial development using an energy-protein model. – *Rangifer* 34: 1.