FORAGE QUALITY AND MOOSE (*ALCES ALCES*) NUTRITION IN A LOGGED LANDSCAPE

by

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ABSTRACT

Forest dynamics are increasingly being influenced by forest management practices such as logging and salvage operations. These practices alter forest landscapes by shifting forest patches from mature forest dominated by coniferous trees to younger seral stages represented by grasses, forbs, shrubs, and deciduous trees. These changes affect the conditions (e.g. sunlight, water, soil nutrients) under which the regenerating plants grow, further influencing species composition and plant nutritional quality. Of note is the fact that many plants growing in full sunlight can produce more tannins (secondary metabolites produced to defend against herbivory) than plants growing in shade. Tannins decrease the digestible protein available in plants, reducing the nutritional value for herbivores such as moose.

Many moose populations in central interior British Columbia (BC) have been declining in tandem with a dramatic increase in salvage logging that followed a mountain pine beetle epidemic in the 1990s and 2000s. Cutblocks are typically thought to benefit moose, as the early-seral plant regrowth provides abundant forage. However, moose populations have declined despite an increase in this habitat type. Hypothetically, these declines may be due at least in part from forage plants growing in sun-rich cutblocks producing more tannins and thus affording relatively lower digestible protein to the moose. Following this, I studied whether individual moose that foraged more in cutblocks would have poorer body condition and lower rates of pregnancy and calf survival than individuals that foraged more in unlogged forests.

Working near Logan Lake, BC, I used a cohort of collared adult female moose (n=16) to select areas for forage sampling. I analyzed key forage species in cutblocks, cutblock edges, and unlogged forests over two summers (2021 and 2022) and found that plants in cutblocks did indeed produce more tannins and had lower digestible protein than those in forests. I also found that forages provided insufficient protein to support lactating moose throughout most of the summer. There were significant differences in plant nutritional quality year to year, with plants being of relatively poorer quality after the hot, dry growing season of 2021. I also followed the cohort of collared moose over the course of the study and repeatedly measured their body condition. I found that all individuals were classified as mildly to moderately nutritionally limited, but that poor body condition of adult females was not associated with depressed pregnancy or calf survival rates. Finally, I quantified each individual's use of cutblocks and burned habitats during the summer, and counter to the results of my nutritional work, I found no effect of cutblock use on adult female moose condition or reproduction. Use of burned habitats by moose, however, was linked to calf survival. Differences in adult female moose body fat were best explained by year, with individuals being in relatively poorer condition after the hot, dry spring and summer of 2021, likely due to a combination of reduced forage quality and increased thermal stress.

In summary, the cutblocks in my study area provided forage of poorer nutritional quality than forests, with cutblock edges providing forage of intermediate quality. Moreover, this landscape provided insufficient digestible protein to support lactating moose for most of the summer. However, these differences in nutritional quality between cutblocks and forests did not seem to translate into differences in adult female moose body condition or reproduction. Further work should explore whether other factors such as climate change or moose harvest are more directly linked to recent population declines in this area.

Keywords: moose, *Alces alces*, nutrition, condition, salvage logging, forage, British Columbia

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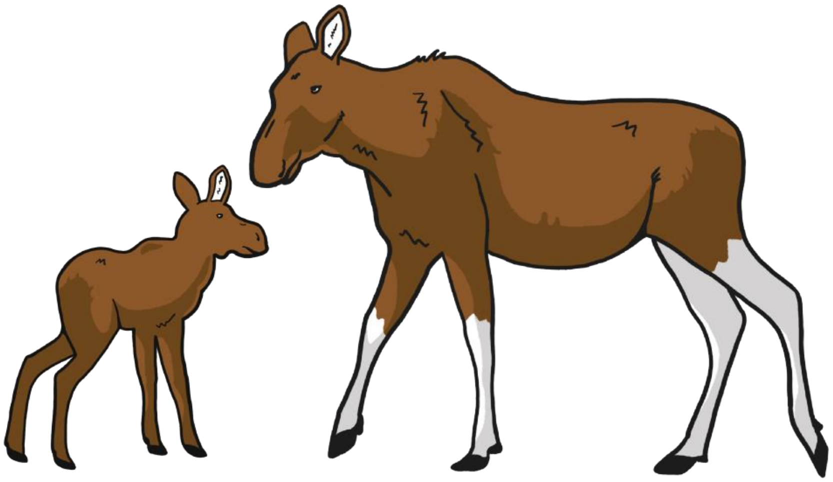

The moose is singularly grotesque and awkward to look at. Why should it stand so high at the shoulders? Why have so long a head? Why have no tail to speak of?

- Henry David Thoreau, The Maine Woods (1864)

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CHAPTER 1: INTRODUCTION TO THE THESIS

Ungulate Population Dynamics

Ungulate populations often exist in flux, their dynamics driven by temporal variation in demographic rates such as birth and death, that in turn are influenced by abiotic conditions and a suite of biotic forces acting from higher (top-down) or lower (bottom-up) in the food web (Gaillard et al. 2000, Vucetich & Peterson 2003, Joly et al. 2017).

Availability of key resources such as palatable forages is a strong bottom-up influence on ungulates. Forage quantity is limited by accessibility, such as when forages are covered by deep snow (Robinson & Merrill 2012), and forage quality is determined by both the nutritional (e.g., carbohydrates, fats, proteins, vitamins, minerals) and anti-nutritional (e.g., indigestible fiber, many plant primary and secondary metabolites) components of the plant material. Bottom-up influences may limit or regulate populations; limiting factors set a limit on population growth while regulating factors control population size, density, and dynamics within those limits through density-dependent negative feedback mechanisms (Messier 1991). One clear example is the moose (*Alces alces*) population on Isle Royale (Michigan, USA) which was limited by forage quality at low to moderate population densities but regulated by competition for high-quality forage at high densities (Messier 1991). Many other ungulate populations that are controlled by forage quantity (Desforges et al. 2021) and quality (McArt et al. 2009, Cook et al. 2013, Cook et al. 2016) have been described.

Top-down control of ungulate populations is exerted by organisms at higher trophic levels. Predation can influence populations directly through mortality and indirectly through risk aversion, where perceived danger alters ungulate movement and foraging, potentially reducing access to resources (Lowrey et al. 2019). Top-down controls also can be either limiting or regulating. For example, some moose populations are limited by wolf (*Canis lupus*) and bear (*Ursus* spp.) predation (Gasaway et al. 1992) while others are regulated by wolf predation and human harvest (Marrotte et al. 2022).

Typically, top-down and bottom-up controls work in tandem and alongside abiotic factors such as weather (Vucetich & Peterson 2003, Joly et al. 2017, Forrester & Wittmer 2019). Their relative influence varies spatially and temporally, often due to density-dependent feedback (Peterson et al. 2003, Gripenberg & Roslin 2007, Oates et al. 2021). For example, predation by wolves can regulate moose populations at low moose densities but has relatively little effect on population dynamics at high moose densities (Messier 1994, Marrotte et al. 2022). Conversely forage availability can support ungulate populations at low densities but can be limiting at high population densities, as competition for forage leads to decreased body condition, productivity, and survival and, ultimately, population growth (Simard et al. 2010). Resource availability can also exert density-independent population regulation or limitation, such as in unproductive habitats where forage quantity and/or quality is insufficient regardless of population density (Crête & Courtois 1997).

Humans increasingly are driving ungulate population dynamics. Humans exert top-down control directly through hunting, indirectly through risk aversion, and by hunting, trapping, and persecuting their predators (Berger et al. 2001, Tveraa et al. 2007). Humans also exert bottom-up control through activities that alter the quantity, quality, and spatial arrangement of critical resources on the landscape, such as logging, livestock grazing, urbanization, and wildfire management (Laliberté & Ripple 2004, Tveraa et al. 2007, Hebblewhite et al. 2009, Filazzola et al. 2020). Moreover, humans also influence the relative importance of top-down and bottom-up controls on ungulate populations. For example, regulation of the moose population in Isle Royale switched from top-down control via wolf predation to bottom-up regulation via balsam fir (*Abies balsamifera*) production following human introduction of canine parvovirus which decimated the wolf population (Wilmers et al. 2006). In an increasingly managed world, ungulate and other wildlife populations are affected by nearly every aspect of human life, including climate change. Effective wildlife management and conservation will depend upon understanding the relative effects of these factors on wildlife populations; this is especially important in

Canada, where a significant portion of the human population relies on game species such as moose for sustenance, as well as for spiritual and cultural purposes (Timmerman & Rodgers 2005).

Moose Ecology

Moose are the largest living deer (Family Cervidae) and are native to the northern forests of Eurasia and North America (Franzmann 1981). They first arrived in North America over the Bering Land Bridge approximately 11,000 – 14,000 years ago from present day Russia (Hundertmark et al. 2002). Their range then expanded across North America to include present-day Alaska and northern Canada (Alaskan moose, *A. a. gigas*), western Canada and some north-central states (Northwestern moose, *A. a. andersoni*), eastern Canada and some northeastern states (Eastern moose, *A. a. americana*), and some northwestern states and Canadian provinces in the Rocky Mountain cordillera (Shiras moose, *A. a. shirasi*).

Moose generally inhabit boreal forest, mixed forest, subalpine shrub, tundra, and alluvial environments (Telfer 1984). There, they primarily browse on deciduous and coniferous shrubs and trees, but also forage on a wide variety of other plants such as forbs, grasses, mushrooms, and aquatic vegetation (Dungan & Wright 2005, Tischler et al. 2019, Felton et al. 2020). Moose typically occur in coexistence with a suite of predators including wolves, cougars (*Puma concolor*), grizzly bears (*U. arctos*), black bears (*U. americanus*), and humans. Wolves, cougars, and humans predate moose of all sizes, while bears typically only predate on relatively young moose calves (Ross & Jalkotzy 1996, Sand et al. 2012, Patterson et al. 2013, Severud et al. 2015).

Moose rely on a mosaic of habitat types on the landscape to meet their physiological requirements: (a) early seral forest for abundant forage; (b) mature forest for relief from deep snowfall and from extreme hot and cold, as well as concealment from predators; and (c) wetlands, water bodies, and lowland habitats for thermoregulation in moist soils and surface water, for refuge from insects, and for access to nutritious aquatic vegetation (reviewed by Timmermann and McNicol 1988). An individual's reliance on these habitat types is dependent upon season, sex, age, and reproductive status

(Bjørneraas et al. 2011). For example, females with calves trade off high quality forage for cover, while males and females without calves will prioritize forage quality at the expense of higher predation risk (Bjørneraas et al. 2011), though this is not always the case (Francis et al. 2020, Mumma et al. 2021). Additionally, in winter moose often use mature coniferous forest stands where snowfall is intercepted (Bjørneraas et al. 2011), while in summer they take advantage of thawed water bodies to feed on nutritious aquatic vegetation (Tischler et al. 2019).

Moose and Logging in British Columbia

Moose slowly expanded across British Columbia (BC) in the 1800s, moving into the southern areas of the province as late as the mid-1900s (Bergerud & Elliot 1986). There, they became an important species ecologically, economically, and culturally. Moose are considered secure in BC and at federal and international levels (provincial status of S5, federal status of 4, and global status of G5; BC CDC 2020). However, several populations in BC's central interior have been declining over the past several decades, a trend concerning managers, Indigenous peoples, and other stakeholders (Kuzyk 2016). These population declines coincided both spatially and temporally with a surge in salvage logging following a mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the 1990s and 2000s. This epidemic was the largest mountain pine beetle outbreak ever recorded in western Canada, killing 54% of BC's merchantable pine (British Columbia Ministry of Forests 2023). The outbreak was followed by a dramatic increase in cutblocks and roads associated with salvage logging of the infested forest stands (Parfitt 2007). Cutblocks of 5-40 years post-logging classically are considered beneficial to moose, as they typically provide abundant early seral forage consumed by moose (Bunnell et al. 2004, Janz 2006). Therefore, wildlife managers expected increased cutblocks on the landscape to result in healthier moose and increasing populations (Bunnell et al. 2004, Janz 2006). However, the opposite has occurred: moose populations in some areas affected by the outbreak and associated salvage logging have declined by 50-70% (Kuzyk & Heard 2014).

Logging practices attempt to approximate the effects of natural stand-replacing disturbances such as wildfire, pest outbreaks, and windstorms (McRae et al. 2001). However, salvage logging naturally disturbed forests drastically changes their ecological value to moose: residual live trees are removed, plant communities are altered, understories are often less developed and diverse, and road networks are built (Dykstra & Braumandl 2006, Lindenmayer & Noss 2006, Lewis 2009, Steinke et al. 2020). Thus, even in ecosystems historically driven by frequent natural stand-replacing events, salvage logging can affect both top-down and bottom-up influences on moose populations (Hebblewhite et al. 2009, Boucher et al. 2022, Koetke et al. 2023).

Other recent research suggests that landscape change due to salvage logging has altered both top-down and bottom-up influences on moose populations. In central interior BC, moose have been shown to be more susceptible to wolf predation in regenerating cutblocks (Boucher et al. 2022). Moose diets also differ between areas with high and low cutblock densities, with a greater proportion of moose mortalities attributed to starvation in the former (Koetke et al. 2023). Population monitoring conducted by Kuzyk et al. (2019) across central interior BC reported high adult survival rates, poor calf recruitment rates, and poor body condition of some adult females within declining populations. Poor calf recruitment has been proposed as the mechanism of population decline, with poor nutritional condition of adult females suggested as one important potential driver in declining recruitment that needs to be evaluated (Kuzyk et al. 2019). Kuzyk et al. (2019), Mumma et al. (2021), and Koetke et al. (2023) identified the need for further research into effects of logging on forage quality and moose nutritional condition in BC; the current study was designed to address this need.

Research Objectives

I conducted my research in southern interior BC on a population of moose inhabiting a landscape highly impacted by both mountain pine beetle mortality and salvage logging. The research objectives of my thesis were to determine (i) whether forage nutritional quality differed between logged and unlogged sites, (ii) whether adult female moose in my study area were nutritionally limited, and (iii) whether foraging in cutblocks affected these animals in terms of body condition and reproduction.

My thesis is organized into four chapters. In this chapter I have presented an overview of the concepts and knowledge of moose that frame my study and my research objectives; in the section below, I describe in detail my study area and study population.

In Chapter 2 (*Patterns in nutritional quality of moose forage in a logged landscape*) I examine whether logging affects the nutritional quality of forage for moose in this landscape through changes in plant secondary metabolites, protein, and energy by comparing vegetation quality at moose foraging locations in, out, and on the edges of cutblocks. I also calculate nutritional requirements for moose and determine whether the nutritional quality of available forages is sufficient to support lactating female moose during the summer.

In Chapter 3 (*A preliminary examination of moose nutritional status in a disturbed landscape*) I examine whether individual moose are nutritionally limited and whether use of cutblocks for foraging is associated with poorer body condition and reproductive success. I accomplished this by following a cohort of collared adult female moose throughout two summers and recapturing them each winter to assess condition, pregnancy, and calf survival.

In Chapter 4, *Conclusions and Management Implications*, I provide a synthesis of my findings and discuss conclusions, management implications, and future research.

Study Area and Population

The study was conducted in Wildlife Management Unit (WMU) 3-18 (50.504708, -121.040319), a ~2,000,000 km^2 region in southern interior BC. This WMU spans the area between the towns of Ashcroft and Merritt, bounded by Highway 1 to the north and west, Highway 8 to the south, and Highway 97C from Merritt to Logan Lake and the Tunkwa Lake Road to the east (Figure 1-1).

The study site lies within one of the hottest and driest regions in Canada (Alldritt McDowell & Coupé 1998). Biogeoclimatic zones (Meidinger & Pojar 1991) within the study area consist primarily of Interior Douglas Fir (IDF) and Montane Spruce (MS) zones. Mean annual temperature is 4.0 °C in the IDF zone and 1.9 °C in the MS zone (Moore et al. 2010). The hottest month is July, with a mean temperature of 15.1 °C (based on hourly readings) in the IDF zone and 12.8 °C in the MS zone (Moore et al. 2010). The coolest month is February, with a mean temperature of -7.7 °C in the IDF zone and -9.3 °C in the MS zone (Moore et al. 2010). Mean annual precipitation is 493 mm in the IDF zone and 648 mm in the MS zone (Moore et al. 2010). The study was conducted between December 2020 and December 2022. Weather in 2021 was drier than average in winter and spring, and hotter and drier than average in June and July, including a record-breaking heatwave in late June (Bratu et al. 2022), and wetter than average in autumn (Figures 1-2 and 1-3). Summer 2021 also was characterized by several large wildfires, that burned 31% of WMU 3-18 between July 12 and September 8. Weather in 2022 was cooler and wetter than average in spring, hotter than average in July and August, and drier than average in fall, with unusually cold weather in November and December (Figures 1-2 and 1-3).

The valley bottoms of WMU 3-18 are characterized by bunchgrasses (e.g. bluebunch wheatgrass [*Pseudoroegneria spicata*]) and drought-resistant shrubs such as big sagebrush (*Artemisia tridentata*) (Alldritt McDowell & Coupé 1998). Douglas fir (*Pseudotseuga menziesii*) forests dominate at higher elevations, with ponderosa pine (*Pinus ponderosa*) forests at drier sites, Engelmann spruce (*Picea engelmannii*) forests at cooler and wetter sites, and lodgepole pine forests at recently burned sites (Egan 1996). The forests in WMU 3-18 have been heavily logged since the 1950s and are intersected with forestry and recreational roads, seismic lines, and power lines. At the time of the study (2022), 27% of WMU 3-18 had been logged (0.6% of the land base was 0-2 years post-logging, 13% was 3-14 years, 7% was 15-25 years, and 6% was 26-79 years). Wildfires burned 31% of the land base in summer 2021 (British Columbia Wildfire Service 2023). The Highland Valley Copper Mine takes up roughly 4% of the land base in WMU 3-18. There are several protected areas, including Tunkwa Provincial Park and Mount Savona Provincial Park.

The moose density in WMU 3-18 was estimated at 0.26 moose/km^2 in 2016 and 0.14 moose/km^2 in 2022 (C. Procter, British Columbia Ministry of Forests, unpublished data), indicating a population decline of 46% over the past 6 years. Moose in WMU 3-18 co-exist with mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), and a very small number of elk (*Cervus canadensis*) (Procter & Iredale 2017). Predators include abundant black bears (*Ursus americanus*) and cougars (*Puma concolor*), and a low density of grey wolves (*Canis lupus*) (Procter & Iredale 2017). Human harvest included a general open season for spike-fork male moose from November 1-15 (BC FLNRORD 2020a), limited entry hunting for adult females and calves from November 1-10 and adult males from October 1-31 (BC FLNRORD 2020b), and year-round harvest by Indigenous peoples (Procter & Iredale 2017). Unregulated harvest of adult female moose is suspected to be contributing to population declines in this area (C. Procter, personal communication, July 2022), although the number of animals harvested in this fashion is unknown, as is the relationship with other factors such as forage nutritional quality (examined in this thesis).

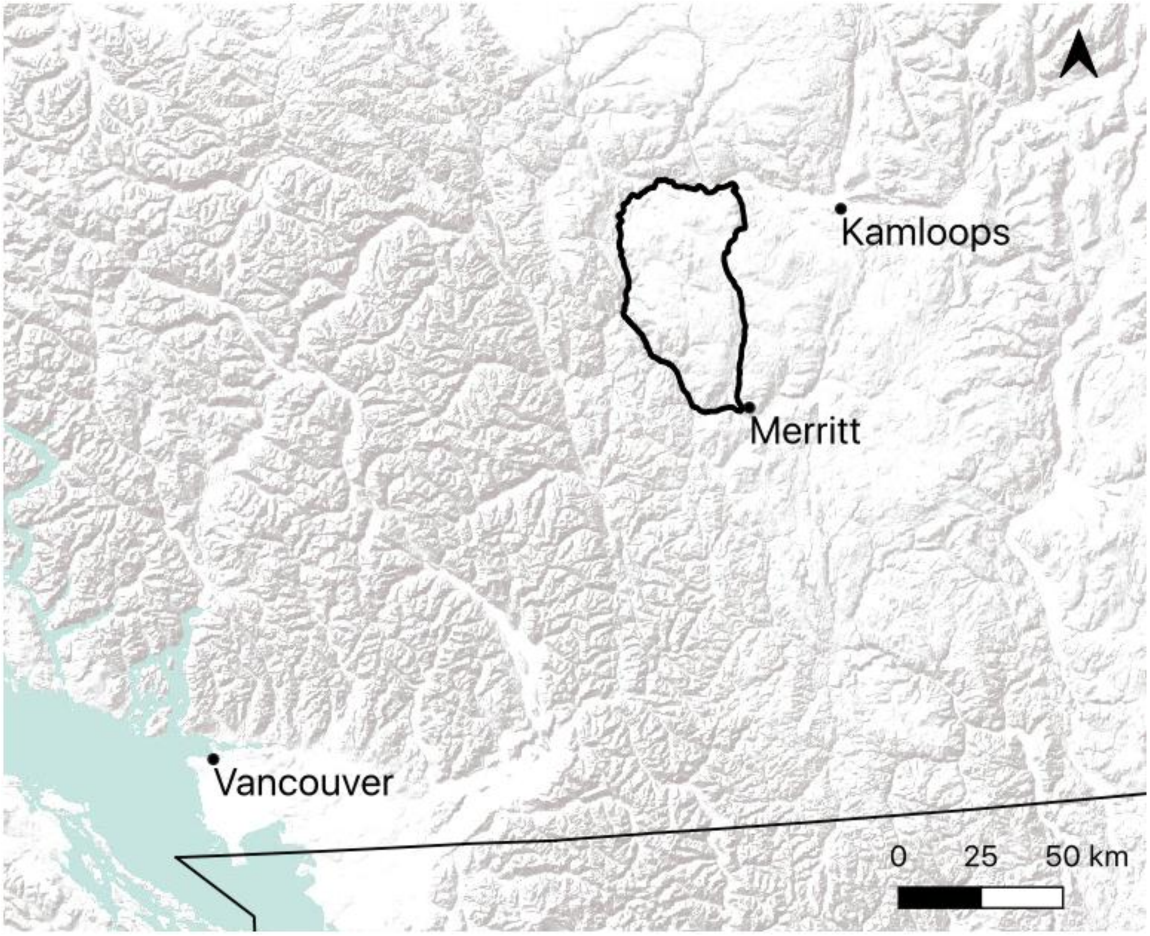

Figure 1-1. Location of Wildlife Management Unit 3-18 (the study area) in southern interior British Columbia, Canada.

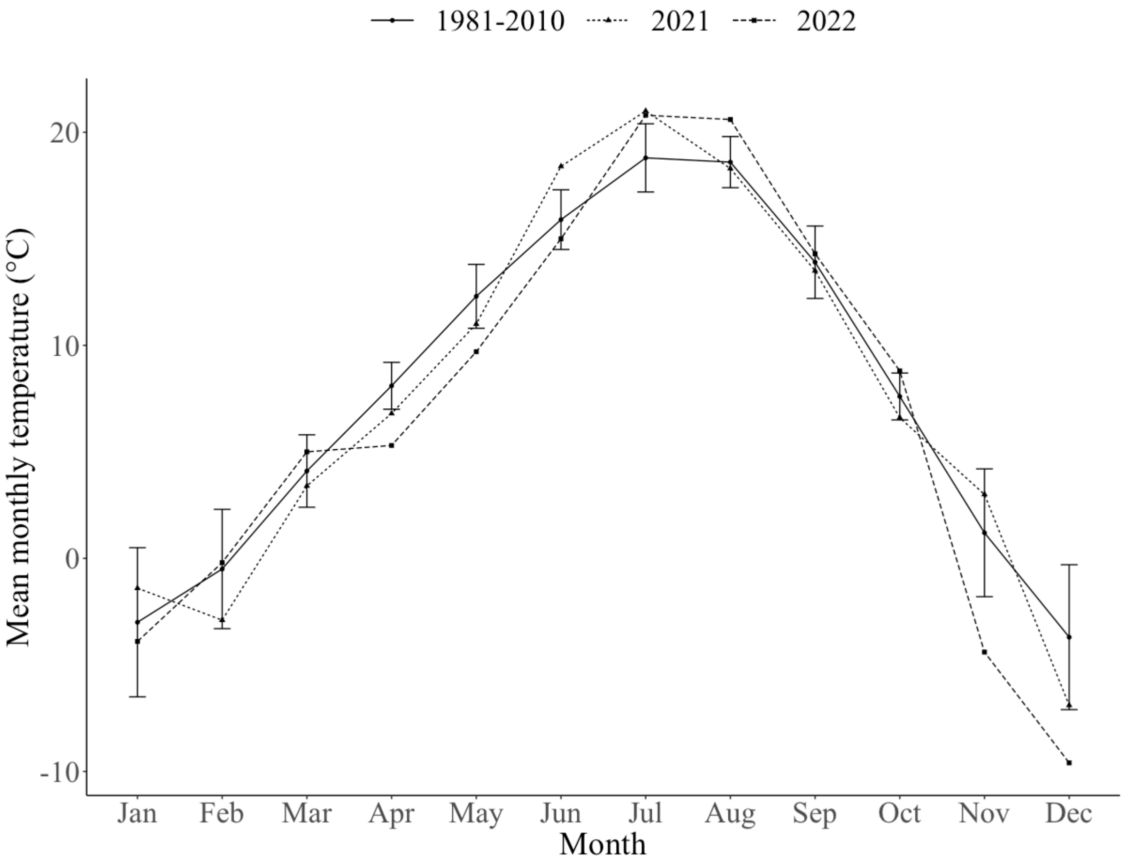

Figure 1-2. Mean monthly temperatures in Merritt, British Columbia, Canada during the study years (2021 and 2022) compared to the historical 30-year mean (1981-2010) with standard deviation represented as error bars. Data from Environment and Climate Change Canada (2023).

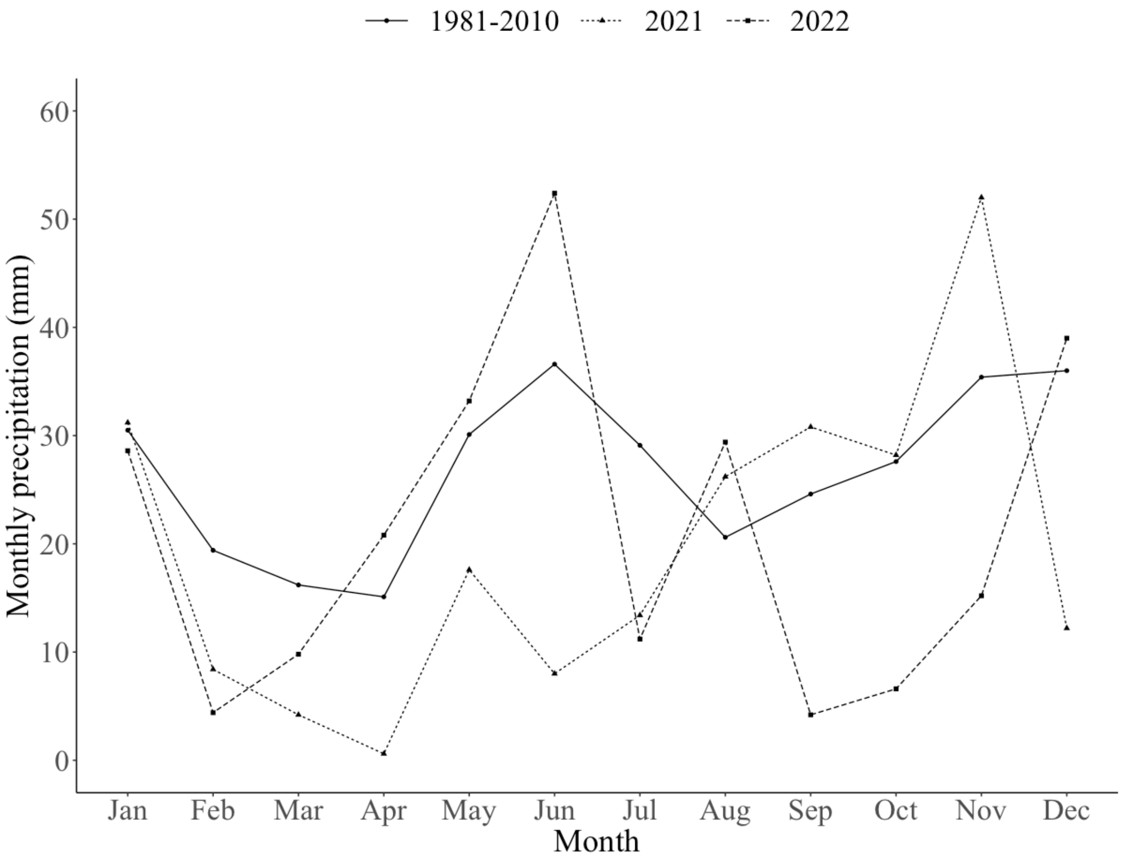

Figure 1-3. Total monthly precipitation in Merritt, British Columbia, Canada during the study years (2021 and 2022) compared to the historical 30-year mean (1981-2010). Data from Environment and Climate Change Canada (2023).

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CHAPTER 2: PATTERNS IN NUTRITIONAL QUALITY OF MOOSE FORAGE IN A LOGGED LANDSCAPE

Introduction

Nutrition is fundamental to individual growth, reproduction, survival, and ultimately population productivity (McArt et al. 2009, Parker et al. 2009). For herbivores, nutrition depends on both plant quantity and quality (Ma et al. 2020). Forage quantity limits food intake when abundance is low, while quality can limit food intake even when abundance is high, by increasing food retention time in the digestive tract (Hjeljord et al. 1982, Renecker & Hudson 1989, Cook et al. 2004, Meyer et al. 2010).

Several nutritional currencies are essential to ungulates, including energy, protein, minerals, vitamins, and water (Robbins 1983, Parker et al. 2009). Energy and protein typically are the limiting factors for cervids (Wallmo et al. 1977, Robbins 1983, van Soest 1994, McArt et al. 2009) and protein typically is the limiting factor for moose (McArt et al. 2009, Peterson et al. 2022). Protein is critical for maintenance, growth, reproduction, and lactation (Parker et al. 2009, Hackmann 2011), and it supports rumen microorganisms that break down forage (Hoover & Stokes 1991). Only a portion of the protein in plant tissues is available to herbivores; this amount is a function of the crude protein content (i.e., nitrogen [N] content), the amount of non-digestible fiber-bound protein, and the degree of protein precipitation by tannins (Robbins et al. 1987, Wallis et al. 2012).

Tannins are a diverse class of secondary metabolites synthesized by plants to defend against damage from abiotic stressors, pathogens, and herbivores (Hartley et al. 2012). Tannins can have both positive and negative effects on herbivores, depending on their concentration and chemical structure, and the herbivore's physiology (Frutos et al. 2004). Beneficial effects of tannins include antioxidant, anti-inflammatory, and antiparasitic properties (Huang et al. 2018). However, tannins can be toxic to herbivores by binding plant proteins, reducing the amount of protein available to the herbivore during digestion (i.e., digestible protein) (Robbins et al. 1987, DeGabriel et al. 2009).

Tannins are energetically costly to produce (Koricheva et al. 1998). Therefore, plants growing in sunnier sites tend to produce more tannins (Waterman et al. 1984, Molvar et al. 1993, Lawler et al. 1996, Yan et al. 2014), as they have more energy and carbon left after growth, development, and reproduction (i.e., primary metabolism) to allocate to tannin production in secondary metabolism (Koricheva et al. 1998). Forest management practices such as logging create early seral habitat with abundant forage (Parker & Morton 1978, Smolko et al. 2018), but also create high-sunlight conditions (Harper et al. 2004, Domke et al. 2007) conducive to tannin production. However, whether plants in logging cutblocks actually increase tannin production, and whether that translates to reduced digestible protein for herbivores, seems to be both species- and site-specific (Happe et al. 1990, Ford et al. 1994).

In some areas of central interior British Columbia (BC), Canada, moose populations have declined by 50-70% (Kuzyk & Heard 2014). This has occurred in tandem with a dramatic increase in salvage logging following the largest mountain pine beetle (*Dendroctonus ponderosae*) epidemic recorded in the province, that lasted from the 1990s through the 2010s and killed 54% of BC's merchantable pine (British Columbia Ministry of Forests 2023). Annual logging quotas were increased by up to 80% in affected areas in order to recover economic value from infested forest stands (Forest Practices Board 2009). Salvaged cutblocks often exceed the 60-hectare (ha) maximum cutblock size, even connecting previously logged cutblocks to create exceptionally large logged patches (Forest Practices Board 2009). Post-salvage monitoring of moose populations in interior BC has revealed low body fat levels (~8-10%) in many individuals and ≥8% of mortalities attributed to apparent starvation (Procter et al. 2020). Moreover, research by Koetke et al. (2023) identified differences in moose diets in areas with high and low cutblock densities and noted a greater proportion of moose mortalities attributed to starvation in high cutblock density areas. Mumma and Gillingham (2019) also found that moose occupying areas with higher proportions of cutblock were more likely to die of apparent starvation, though this may be attributed to factors other than, or in addition to, reduced plant nutritional quality. All told, these responses warranted further investigation into the effects of large-scale salvage logging on moose forage.

I conducted this work in an area where over a quarter of the landscape had been logged in the past few decades. My objectives were to determine whether plants growing in cutblocks produced more tannins and provided less digestible protein than plants growing in unlogged forests, to calculate daily digestible protein and energy requirements for lactating adult female moose in summer, and to examine whether plants in cutblocks and unlogged forests provided adequate nutrition to support healthy moose. Overall, I sought to reveal whether logging cutblocks provide forage of poor plant nutritional quality and whether this could be considered a potential driver of regional moose population declines.

Methods

Study Area

The study was conducted from December 2020 to December 2022 in Wildlife Management Unit (WMU) 3-18 (50.504708, -121.040319, elevation: 1,277 metres), a ~2,000,000-km^2 area situated in southern interior BC (Figure 1). Located in one of the hottest and driest regions of the country and in the rain shadow of the Coast, Cascade, and Columbia mountains (Egan 1996), WMU 3-18 received a long-term average of only 321mm of precipitation a year (Environment and Climate Change Canada 2023). Conditions in summer 2021 were hotter and drier than average in June and July, including a record-breaking heatwave in late June (Bratu et al. 2022), and relatively average temperatures in August and September. Several large wildfires burned 31% of WMU 3-18 in summer 2021 (British Columbia Wildfire Service 2023). Summer 2022 was wetter than average in June, hotter than average in July and August, and drier than average in July and September.

Two forest ecosystems dominated the study area: Interior Douglas-Fir (IDF) zones at lower elevations and Montane Spruce (MS) zones at higher elevations (Meidinger & Pojar 1991). The IDF zone was characterized by open Douglas-fir (*Pseudotseuga menziesii*) forests with grassy understories, with stands of ponderosa pine

(*Pinus ponderosa*) growing on hotter and drier sites, spruce (*Picea* spp.) on cooler and wetter sites, and lodgepole pine (*Pinus contorta*) on recently burned sites (Egan 1996). The MS zone was characterized by hybrid white spruce (*Picea glauca x engelmannii*) forests as well as extensive lodgepole pine stands (Alldritt McDowell & Lloyd 1999). The area has been heavily logged since the 1950s, with an increase in logging activity due to salvage logging operations following a mountain pine beetle outbreak in the area (Corbett et al. 2016). This started around 2004, peaked in 2007, and declined by 2010 (Nicholls 2016). As of 2022, 27% of the land base had been logged, 0.6% of the land base was 0-2 years post-logging, 13% was 3-14 years, 7% was 15-25 years, and 6% was 26-79 years. The majority of WMU 3-18 also was under active range tenures held as cattle, sheep, or horse grazing leases and/or hay cutting areas.

The moose density in WMU 3-18 was estimated to be 0.14 moose/km^2 in 2022, 46% lower than in 2016 when it was estimated as 0.26 moose/km^2 (C. Procter, British Columbia Ministry of Forests, unpublished data). Moose were sympatric with mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), and a low density of elk (*Cervus canadensis*) (Procter & Iredale 2017). Predators included black bears (*Ursus americanus*), cougars (*Puma concolor*), and a small number of grey wolves (*Canis lupus*) (Procter & Iredale 2017). Human harvest included a general open season for spike-fork male moose (BC FLNRORD 2020a), limited entry hunting for adult males, adult females, and calves (BC FLNRORD 2020b), and year-round harvest by Indigenous peoples (Procter & Iredale 2017).

Moose Capture and Handling

We captured 13 adult female moose at random between December 2020 and February 2021. We recaptured these individuals annually between December and January for 2 successive years (winter 2021/2022 and winter 2022/2023). Three additional moose were captured in the second winter (2021/2022). We chemically immobilized moose from helicopter using the Pneudart (Pneudart Inc., Williamsport, Pennsylvania, USA) remote delivery system with a 3.5 milliliter (ml) dose of BAM II (Chiron Compounding Pharmacy Inc., Guelph, Ontario, Canada), a premixed combination of butophanol (27.3

milligram (mg)/ml), azaperone (9.1 mg/ml), and medetomidine (10.9 mg/ml). We reversed immobilization by administering naltrexone hydrochloride (1 ml at 50 mg/ml; Chiron Compounding Pharmacy Inc, Guelph, Ontario, Canada) and atipamezole hydrochloride (7 ml at 25 mg/ml; Chiron Compounding Pharmacy Inc, Guelph, Ontario, Canada). Captures were conducted by a Wildlife Officer in accordance with the British Columbia *Wildlife Act*. We outfitted each captured moose with a Telonics TWG-4667-4 GPS collar (Telonics Inc., Mesa, Arizona, USA) programmed with a 2-hour GPS fix rate, activity recorded as active seconds (defined as movement along ≥1 axes in an internal 3-axis accelerometer) in a 10-minute period prior to each GPS fix, and mortality reported via email alert after 8 hours of inactivity.

Foraging Sites

Using the locational data from the collars, I identified likely moose foraging sites in cutblocks, cutblock edges (i.e., within 25 metres [m] of a cutblock edge), and unlogged forests. Cutblock edges were included in this design as moose are known to forage extensively at these ecotones (Hjeljord et al. 1990, Dussault et al. 2005). Relocation data were parcelled into 10-day periods in summer 2021 and three periods (early, mid-, and late summer) in 2022. Summer was defined as June 28 - September 20 based on biological moose seasons in BC (Francis et al. 2020), though sampling began one week earlier in 2021. Summer was chosen as the focal season as during this time foraging has the greatest influence on growth and reproduction (Hjeljord & Histøl 1999, Cook et al. 2004).

To identify likely foraging sites, GPS location data were constrained to those recorded from dusk through dawn, when moose are most likely to be foraging during the summer (Ditmer et al. 2018, Montgomery et al. 2019). Only GPS fixes where moose were active, rather than resting, were considered (i.e., ≥1 active second/minute detected on the collar's activity sensors during the 10 minutes prior to the GPS fix) (Street et al. 2015, Battle 2016). Each putative foraging site was visited in the field within 10 days of identification and searched for evidence of recent foraging on at least one preferred forage species (Table 2-1). If no evidence of foraging was found another putative foraging site was visited; this process was repeated until a foraging site was confirmed or until all possible GPS locations had been visited and ruled out for that particular moose during the time window.

Given that sunlight is a driver in tannin production (Yan et al. 2014), canopy cover was measured at each foraging site. Canopy cover was measured at plot centre (i.e., the moose's recorded GPS location) and at 25 m from plot centre in each cardinal direction using the modified spherical densiometer method described by Strickler (1959). Densiometer readings were averaged, and the mean was reported as the site canopy cover.

Forage Nutritional Quality

A composite sample of leaves and stems (≥40 gram (g)) was collected for each preferred forage species (see Table 2-1) present within a 25 m radius of plot centre. When possible, samples were taken from ≥10 individual plants and from a variety of aspects and heights between 0 and 2 m above ground (Shipley et al. 1998).

Samples were immediately placed on ice in the field and sent to the BC Government Analytical Chemistry Services Laboratory in Victoria, BC. Once there, samples were freeze-dried and milled using a Wiley Mill with 2 mm screen, and the following four analyses were conducted:

Total N was determined by dynamic flash combustion (modified Dumas method) using a FLASH 2000 Organic Elemental Analyzer (Thermo Scientific, Bremen, Germany). Following (Hanley et al. 1992), crude protein (CP) was calculated as:

$$\text{Crude Protein} = -6.25N \tag{1}$$

Protein precipitation capacity (PPC) of tannins (mg BSA ppt/mg) was analyzed using a 50% methanol extraction method modified from Martin & Martin (1982).

Digestible protein (in g/100g of forage) was calculated following equation 2 (Robbins et al. 1987).

$$\text{Digestible Protein} = -3.87 + 0.9283CP - 11.82PPC \tag{2}$$

Acid detergent fiber (ADF), acid detergent lignin (ADL), and neutral detergent fiber (NDF) were quantified using Ankom Technology Methods 12, 8, and 13, respectively (Ankom Technology 2017a, 2017b, 2020).

Digestible dry matter (DDM, in g/100g of forage) was calculated following equation 3 (Hanley et al. 1992), where A = (ADL + cutin) content as a percentage of NDF (cutin assumed to be 0), B = biogenic silica content (assumed to be 0), NDS = percent neutral detergent solubles (100 – percent NDF), and P = the reduction in protein digestion calculated in the term 11.82PPC expressed in equation 2.

$$DDM = [(0.9231e^{-0.0451A} - 0.03B)(NDF)] + [(-16.03 + 1.02\ NDS) - 2.8P] \qquad (3)$$

Digestible energy (in g/100g of forage) was calculated from DDM following equation 4 (Schwartz et al. 1987b):

$$\text{Digestible Energy} = -2.42 + 1.04DDM \qquad (4)$$

Table 2-1. Preferred moose forage species identified from the literature and present in Wildlife Management Unit 3-18 (Hosley 1949[1], Hatter 1950[2], LeResche & Davis 1973).

Common Name	Scientific Name
birches	*Betula* spp. [1, 2, 3]
Douglas maple	*Acer glabrum* [1, 2]
fireweed	*Chamaenerion angustifolium* [1, 3]
highbush cranberry	*Viburnum edule* [1, 2]
mountain ashes	*Sorbus* spp. [1]
red-osier dogwood	*Cornus stolonifera* [1, 2]
Saskatoon	*Amelanchier alnifolia* [2]
trembling aspen	*Populus tremuloides* [1, 2]
willows	*Salix* spp. [1, 2, 3]

Digestible energy was converted to kilocalories (kcal)/g DM using the following average gross energy values calculated from values provided by Shipley & Felicetti (2002) and Spalinger et al. (2010): 4.85 kcal/g (n=5) for willows, 5.21 kcal/g (n=1) for trembling aspen, and 4.57 kcal/g (n=2) for fireweed. Analogous values for Saskatoon were not found, so the average of the other two shrub species (4.91kcal/g; n=6) was used.

Nutritional Requirements

Available crude protein was compared to a minimum dietary crude protein content of 6.8% (Schwartz et al. 1987) as well as an ideal crude protein content of 12.7%, which was successfully used by Schwartz et al. (1985) to rear healthy captive moose.

The daily digestible protein requirement (g/100g DM) for a healthy adult female Northwestern moose raising a singleton calf was calculated by adding the excretion of metabolic fecal N (0.458g N/100g DM) and endogenous urinary N (56 mg/kg body weight$^{0.75}$) (Schwartz et al. 1987a) to the protein costs of lactation and mass gain, assuming a protein digestion efficiency of 80% (Robbins 1983). The excretion of metabolic fecal N reported by Schwartz et al. (1987a) is similar to the 0.389g N/100g DM reported by Spalinger et al. (2010) for moose and within the range reported for domestic and wild ruminants by Robbins (1983). Total daily protein cost of lactation was estimated on a daily basis throughout the summer by multiplying the protein content of moose milk by the daily milk intake of moose calves (Reese & Robbins 1994), with intermediate daily values assumed to increase/decrease linearly between reported observations. Lactation was assumed to begin on May 21, the mean date of parturition for moose in central interior BC (Procter et al. 2020). Protein required to synthesize 0.2 kg/day of body mass over the summer (Reese & Robbins 1994) was calculated assuming 20% of body mass is made of protein, as in deer (Robbins 1973). The minimum daily requirement was converted to a concentration of digestible protein required in the diet by multiplying it by the average daily dry matter intake measured by Renecker & Hudson (1985), which is within the range reported by Schwartz et al. (1984), with intermediate daily values assumed to increase/decrease linearly between reported observations. Because the moose studied by Renecker & Hudson (1985) were not rearing calves, the daily dry matter intake was increased by 11% to account for additional forage intake to support a singleton calf (D. Spalinger, University of Alaska Anchorage, unpublished data [provided by L. Shipley, Washington State University]). Moose body mass was not measured during capture, so an estimate of 344kg at parturition was used (Reese & Robbins 1994). See Appendix A for detailed calculations.

The daily digestible energy requirement (kJ/g DM) for a healthy adult female Northwestern moose raising a singleton calf was calculated similarly to the digestible protein requirement, but by adding the digestible energy requirement for maintenance at 0.2kg mass gain per day (170 kcal digestible energy/kgBW$^{0.75}$) (Schwartz et al. 1988) to the energy costs of lactation reported by Reese & Robbins (1994). This was calculated assuming an 88.5% efficiency converting digestible energy to metabolizable energy (Schwartz et al. 1988) and a 70% efficiency converting metabolizable energy to gross milk energy (Blaxter 1962, Reid 1968). See Appendix A for detailed calculations.

Most of the daily variation in the digestible protein and energy requirements was due to differences in moose forage intake over the course of the summer. In order to limit the influence of this variable on interpretations of nutritional quality, the highest daily requirement value was extrapolated over the course of the whole summer. Therefore, all forage samples collected over the course of the summer were compared to only one benchmark requirement for each of digestible protein and digestible energy.

Statistical Analysis

Canopy cover was compared between site types (cutblock, edge, forest) using analysis of variance (ANOVA) and Tukey’s post hoc test. Crude protein, digestible protein, and digestible energy content of forages were analyzed using linear regression. Given that a portion (16%) of samples had no detectable tannin PPC (i.e., had either no tannin PPC or had an unknown value below the detection limit of 0.05 mg BSA ppt/mg), tannin PPC was analyzed with Tobit regression using the censReg package (Henningsen 2017) to account for the left-censored data (Lubin et al. 2004, Lorimer & Kiermeier 2007). Tannin PPC values were required for calculation of digestible protein and digestible energy. Therefore, a sensitivity analysis was completed for these response variables whereby the analyses were completed twice, once with unknown values assumed to be 0 and once with unknown values assumed to be 0.049 (just below the detection limit of 0.05 mg BSA ppt/mg). For each response variable, a set of 16 candidate models was compared – a null model and all additive combinations of the following variables: Julian date, year, species, and site type. The reference site type always was forest. The reference species was the species with the lowest mean value for the response variable. Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002) was used for model selection. For each response variable, the top two models were reported, as well as any other candidate models within <2 ΔAICc units from the best-approximating model. Reduction in protein digestibility due to tannins was analyzed with a paired Student's t-test. All statistical analyses were conducted in the program R, version 4.2.3 (R Core Team 2023).

Results

Moose Capture and Handling

A total of 13 adult female moose were collared during winter 2020/2021 captures. Mortalities, collar failure, and wildfires limited the effective sample size of the summer 2021 field season to 11 individuals from June 28 – July 2, 10 individuals from July 3 – July 31, and 5 – 6 individuals from August 1– September 20. Surviving individuals were recaptured in winter 2021/2022 and an additional three individuals were fitted with GPS collars. Mortalities and use of burned areas limited the effective sample size of the summer 2022 field season to 8 individuals from June 28 – August 5 and 7 individuals from August 6 – September 20. All 10 surviving moose were recaptured in winter 2022/2023 and collars were removed. See Chapter 3 for detailed mortality information.

Foraging Site Characteristics

In summer 2021, 160 likely foraging sites were visited, of which 18 sites (11%) lacked evidence of browsing and were not sampled, and 142 sites (53 forest, 42 edge, and 47 cutblock sites) were sampled. In summer 2022, 44 likely foraging sites were visited, of which 3 sites (7%) lacked evidence of browsing and were not sampled, and 41 sites (14 forest, 14 edge, and 13 cutblock sites) were sampled. Cutblock and edge sites were located in cutblocks aged 4 – 41 years post-logging.

Canopy cover differed by site type (ANOVA, $F_{2,180} = 54.04$, $P < 0.001$). Post hoc comparisons using Tukey's test indicated that mean canopy cover was significantly higher in forests than in edges (mean difference = 28.53, 95% CI = 18.91 – 38.15], $P < 0.001$) and in forests (mean difference = 40.18, 95% CI = 30.73 – 49.63, $P < 0.001$) and edges than in cutblocks (mean difference = 11.65, 95% CI = 1.78 – 21.52, $P < 0.016$; Table 2-2).

Table 2-2. Comparison of percent canopy cover at moose foraging locations in British Columbia, Canada grouped by site type.

Site Type	Sample Size	Canopy Cover (%), Mean ± SD
Forest	67	60 ± 23.5
Edge	56	32 ± 19.5
Cutblock	60	20 ± 23.9

Forage Nutritional Quality

Four of the 10 focal plant species were detected frequently enough to warrant nutritional analysis: fireweed (n = 155 samples), Saskatoon (n = 49), trembling aspen (n = 137), and willow (n = 161).

Crude Protein

Of the 16 candidate models predicting crude protein, the top model (as ranked through AICc) included all covariates (Table 2-3; adjusted $R^2 = 0.47$, $F_{7,494} = 64.92$, $P \leq 0.001$). The crude protein content of forages decreased throughout the summer (i.e. by Julian date; $t = -20.59$, $P < 0.001$), was higher in 2022 than 2021 ($t = 4.82$, $P < 0.001$), was lower in cutblocks than forests ($t = -3.00$, $P < 0.01$), and was higher in fireweed than Saskatoon ($t = 2.81$, $P < 0.01$), the reference species. On average, crude protein was estimated to be lower in cutblocks than forests by 0.74g/100g DM, while keeping all other variables constant. No other models were <2 ΔAICc of the best-approximating model.

When forage species were assessed separately, all species showed a decrease in crude protein over the course of the summer ($t = -15.26 – -4.05$, $P < 0.001$). Trembling aspen and willows both had higher crude protein in 2022 than 2021 ($t = 5.34$, $P < 0.001$; $t = 4.05$, $P < 0.001$, respectively), but this trend was not found in the other species. Crude protein was lower in cutblocks ($t = -3.67$, $P \leq 0.001$) and edges ($t = -2.30$, $P = 0.023$) than forests for fireweed only, with no differences in crude protein by site type for Saskatoon, trembling aspen, or willows (Table 2-4).

The crude protein content of forages met or exceeded the minimum requirement of 6.8% in all but four samples collected in late summer, 3 from forests and 1 from a cutblock. Forages met or exceeded the ideal crude protein benchmark concentration of 12.7% in early summer but trend lines declined below 12.7% at approximately day 209 (July 28) in cutblocks, 213 (August 1) in edges, and 217 (August 5) in forests (Figure 2-1).

Table 2-3. Summary of models comparing crude protein, digestible protein, tannin protein precipitation capacity (PPC), and digestible energy content of moose forages sampled in British Columbia, Canada (n=502) to Julian date, year, site type (cutblock, edge, forest), and species (fireweed, Saskatoon, trembling aspen, and willows).The top two competing models were reported for each response variable, based on Akaike's Information Criterion corrected for small sample sizes (AICc). Number of model parameters (K), change in AIC from the best model (ΔAICc), model weights (wi), and the log likelihoods (LL) for competing models are also reported. Crude and digestible protein and digestible energy were best explained by the full model, while tannin PPC was best explained by year, site type, and species.

	K	**AICc**	**ΔAICc**	**w_i**	**LL**
Crude Protein					
Julian Date + Year + Site Type + Species	9	2260.80	0.00	0.67	-1121.22
Julian Date + Year + Site Type	8	2263.00	2.20	0.22	-1125.41
Digestible Protein					
Sensitivity Analysis iteration #1: assuming tannin PPC values <DL = 0					
Julian Date + Year + Site Type + Species	9	2355.76	0.00	0.99	-1168.70
Julian Date + Year + Species	8	2365.17	9.41	0.01	-1175.47
Digestible Protein					
Sensitivity Analysis iteration #2: assuming tannin PPC values <DL = 0.049					
Julian Date + Year + Site Type + Species	9	2337.39	0.00	0.99	-1159.51
Julian Date + Year + Species	8	2346.49	9.10	0.01	-1166.13
Tannin PPC					
Year + Site Type + Species	8	-838.53	0.00	-	427.27
Year + Site Type + Species + Julian Date	9	-838.43	0.10	-	428.21
Digestible Energy					
Both iterations of the Sensitivity Analysis					
Julian Date + Year + Site Type + Species	9	1389.80	0.00	0.92	-685.72
Julian Date + Year + Species	8	1394.79	4.99	0.08	-690.28

Table 2-4. Comparison of crude protein (g/100g DM), digestible protein (g/100g DM), tannin protein precipitating capacity (PPC; mg BSA ppt/mg), and digestible energy (kJ/100g DM) content of forages sampled in British Columbia, Canada between site types. The percentage of samples exceeding the requirements for digestible protein and digestible energy also are reported.

	Site Type	**n**	**Crude Protein**	**Digestible Protein**		**Tannin PPC[1]**	**Digestible Energy[1]**	
			Mean ± SD	Mean ± SD	Samples ≥ Requirement	Mean ± SD	Mean ± SD	Samples ≥ Requirement
Fireweed	**Forest**	53	14.0 ± 3.89 ^{a}	6.5 ± 3.85 ^{a}	15%	0.23 ± 0.07 ^{a}	12.31 ± 0.67 ^{a}	100%
	Edge	48	13.3 ± 3.66 ^{b}	5.2 ± 3.62 ^{b}	10%	0.28 ± 0.07 ^{b}	12.17 ± 0.73 ^{a}	100%
	Cutblock	54	12.5 ± 3.70 ^{b}	4.5 ± 3.70 ^{b}	6%	0.28 ± 0.07 ^{b}	12.19 ± 0.71 ^{a}	100%
Saskatoon	**Forest**	28	12.2 ± 2.25 ^{c}	5.9 ± 2.12 ^{c}	4%	0.13 ± 0.04 ^{c}	10.76 ± 1.14 ^{c}	75%
	Edge	11	13.0 ± 3.91 ^{c}	6.9 ± 3.98 ^{c}	18%	0.11 ± 0.05 ^{cd}	11.38 ± 1.59 ^{c}	91%
	Cutblock	10	11.8 ± 2.65 ^{c}	5.9 ± 2.78 ^{c}	10%	0.09 ± 0.04 ^{d}	11.24 ± 1.54 ^{c}	90%
Trembling	**Forest**	52	13.4 ± 2.63 ^{e}	8.0 ± 2.83 ^{e}	19%	0.05 ± 0.1$^{0\ e}$	13.70 ± 1.14 ^{e}	100%
	Edge	43	12.8 ± 2.92 ^{e}	7.2 ± 3.11 ^{f}	21%	0.06 ± 0.10 ^{ef}	14.09 ± 1.20 ^{e}	100%
	Cutblock	42	12.6 ± 2.19 ^{e}	6.8 ± 2.67 ^{f}	12%	0.09 ± 0.11 ^{f}	14.04 ± 1.20 ^{e}	100%
Willows	**Forest**	57	12.4 ± 2.77 ^{g}	5.6 ± 2.63 ^{g}	5%	0.17 ± 0.06 ^{g}	11.46 ± 1.18 ^{g}	87%
	Edge	50	13.1 ± 3.24 ^{g}	6.3 ± 3.24 ^{g}	8%	0.17 ± 0.06 ^{g}	12.23 ± 0.97 ^{g}	98%
	Cutblock	54	13.0 ± 2.90 ^{g}	6.0 ± 2.95 ^{g}	11%	0.18 ± 0.06 ^{g}	12.04 ± 1.16 ^{g}	93%

[1] Tannin PPC values below the detection limit were assumed to be zero.

[a, b] Within each species, identical superscript letters denote non-significant differences between site types; different letters denote significant differences

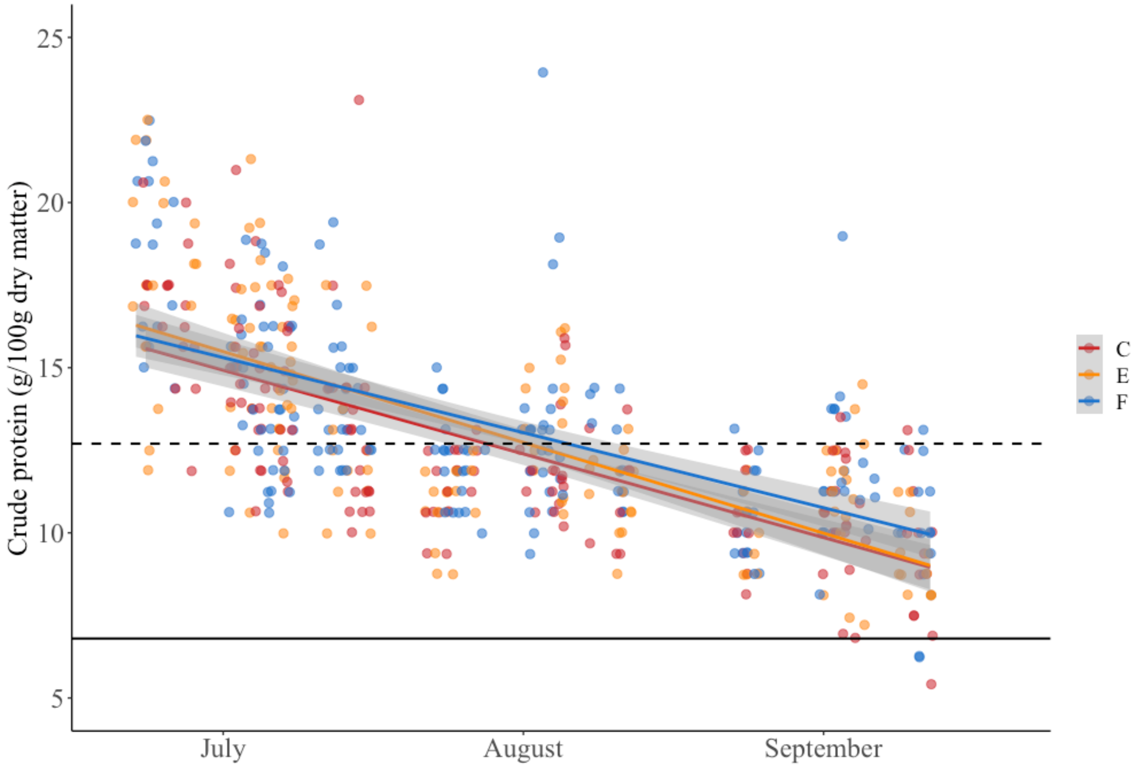

Figure 2-1. Crude protein content of forages sampled in cutblocks (red), cutblock edges (orange) and forests (blue) in British Columbia, Canada. Trend lines are shown in matching colours with grey 95% confidence intervals. An ideal crude protein benchmark concentration of 12.7% (Schwartz et al. 1985) is shown in dashed black, and a minimum requirement of 6.8% (Schwartz et al. 1987) is shown in solid black.

Digestible Protein

Digestible protein content of forages was best explained by the combination of all the putative explanatory variables (Table 2-3; adjusted $R^2 = 0.42$, $F(7, 494) = 52.74$, $P < 0.001$). The digestible protein content of forages decreased throughout the summer ($t = -16.94$, $P < 0.001$), was higher in 2022 than 2021 ($t = 5.48$, $P < 0.001$), was lower in cutblocks ($t = -3.65$, $P < 0.001$) and edges ($t = -2.06$, $P < 0.05$) than forests, and was higher in trembling aspen ($t = 6.61$, $P < 0.001$) and in willows ($t = 2.25$, $P < 0.05$) than fireweed, the reference species. On average, digestible protein was estimated to be 0.989g/100g DM lower in cutblocks and 0.567 g/100g DM lower in edges than in forests, while keeping all other variables constant. No other models were <2 ΔAICc of the best-approximating model.

When forage species were analyzed separately, all species showed a decrease in digestible protein over the course of the summer ($t = -12.45 – -4.84$, $P < 0.001$). Trembling aspen and willows both had higher digestible protein in 2022 than 2021 ($t = 5.30$, $P < 0.001$; $t = 4.69$, $P < 0.001$, respectively), but this trend was not found in the other species. Both fireweed and trembling aspen had lower digestible protein in cutblocks ($t = -4.23$, $P < 0.001$; $t = -2.22$, $P < 0.05$, respectively) and edges ($t = -3.08$, $P < 0.01$; $t = -1.96$, $P = 0.053$, respectively) than forests but there were no differences by site type for Saskatoon or willows (Table 2-4).

Calculated daily digestible protein requirements for lactating moose in summer ranged from 8.19 – 10.29 g/100g DM (mean = 9.24 ± 0.67 g/100g DM). Digestible protein content was close to the requirement (10.29 g/100g) at the start of the summer, but decreased throughout the season, with most samples collected in August and September falling below the requirement, some even having negative values (Figure 2-2).

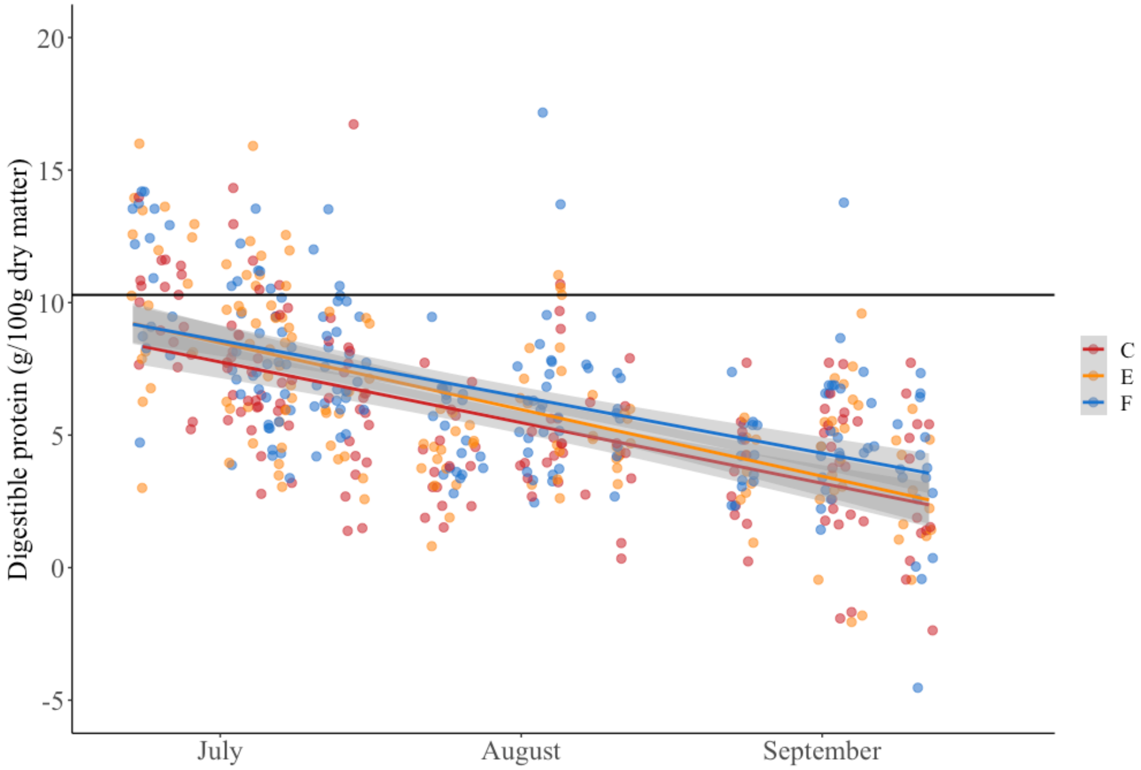

Figure 2-2. Digestible protein content of forages sampled in cutblocks (red), cutblock edges (orange) and forests (blue) in British Columbia, Canada. Trend lines are shown in matching colours with grey 95% confidence intervals. The calculated daily digestible protein requirement is shown in black.

Tannin Protein Precipitation Capacity

Tannins decreased the digestibility of protein (t = 120.40, df = 501, $P < 0.001$) by a mean of 53% in forests, 55% in edges, and 58% in cutblocks. The top model for tannin PPC included year, site type and species (Table 2-3) and was statistically significant (χ^2(df = 2, N = 502) = 362.12, $P < 0.001$). One other candidate model was <2 ΔAICc of the best-approximating model. However, this model differed only in the addition of another parameter, Julian date, which was therefore not considered to have additional explanatory power (Arnold 2010). Tannin PPC was lower in 2022 than 2021 (t = -4.082, $P < 0.001$), higher in cutblocks (t = 3.29, $P < 0.001$) and edges (t = 2.10, $P < 0.05$) than forests, and higher in fireweed (t = 20.53, $P < 0.001$), willows (t = 11.85, $P < 0.001$), and Saskatoon (t = 4.70, $P < 0.001$) than trembling aspen, the reference species (Figure 2-3). On average, tannin PPC was estimated to be 0.028 mg BSA ppt/mg higher in cutblocks and 0.018mg BSA ppt/mg higher in edges than forests, while keeping all other variables constant.

When forage species were analyzed separately, Saskatoon, trembling aspen, and willows had lower tannin PPC in 2022 than 2021 (t = -3.00 – -2.15, $P < 0.05$), but there were no significant differences between years for fireweed. Tannin PPC was higher in both cutblocks (t = 3.80, $P < 0.001$) and edges (t = 3.75, $P < 0.001$) than forests for fireweed, was marginally higher in cutblocks than forests for trembling aspen (t = 1.93, P = 0.056), was lower in cutblocks than forests for Saskatoon (t = -2.44, $P < 0.05$), and did not differ between site types for willows (Table 2-4).

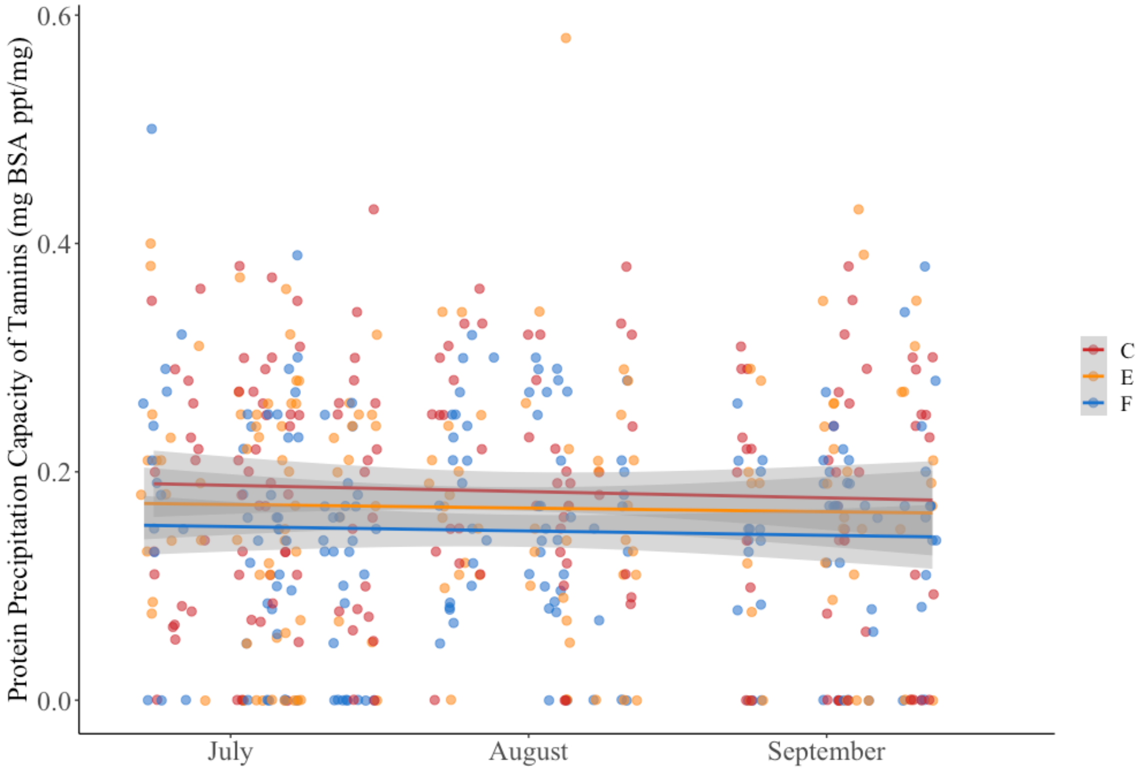

Figure 2-3. Tannin protein precipitating capacity of forages sampled in cutblocks (red), cutblock edges (orange) and forests (blue) in British Columbia, Canada. Trend lines are shown in matching colours with grey 95% confidence intervals.

Digestible Energy

The top model predicting digestible energy included all covariates (Table 2-3) and was statistically significant (adjusted $R^2 = 0.55$, $F(7, 494) = 89.47$, $P < 0.001$). No other models were <2 ΔAICc of the best-approximating model. The sensitivity analysis for digestible energy revealed no differences in top model or significance of model parameters between iterations (values <DL assumed to be 0 or 0.049). Digestible energy content of forages decreased throughout the summer ($t = -8.93$, $P < 0.001$), was higher in 2022 than 2021 ($t = 5.58$, $P < 0.01$), was higher in both cutblocks ($t = 2.33$, $P < 0.05$) and edges ($t = 2.77$, $P < 0.01$) than forests, and was higher in trembling aspen ($t = 17.81$, $P < 0.001$), fireweed ($t = 7.20$, $P < 0.001$) and willows ($t = 5.26$, $P < 0.001$) than Saskatoon, the reference species. On average, digestible energy was estimated to be 0.241g/100g DM higher in cutblocks and 0.291g/100g DM higher in edges than forests, while keeping all other variables constant.

When species were analyzed separately, all species showed a decrease in digestible energy over the course of the summer ($t = -8.20 – -5.91$, $P < 0.001$) except trembling aspen. Digestible energy was higher in 2022 than 2021 for all species ($t = 2.13 – 4.88$, $P < 0.05$) except Saskatoon. Digestible energy in willows was higher in cutblocks ($t = 2.37$, $P < 0.05$) and edges ($t = 3.45$, $P = 0.001$) than forests, but no differences between site types were found in any other species (Table 2-4).

Calculated daily digestible energy requirements for lactating moose in summer ranged from 7.52 – 9.82 g/100g DM (mean = 8.61 ± 0.77 g/100g DM). Twenty samples had digestible energy values below the requirement (9.82 g/100g): 14 samples from forests, 4 from cutblocks, and 2 from cutblock edges (Figure 2-4).

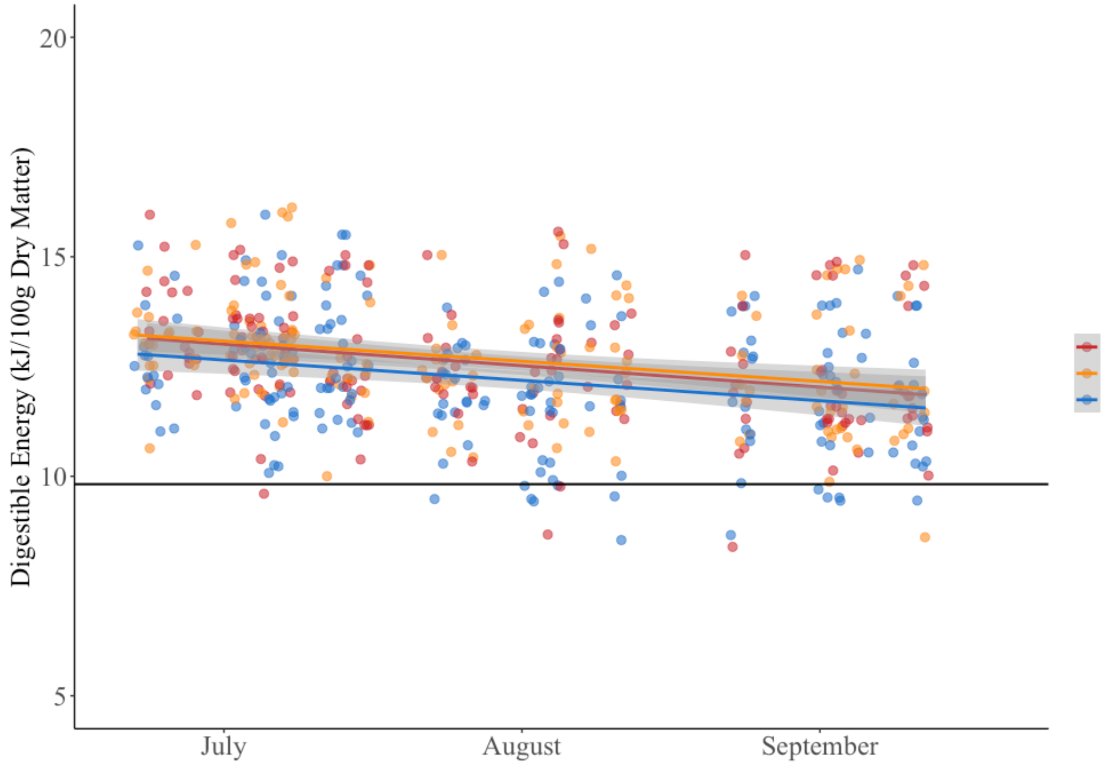

Figure 2-4. Digestible energy of forages sampled in cutblocks (red), cutblock edges (orange) and forests (blue) in British Columbia, Canada. Trend lines are shown in matching colours with grey 95% confidence intervals. The calculated daily digestible energy requirement is shown in black.

Discussion

As predicted, logging negatively influenced the nutritional quality of forage in the study area. I found decreased crude and digestible protein and increased tannin production in forages sampled from cutblocks compared to forests. These results corroborate other studies finding plants growing in high-sunlight conditions to have higher tannin and lower crude and digestible protein content than those growing in shaded conditions (Waterman et al. 1984, Happe et al. 1990, Hjeljord et al. 1990, Molvar et al. 1993, Yan et al. 2014, but see Ford et al. 1994). In this study, forages in forests more often met crude and digestible protein requirements than forages from cutblocks, suggesting that adult female moose in this logged landscape may be protein-limited if they forage extensively in cutblocks. Given that the protein content of forages decreased over the course of the summer, availability of forest habitats likely is of greatest nutritive value for moose in late summer. At this time, digestible protein levels are low and small differences in protein content could make the difference between a nutritionally adequate or inadequate diet.

These results suggest that adult female moose in this logged landscape may be protein-limited during most of the summer, especially those individuals that forage extensively in cutblocks. Cutblocks typically produce more forage than unlogged mature forest for a decade or more post-logging (Parker & Morton 1978, Smolko et al. 2018). Therefore, there is potential that the lower digestible protein per unit mass of forage in cutblocks is balanced out by the greater mass per unit area (Robbins et al. 1987). However, Mumma and Gillingham (2019) and Koetke et al. (2023) noted higher moose mortality due to apparent starvation in areas with more cutblocks, suggesting that this is not always the case. Given that summer and autumn nutrition strongly influence condition, reproduction, and survival of moose (Testa & Adams 1998, Hjeljord & Histøl 1999, Keech et al. 2000, McArt et al. 2009, Bjørneraas et al. 2012), and even small decreases in nutritional quality can lead to disproportionately large effects on ungulate condition and productivity (White 1983, Cook et al. 2004, Parker et al. 2009), there is potential that differences in digestible protein between cutblocks and forests have a biologically significant effect on moose. Research into moose condition, pregnancy rates, calf recruitment, and adult survival are required to confirm whether apparent protein limitation in forage is translating into nutritional limitation in moose.

Though generally plants in cutblocks were of poorer nutritional quality than plants in forests, I found opposing trends in plant nutritional quality when species were assessed separately, highlighting the diversity of plant species phytochemical responses to environmental conditions (Berini et al. 2018). Because the digestible protein content of willows and Saskatoon did not differ between site types, they are likely to be important components of a moose diet in this logged landscape. Willows may be especially important as they were found at the most foraging locations of all the species studied. Trembling aspen had the most samples above the digestible protein requirement, with especially high digestible protein content in forests. Given the ability of moose to discern differences in quality and select the most nutritious plants and plant parts to satisfy metabolic requirements (Hjeljord et al. 1990, Felton et al. 2016, Wam et al. 2018, Felton et al. 2021), moose living in a logged landscape may select specific plants in each habitat type that offer optimal nutritional qualities, potentially balancing out differences between habitat types observed in this study.

All habitat types provided forage with much higher digestible energy content than required, with few samples falling below the requirement, indicating that moose in this region are unlikely to be energy-limited. This agrees with other studies reporting that summer forages provided more energy than required by moose (Coady 1982) and that protein intake was more limiting than energy (McArt et al. 2009, Peterson et al. 2022). Differences in additional nutritional currencies (not studied here) have been identified in moose in other areas, including copper deficiencies in Alaska’s Kenai Peninsula (Flynn et al. 1977) and phosphorus and sodium deficiencies in southern Norway (Ohlson & Staaland 2001). Therefore, this study serves as an initial exploration of the nutritional differences between logged and unlogged forests, highlighting potential implications for moose and other ungulates.

Interestingly, tannins decreased protein digestibility to a much higher degree than reported in other studies. Of the four forage species analyzed, only two, willows and fireweed, had tannin values previously reported, with all studies from Alaska. In this study, tannins decreased the protein digestibility of fireweed by a mean of 65% (± 22.9) compared to 38% reported by Hanley et al. (1992). Similarly, tannins decreased the protein digestibility of willows by a mean of 56% (± 12.7) in this study, noticeably higher than the 38% reported by Spalinger et al. (2010), 46% reported by McArt et al. (2009), and 47% reported for Sitka willow specifically by Hanley et al. (1992), though similar to the 59% reported by Hanley et al. (1992) for a mixture of willow species. Additionally, by late summer we calculated negative protein digestibility in several samples, a phenomenon not previously reported in moose forage studies in Alaska but documented by Happe et al. (1990) in elk forages in Washington, USA, south of our study area. Tannin content of some plant species decreases with increasing latitude (e.g., Abdala-Roberts et al. 2016, Zhang et al. 2021), though this is not consistent across taxa (Adams et al. 2009, Moles et al. 2011, Saihanna et al. 2018). A suite of factors affects tannin production, including factors that change at the site, regional, and latitudinal levels such as soil nutrients (Keski-Saari et al. 2005), precipitation (Abdala-Roberts et al. 2016, Moreira et al. 2018), sunlight (Keski-Saari et al. 2005, Yan et al. 2014), and temperature (Moreira et al. 2018). It seems that tannins play a much greater role in the nutritional quality of forage in southern BC compared to Alaska, though whether this is a regional or latitudinal difference remains unknown.

Forage was of poorer nutritional quality in 2021 (drier than average in spring and hotter than average in June and July, including an extreme heatwave; Bratu et al. 2022) compared to 2022 (cooler and wetter than average in spring, hotter than average in July and August). In 2021, most plant species produced significantly more tannins, and had less crude and digestible protein compared to 2022, and all species had significantly less digestible energy. These results agree with other studies reporting that plants produce more tannins and have lower protein digestibility in sunny, dry summers than cloudy, wet summers (Bø & Hjeljord 1991, Top et al. 2017). Summers in the study region are predicted to become increasingly hot and dry (Spittlehouse 2008), potentially leading to poorer nutritional quality of summer forages for moose and other wildlife in this region. This will be exacerbated by a predicted general decrease in plant nutritional quality with climate change, including reduced protein concentrations and changes in plant secondary metabolism associated with increasing atmospheric CO_2 and O_3 concentrations, ultraviolet radiation, and temperature (Bidart-Bouzat & Imeh-Nathaniel 2008, Muller et al. 2011, Robinson et al. 2012, Rothman et al. 2015).

Hot, dry landscapes pose serious thermoregulatory challenges to moose, which can exacerbate potential nutritional limitations. Hot conditions heighten the toxic effects of plant secondary metabolites as the herbivore's physiological capacity to metabolize the toxins diminishes with heat stress, termed temperature-dependent toxicity (Beale et al. 2018). Additionally, consumption of forages with high concentrations of plant secondary metabolites can interfere with thermoregulatory processes in herbivores, further intensifying thermal stress (Beale et al. 2018). Heat stress also leads to decreased protein synthesis and increased protein catabolism in ruminants (Marai et al. 2007, Baumgard & Rhoads 2012), potentially exacerbating the effects of protein limitation in forages in late summer. Moose respond to heat stress by decreasing forage intake (Renecker & Hudson 1986), decreasing activity (Dussault et al. 2004, Street et al. 2015), and seeking thermal refuge (van Beest et al. 2012, Street et al. 2015). These responses essentially trade off nutritional intake for thermoregulation and may have negative impacts on fitness and population dynamics as a result (van Beest et al. 2012, van Beest & Milner 2013, Shively et al. 2019). Whether these behaviours will be sufficient to overcome increasing temperatures while maintaining sufficient nutritional intake is yet unknown. Potential nutritional limitations for moose in logged landscapes may therefore be of much greater concern in hot, dry regions, including southern BC and many areas near the southern periphery of their range.

Limitations

In this study, we did not differentiate between cutblock age or post-logging silviculture treatments (e.g., herbicide application, mechanical brushing, manual brushing). The diversity, composition (Haeussler et al. 2002), and quality (Wam et al. 2016, 2017) of plant species, including forages for moose, change over time as cutblocks regenerate. Herbicide application can reduce shrub richness, diversity, quantity (Sullivan et al. 1996, Bell et al. 1997) and quality (Werner et al. 2022), and manual and mechanical brushing can increase or decrease forage quantity depending on treatment type and intensity (Bell et al. 1997, Haeussler et al. 2002, Heineman et al. 2007). Further research exploring differences in nutritional quality of forage between cutblock silviculture treatment types and ages would be beneficial.

Daily digestible protein and energy requirements were calculated based on several assumptions, the first being moose body weight, which we did not measure in this study. We assumed the moose weighed 344 kg at parturition, the average (± 29 kg) reported by Reese & Robbins (1994). When 29 kg was added or subtracted from the weight at parturition, the daily digestible protein requirement only differed by 0.04 ± 0.03 g DP/100g DM and -0.05 ± 0.04 g DP/100g DM, respectively. Therefore, the daily digestible protein requirement calculated in this study is likely appropriate for assessing whether forages provide sufficient digestible protein to support moose.

Daily requirements also were calculated assuming that moose consumed the same average dry matter intake as individuals foraging in the boreal mixedwood forest zone of Alberta, Canada (Renecker & Hudson 1985). Forests in this area support different forage species that may differ in quality. Additionally, it is well documented that under heat stress moose will trade off foraging for thermoregulation (Renecker & Hudson 1986, Shively et al. 2019). Given the hot summer conditions experienced in the study area during the two study years, the moose may have consumed less forage than assumed. If that is the case, each bite would need to have a greater percentage of digestible protein to meet the daily requirement. In this case, moose in WMU 3-18 may be more nutritionally limited than estimated due to thermoregulatory limitations.

Management Implications

This study highlights the importance of retaining unlogged forest habitats within managed forests to support adequate nutrition for moose, particularly in late summer. This may be especially important in hot, dry ecosystems such as southern BC where plants produce more tannins and mature forest also serves as important thermal refuge for moose. This study also reveals that cutblock edges generally provide forage of intermediate nutritional value, indicating that the size and configuration of cutblocks may affect forage quality and should be considered in forest planning. As noted by Hjeljord et al. (1990), extensive use of cutblock edges by moose may be partially attributable to preferred consumption of more shaded plants. A significant proportion of cutblocks in our study area were logged to salvage timber impacted by mountain pine beetle; these salvage cutblocks are typically much larger than non-salvage cutblocks (Forest Practices Board 2009) and have low edge ratios as a result. Cutblock edges provide ideal foraging habitat where biomass is higher than in adjacent mature forest and quality is higher than further into the cutblock. Planning smaller cutblocks with higher edge ratios and more retained wildlife tree patches may enhance the quantity and quality of forage on the landscape.

This study found that most forage samples did not provide sufficient digestible protein to support healthy adult female moose rearing a singleton calf. Further research into whether nutritional inadequacies in forage actually result in decreased nutritional condition and productivity of moose is required (see Chapter 3). Potential nutritional limitation likely inter-plays with other factors such as climate change, predation, and harvest rates.

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CHAPTER 3: A PRELIMINARY EXAMINATION OF MOOSE NUTRITIONAL STATUS IN A DISTURBED LANDSCAPE

Introduction

Moose (*Alces alces*) are adapted to disturbance-mediated temperate forests (Geist 1971) where natural disturbances such as wildfire, pest outbreaks, and storms create a mosaic of early- and late-seral forest patches (Swanson et al. 2011). They exploit mature stands for relief from heat, cold, and snowfall, and feed in early seral stands where forage is abundant (Timmermann and McNicol 1988, Bjørneraas et al. 2011). Fire can create particularly valuable early seral stands for moose, as mineralization of organic matter and ash create a nutrient pulse (Fuentes-Ramirez et al. 2008) that can increase forage quality in the short-term (MacCracken & Vierek 1990, van Dyke & Darragh 2007, Proffitt et al. 2019), and fire-disturbed soils are favourable to establishment of deciduous species that persist for decades post-fire (Shenoy et al. 2011). Thus, landscapes disturbed by natural fire regimes often support healthy moose populations (Irwin 1975, Schwartz & Franzmann 1989, DuBois 2008).

In addition to natural disturbances, forest heterogeneity is increasingly shaped by forest management practices such as logging, salvage logging, and fire suppression (Brown et al. 1994, Cyr et al. 2009). While logging practices aim to approximate the effects of natural forest disturbances (McRae et al. 2001), there are key differences that greatly affect the habitat value for moose and other wildlife. For example, forest management practices involve road building and removal of key biological structures such as residual live trees, snags, and coarse woody debris, resulting in reduced structural diversity, altered plant and animal communities, and disturbed hydrological and nutrient cycles (Dykstra & Braumandl 2006, Lindenmayer & Noss 2006, Lindenmayer et al. 2008, Lewis 2009, Dhar et al. 2016, Thorn al. 2017, Steinke et al. 2020).

Both logging and wildfire alter the nutritional value of the landscape for moose (Happe et al. 1990, Lord & Kielland 2015**,** Brown et al. 2018), affecting their nutritional condition, which, in turn, influences age of sexual maturity (McNicol & Timmermann

1981), pregnancy and twinning rates (McNicol & Timmermann 1981, Franzmann & Schwartz 1985), offspring size and survival (Keech et al. 2000), and ultimately, population dynamics (McArt et al. 2009). Individuals that efficiently use those habitats providing the forage of highest nutritional quality (in adequate amounts) should reap the fitness benefits of maximized nutritional condition (Long et al. 2016, Merems et al. 2020).

Moose respond positively to logging in many areas (Forbes & Théberge 1993, Potvin et al. 2005), though this is not always the case (Potvin & Courtois 2004, Koetke et al. 2023). Many moose populations in British Columbia (BC), Canada have declined precipitously, despite inhabiting areas with extensive logging disturbances over the past 70 years as well as recent wildfires (British Columbia Wildfire Service 2023a). In Chapter 2, I investigated the nutritional quality of moose forage in one such area, focusing on digestible protein, a known limiting nutrient for moose (McArt et al. 2009, Peterson et al. 2022), particularly during lactation (Parker et al. 2009, Hackmann 2011). I found that the digestible protein content of forages was marginal to insufficient for supporting healthy moose in late summer and was lower in plants growing in cutblocks than in forests (Chapter 2). These findings spurred me to understand (1) whether moose in the same region were nutritionally limited, and (2) whether summer habitat use within this disturbed landscape affected moose in terms of body condition and reproduction. Given that forage quality in this area seemed marginal, especially in cutblocks, and that ~1/3 of the area has been logged, I predicted that the animals would be nutritionally limited. Because forage in cutblocks can be of poorer nutritional quality than forage in forests (Happe et al. 1990, Chapter 2) I predicted that moose that used cutblocks more would be in poorer condition and have lower calf survival. Conversely, I predicted that moose that used recently burned habitats would be in better condition and have higher calf survival, as they would reap the benefits of high-quality post-fire forage regeneration (MacCracken & Vierek 1990, van Dyke & Darragh 2007, Proffitt et al. 2019).

Methods

Study Area

The study area, Wildlife Management Unit (WMU) 3-18, is located in the Thompson Okanagan Region of BC, Canada (Figure 3-1). This region is characterized by short hot summers and long cool winters. The long-term mean annual temperature is 7.8°C, with mean monthly temperatures (based on hourly temperature readings) ranging from -3.7 – 4.1°C in winter (December-March) and from 15.9 – 18.8°C in summer (June-August) (Environment and Climate Change Canada 2023). The study area receives a long-term average of 321 mm of precipitation a year (Environment and Climate Change Canada 2023). My research was conducted from December 2020 to December 2022, including three winter capture events in 2020, 2021, and 2022 and two summers from June 28 – September 20 (Francis et al. 2020) 2021 and 2022. Weather in 2021 was drier than average in spring and hotter and drier than average in June and July, including a record-breaking heatwave in late June (Bratu et al. 2022). In 2022 it was cooler and wetter than average in spring, and hotter than average in July and August. Several large wildfires burned 31% of WMU 3-18 between April and September 2021, including three wildfires of note: the Tremont Creek, Petit Creek, and Lytton Creek Wildfires (British Columbia Wildfire Service 2023a).

At lower elevations, the study area included the open Douglas fir (*Pseudotseuga menziesii*) forests associated with the Interior Douglas-Fir Biogeoclimatic Ecosystem Classification Zone (Egan 1996), as well as stands of ponderosa pine (*Pinus ponderosa*) on drier sites, spruce (*Picea* spp.) on wetter sites, and lodgepole pine on recently burned sites. At higher elevations the hybrid white spruce (*Picea glauca x engelmannii*) forests and lodgepole pine stands typical of the Montane Spruce zone prevailed (Alldritt McDowell & Lloyd 1999). The study area has been logged since 1950 (27% of the land base as of 2022), with a marked increase from 2005 – 2010 as a result of salvage logging operations following a mountain pine beetle (*Dendroctonus ponderosae*) epidemic (Corbett et al. 2016). As of 2022, ~0.5% of the land base was 0-2 years post-logging, ~13% was 3-14, ~7% was 15-25, and ~6% was 26-79 years post-logging.

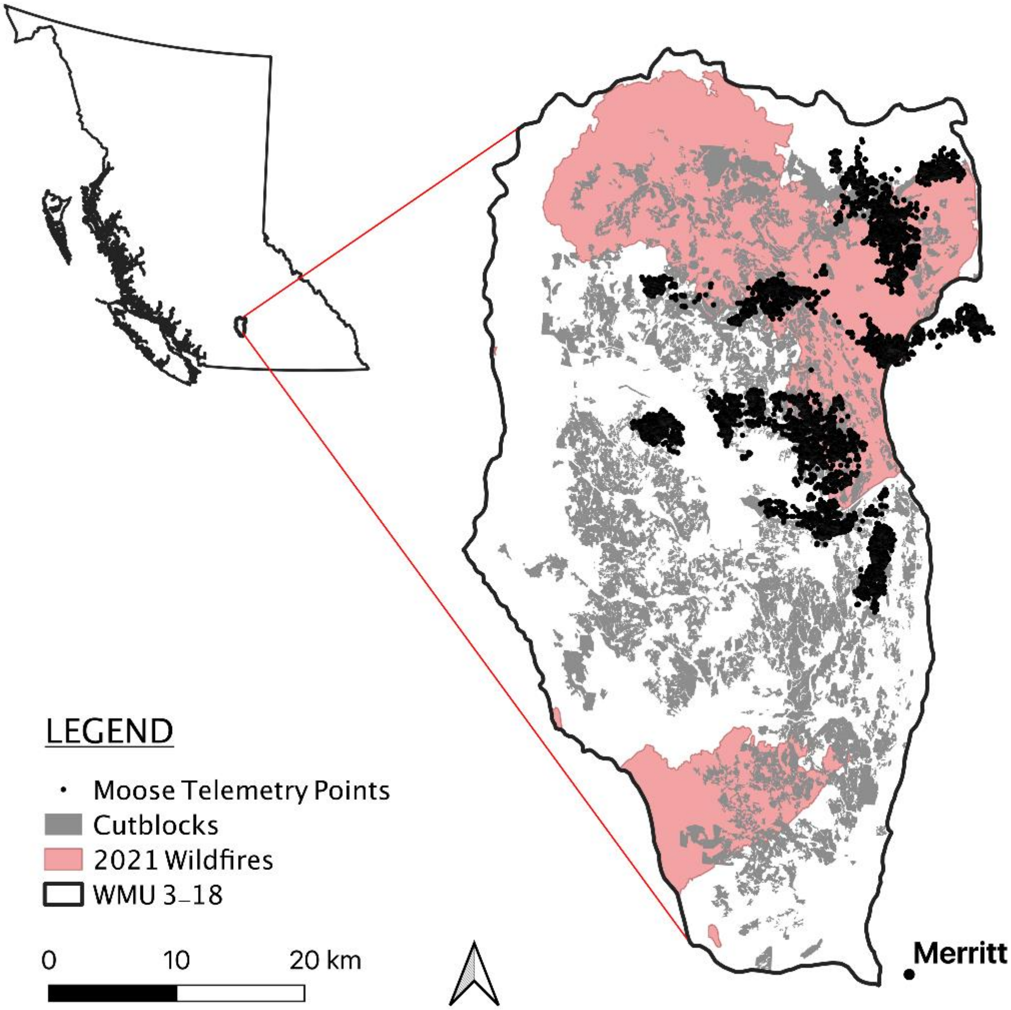

Figure 3-1. Distribution of moose location data (black dots; n = 12, 19,136 locations points) in Wildlife Management Unit (WMU) 3-18 in southern British Columbia, Canada, 2021-2022. Logging cutblocks are shown in grey and areas burned by wildfire in 2021 are shown in red.

The moose density in WMU 3-18 was estimated at 0.26 moose/km^2 in 2016 and 0.14 moose/km^2 in 2022 (C. Procter, British Columbia Ministry of Forests, unpublished data), indicating a population decline of 46% over the past 6 years. Human harvest included a general open season for spike-fork male moose from November 1-15 (BC FLNRORD 2020a), limited entry hunting for adult females and calves from November 1-10 and adult males from October 1-31 (BC FLNRORD 2020b), and year-round harvest by Indigenous peoples (Procter & Iredale 2017). It is suspected that unregulated harvest of adult female moose may be a contributing factor in the population's recent decline (C. Procter, personal communication, July 2022). Predators included abundant black bears (*Ursus americanus*) and cougars (*Puma concolor*), and a low density of grey wolves (*Canis lupus*) (Procter & Iredale 2017).

Moose Nutritional Condition

Thirteen adult female moose were captured between December 2020 and February 2021, and an additional three adult female moose were captured in January 2022. Moose were chemically immobilized with a dose of BAM II (Chiron Compounding Pharmacy Inc., Guelph, Ont.) administered via Pneudart remote delivery system from helicopter (Kuzyk et al. 2019). Moose were outfitted with Telonics TWG-4667-4 GPS collars (Telonics Inc., Mesa, Arizona) with a 2-hour GPS fix rate and activity recorded as active seconds (defined as movement along one or more axes in an internal 3-axis accelerometer) in a 10-minute period prior to each GPS fix. Collars were programmed to send a mortality alert via email if no movement was detected by the internal tip switch for 6 hours. See Chapter 2 for detailed capture methodology.

During capture, each animal's body condition was evaluated by measuring maximum subcutaneous rump fat thickness (i.e., MAXFAT) in centimeters (cm) via ultrasonography (Stephenson et al. 1998) using a FUJIFILM Sonosite M-Turbo ultrasound machine (FUJIFILM Canada, Toronto, ON). Blood samples (35 milliliters [ml]) were drawn using an 18-gauge x 1.5-inch needle to determine pregnancy status through the detection of pregnancy-specific protein B. Presence of offspring also was noted and was assumed to represent calf survival to ~8 months of age (i.e. early winter calf survival). Surviving moose in the cohort were recaptured one and two years after initial capture using the same methods, and collars were removed during the final captures in December 2022.

Percent ingesta-free body fat (IFBF) was calculated as IFBF = 5.61 + 2.05MAXFAT (Stephenson et al. 1998). To determine whether moose were nutritionally limited, IFBF was compared to body fat thresholds determined by Cook et al. (2004) for elk and applied to moose by Cook et al. (2021b). Specifically, individuals with ≤5%, 6-8%, 9-12%, and >12% IFBF were categorized as severely, moderately, mildly, and not nutritionally limited, respectively.

Given that poor maternal condition can lead to depressed pregnancy rates (Keech et al. 2000, Murray et al. 2006), MAXFAT was compared to a 0.20 cm threshold determined by Ruprecht et al. (2016), above which the probability of pregnancy in Shiras moose (*A. a. shirasi*) becomes highly likely (~95%), and to a threshold of 2.33 cm for a high probability of pregnancy (85%) in Alaskan moose (*A. a. gigas*) calculated by Procter et al. (2020) using data from Testa & Adams (1998). As there were no published thresholds for the subspecies studied here, Northwestern moose (*A. a. andersoni*), I assumed the rump fat required for a high probability of pregnancy was within the range of 0.20 – 2.33 cm, given that Northwestern moose are intermediate in size to the Shiras and Alaskan subspecies.

Annual (week of December 15 to week of December 15) adult survival rates were estimated using the Kaplan Meier method (Pollock et al. 1989), excluding the single individual that was poached (to focus on natural mortality factors only) and the single individual that died <5 days post-capture (to avoid bias from capture-related mortality; Neumann et al. 2011). Annual survival estimates were compared to a threshold of 85% indicative of potential for stable moose populations (Bangs et al. 1989, Ballard et al. 1991, Bertram & Vivion 2002).

The recruitment-mortality (R/M) equation was used to estimate the annual finite rate of change in the population (λ) based on adult female and calf survival data collected during captures in early winter, assuming 50% of calves were females (Hatter & Bergerud 1991).

Habitat Use

Habitat type at each GPS location was characterized using a geographic information system (QGIS 3.8 Esri). The Harvested Areas of BC (Consolidated Cutblocks) spatial layer (BC Forest Analysis and Inventory Branch 2022) was used to identify GPS relocations in cutblocks, and fire perimeter shapefiles mapping the progression of the Tremont Creek Wildfire (n=16, supplied by the BC Wildfire Service) were used to identify GPS relocations in burned habitats.

The percentage of time each individual spent in cutblocks and burns each summer (i.e. percent use) was estimated by comparing the number of GPS relocations in cutblocks and burns, respectively, to the total number of successful GPS relocations for each individual taken during summer (June 28 – September 20; Francis et al. 2020). Summer was selected as the focal season because the short summer growing season is the critical period for nutrient intake when individuals must replenish fat and protein reserves to support growth, breeding, and overwinter survival (Crête & Huot 1993, McArt et al. 2009, Shively et al. 2019). This is especially true for reproducing females that must also support lactation (Oftedal 1985).

Statistical Analysis

Measurements of IFBF were related to use of cutblocks and burns in summer, calf-at-heel, calf-at-heel the previous year, and year using linear mixed-effects models with moose ID treated as a random effect to account for multiple observations. The presence of a calf-at-heel was related to use of cutblocks and burns in summer, IFBF, IFBF the previous year, calf-at-heel the previous year, and year using generalized linear mixed effects models with a binomial distribution and moose ID treated as a random effect. For each response variable, a set of candidate models was compared, including a null model and all additive combinations of the predictor variables. Multicollinearity (i.e., variance inflation factor >5) was checked for all full models. Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002) was used for model selection. For each response variable, all candidate models <2 ΔAICc from the best-approximating model were reported. Because small sample sizes are susceptible to the influence of outliers, a jackknife analysis was conducted for each top-ranking regression (Efron 1982). This consisted of iteratively eliminating one data point from the data set, re-calibrating the regression model, and determining the mean r^2 and the proportion of regression iterations that yielded statistically significant results. All statistical analyses were conducted in program R, version 4.2.3 (R Core Team 2023).

Results

Moose Capture and Handling

Thirteen adult female moose were collared during winter 2020 captures. One individual (M11) died of capture-related causes shortly after capture, another individual (M17) died of an unknown cause in July 2021, and a third individual (M12) was poached in October 2021.

In winter 2021, the surviving collared moose (n=10) were recaptured, and three additional individuals were fitted with GPS collars, for a total of 13 collared moose. One individual (M25) died of unknown causes in May 2022, another (M32) died in May 2022 after becoming stuck in a deep mud pit (appearance of bone marrow fat indicated poor condition), and a third (M16) died of apparent starvation in August 2022. All surviving individuals (n=10) were recaptured in winter 2022, and all collars were removed.

Moose Nutritional Condition

On average, moose were in the worst condition in winter 2021, intermediate condition in winter 2020, and best condition in winter 2022 (Table 3-1). All individuals lost IFBF from winter 2020 to winter 2021 and gained IFBF from winter 2021 to winter 2022, though the extent gained in winter 2022 varied greatly (Figure 3-2). However, when individual IFBF was compared over time, there was no significant difference between capture years ($F_{1.07,6.41} = 4.418$, $P = 0.076$), even though 30% of the variance in IFBF could be accounted for by year. Post-hoc analyses revealed significant differences in IFBF between 2020 and 2021 ($P < 0.001$) and 2021 and 2022 ($P = 0.013$). These post-hoc results demonstrate that while the overall effect of year was not significant, there were notable differences between specific years when analyzed pairwise. Based on the

Table 3-1. Maximum thickness of rump fat (MAXFAT), ingesta-free body fat (IFBF), pregnancy, calf survival to ~8 months of age, and mortality of adult female moose in British Columbia, Canada over three years. Mean (± standard deviation) MAXFAT and IFBF, pregnancy rate, and percentage of moose with a surviving offspring at 8 months of age are reported on the bottom row for each year.

	Winter 2020				**Winter 2021**				**Winter 2022**			
ID	**MAXFAT (cm)**	**IFBF (%)**	**Pregnant**	**Calf at heel**	**MAXFAT (cm)**	**IFBF (%)**	**Pregnant**	**Calf at heel**	**MAXFAT (cm)**	**IFBF (%)**	**Pregnant**	**Calf at heel**
M11	1.02	7.70	Y	1	–	–	–	–	–	–	–	–
M12	0.20	6.02	N	0	–	–	–	–	–	–	–	–
M13	1.18	8.03	Y	1	–	–	–	0	1.49	8.66	Y	0
M14	2.67	11.08	Y	0	1.36	8.40	Y	1	2.09	9.89	Y	0
M15	1.62	8.93	Y	0	1.29	8.25	Y	0	1.45	8.58	Y	1
M16	1.60	8.89	Y	0	0.82	7.29	Y	0	–	–	–	–
M17	0.27	6.16	N	0	–	–	–	–	–	–	–	–
M18	1.26	8.19	Y	1	0.76	7.17	Y	0	4.71	15.27	Y	0
M20	0.64	6.92	Y	1	0.40	6.43	Y	1	2.8	11.35	Y	1
M21	1.00	7.66	Y	0	0.29	6.20	Y	1	0.4	6.43	Y	1
M23	1.91	9.53	N	0	1.10	7.87	Y	0	1.78	9.26	–	1
M24	1.91	9.53	Y	1	1.20	8.07	Y	1	2.8	11.35	Y	1
M25	1.15	7.97	Y	1	0.31	6.25	Y	0	–	–	–	–
M31	–	–	–	–	1.80	9.30	Y	2	2.5	10.74	Y	1
M32	–	–	–	–	0.22	6.06	N	0	–	–	–	–
M37	–	–	–	–	0.96	7.58	Y	0	2.34	10.41	Y	0
	1.26 ± 0.670	8.20 ± 1.415	77%	46%	0.88 ± 0.501	7.41 ± 1.027	92%	38%	2.24 ± 1.136	10.19 ± 2.330	100%	60%

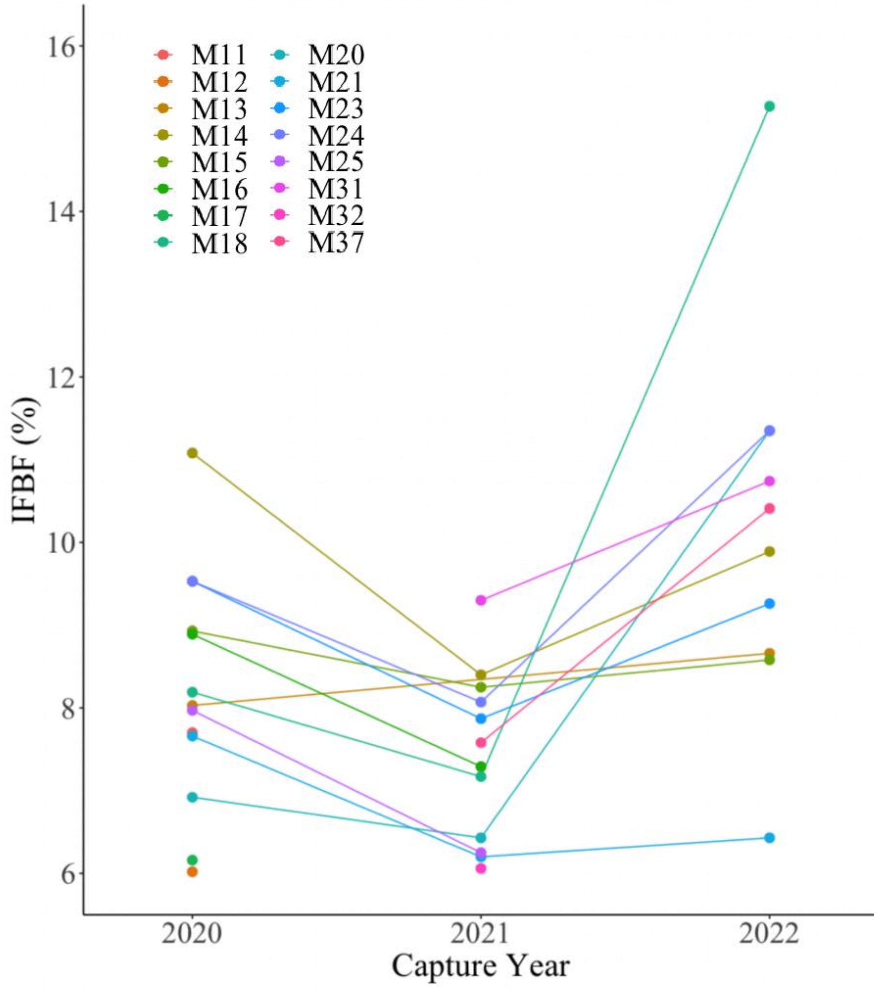

Figure 3-2. Early winter percent ingesta-free body fat (IFBF) of individual adult female moose (n=16) over three consecutive years in British Columbia, Canada.

IFBF index (Cook et al. 2021), 23% and 77% of individuals were mildly- and moderately-nutritionally limited in winter 2020, respectively. In winter 2021, 8% and 92% of individuals were mildly and moderately nutritionally limited, respectively. In winter 2022, one individual (10%) was not nutritionally limited at all, while 60% and 30% of individuals were mildly and moderately nutritionally limited, respectively.

All individuals had at least 0.20 cm of MAXFAT at the beginning of each winter, the threshold for a high probability of pregnancy in Shiras moose (Ruprecht et al. 2016; Table 3-1). However, only one individual in 2020 and no individuals in 2021 met the 2.33 cm threshold for a high probability of pregnancy in Alaskan moose (Procter et al. 2020 based on data from Testa & Adams 1998), while in 2022, 50% of individuals had at least this amount of MAXFAT (Table 3-1). Pregnancy rates ranged from 77 – 100% and the proportion of adult females with a calf at heel during capture (i.e., early winter calf survival) ranged from 38 – 60% (Table 3-1).

Incorporating only non-anthropogenic mortality, annual survival rates for adult female moose were estimated at 0.91 (SE = 0.087, 95% CI = [0.739, 1.000]) from December 15, 2020 to December 15, 2021, and 0.75 (SE = 0.125, 95% CI = [0.505, 0.995]) from December 15, 2021 to December 15, 2022. The survival estimates were not statistically different between years, nor from the 85% survival rate expected to result from a stable moose population (Bangs et al. 1989, Ballard et al. 1991, Bertram & Vivion 2002). The R/M equation revealed that the adult female and calf survival rates (as assessed in early winter) were sufficient to support a growing population in both study years ($\lambda = 1.18$ from 2020-2021, $\lambda = 1.07$ from 2021-2022).

Effect of Summer Habitat Use on Moose Condition and Reproduction

While use of cutblocks, forests, and recently burned habitats varied greatly between individuals and between years (Figure 3-3), IFBF was best explained by year alone, with individuals in worst condition in 2021, intermediate condition in 2020, and best condition in 2022 (Figure 3-2). The top model for IFBF, as ranked through AICc, included only year (Table 3-2). On average, moose IFBF was estimated to be 2.87 (± 0.81) units higher in 2022 than 2021 ($t = 3.51$, $P = 0.003$). All 20 iterations of the

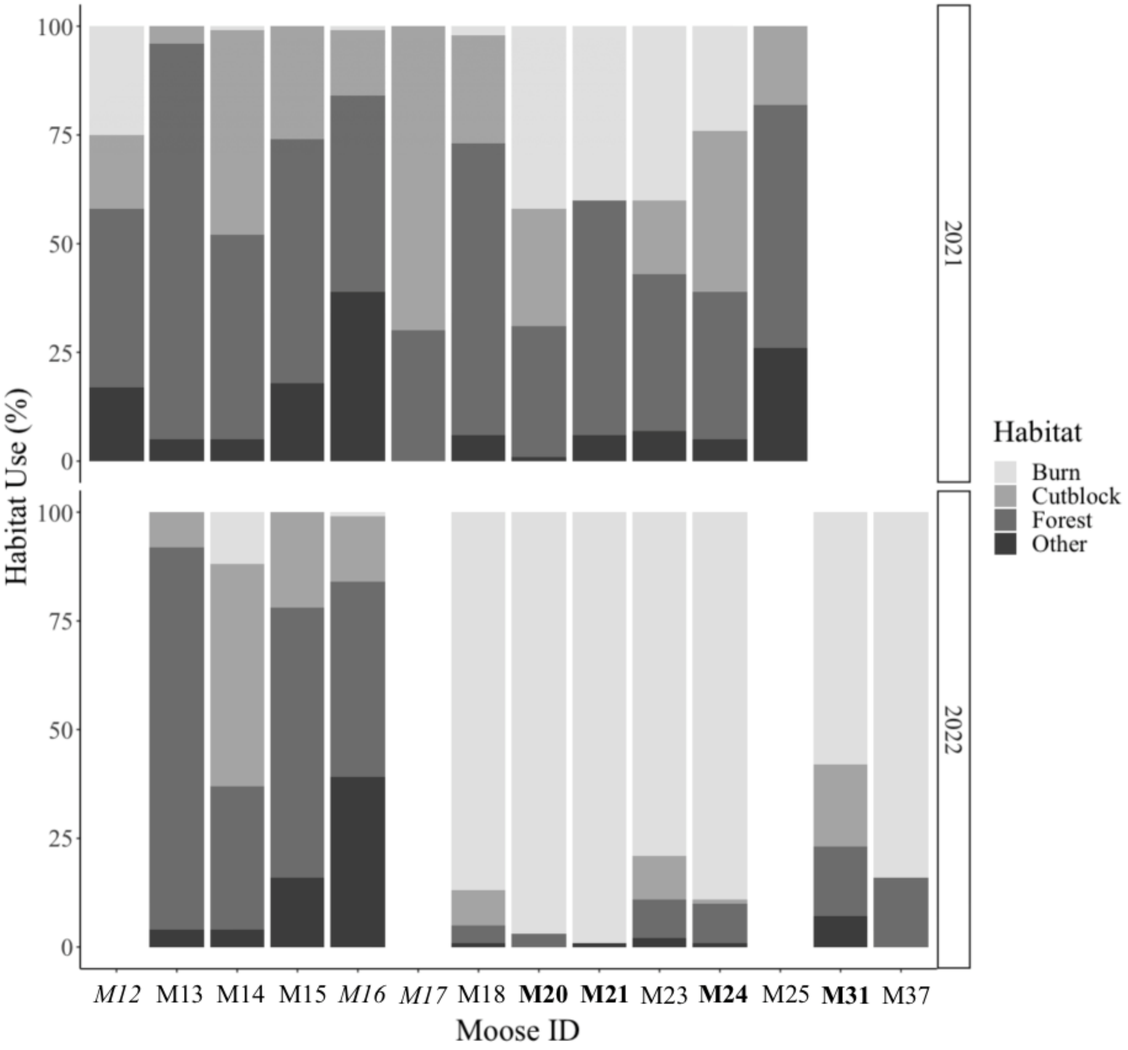

Figure 3-3. Percent use (i.e., percentage of GPS relocations) of recently burned habitats (i.e., burned in 2021), unburned forest, and unburned cutblocks by adult female moose in British Columbia, Canada over two summers. Individuals marked in bold font were classified as the most successful in terms of rearing calves to early winter, while individuals marked in italics were the least successful in calf rearing and/or died of apparent starvation.

Table 3-2. Analysis of factors potentially explaining variation in moose ingesta-free body fat (IFBF) and reproductive success (i.e., calf at heel in early winter). IFBF was best explained by year, while reproductive success was best explained by use of recently burned habitats in the summer. Outlined below are the model variables, number of model parameters (K), Akaike's Information Criterion corrected for small sample sizes (AICc), change in AIC from the best model (ΔAICc), model weights calculated from AICc (wi), and the log likelihoods (LL) for competing models relating moose IFBF to habitat use and reproductive success, and relating reproductive success to habitat use, IFBF, and previous reproductive success. All competing models within <2 ΔAICc of the best-approximating model for each response variable are shown.

	K	**AICc**	**ΔAICc**	**w_i**	**LL**
IFBF					
Year + (1|ID)	4	83.55	0.00	0.45	-36.35
Year + Calf at Heel + (1|ID)	5	84.94	1.39	0.23	-35.16
Year + Calf at Heel the Previous Year + (1|ID)	5	85.08	1.53	0.21	-35.23
Calf at Heel					
Use of Burns + (1|ID)	3	31.82	0.00	0.13	-12.26
Use of Burns + IFBF + (1|ID)	4	32.18	0.36	0.11	-10.66
1 + (1|ID)	2	32.18	0.36	0.11	-13.74
Use of Burns + IFBF the Previous Year + (1|ID)	4	33.45	1.63	0.06	-11.30
Use of Burns + IFBF + Use of Cutblocks + (1|ID)	5	33.56	1.74	0.06	-9/47
Use of Burns + Use of Cutblocks + (1|ID)	4	33.57	1.75	0.05	-11.45
IFBF + (1|ID)	3	33.76	1.95	0.05	-13.08
IFBF the Previous Year + (1|ID)	3	33.80	1.98	0.05	-13.10

jackknife analysis were statistically significant (mean $r^2 = 0.38$). Two additional models were <2 ΔAICc of the best-approximating model. However, these models differed only in the addition of another parameter, calf-at-heel and calf-at-heel the previous year, respectively, and therefore were not considered to have additional explanatory power (Arnold 2010). Neither of these covariates were statistically significant in their respective models (i.e. $P > 0.05$).

The presence or absence of a calf at heel during capture was related primarily to the amount of time the adult female spent in recently burned areas. Individuals with calves used burns to a greater extent (odds ratio = 1.02, CI = 1.00–1.05, $z = 1.63$; Figure 3-4). Three of the four most successful individuals (i.e., those that reared the most calves) used burned habitats almost exclusively after the 2021 wildfires (Figure 3-3). The top model included use of burns only (Table 3-2) but was not statistically significant ($P = 0.103$), and only 2 of 20 jackknife iterations yielded significant results (mean $r^2 = 0.14$; P-values of the two significant iterations were 0.028 and 0.031). Seven additional models were <2 ΔAICc of the best-approximating model. Five of the eight top models included use of burns, but this covariate only was statistically significant in two of the models (Use of Burns + IFBF + Use of Cutblocks + (1|ID): $P = 0.042$; Use of Burns + Use of Cutblocks + (1|ID): $P = 0.049$). Two of the top 8 models included use of cutblocks, three included IFBF, and two included IFBF the previous year, but none of these covariates were statistically significant in any of their respective models.

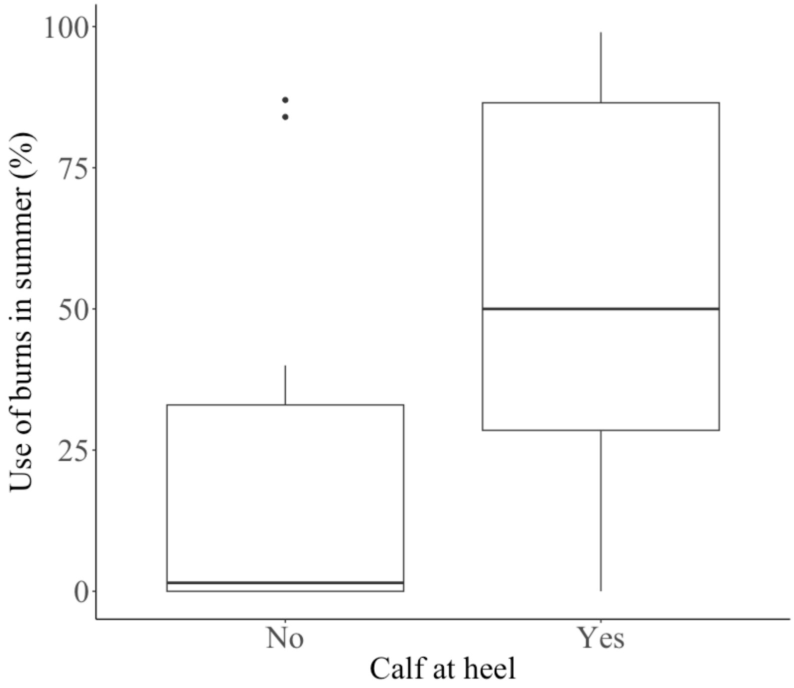

Figure 3-4. Boxplot showing the relationship between percent use of recently burned areas by adult female moose in summer (June 28 – September 20; Francis et al. 2020) and the presence of a calf at heel during winter captures (i.e., early winter calf survival) in British Columbia, Canada.

Discussion

Moose Nutritional Condition

The body fat levels of adult female moose appeared indicative of nutritional limitation but were not associated with depressed pregnancy or calf survival. According to the sole index in the literature (Cook et al. 2021b), all individuals in our study (n=16) were classified as nutritionally limited, except for one individual in one year. This was corroborated by the deaths of two adult females from apparent starvation during the study. However, pregnancy and early-winter calf survival rates were not clearly indicative of poor nutritional condition or declining population trends. If this small sample size is representative of the population, then calf production and survival should be sufficient to support population growth (i.e., λ >1), though true lambda is likely lower than estimated as true calf recruitment is typically lower than early winter calf survival. The pregnancy rates were within typical range for populations across North America (Boer 1992) and for both increasing and declining populations in BC (Procter et al. 2020). Similarly, early winter calf survival rates were within ranges reported in both declining (Arsenault et al. 2016, Harris et al. 2021, Procter et al. 2020) and increasing (Procter et al. 2020) moose populations in North America.

Typically, adult female ungulates are considered nutritionally limited when poor condition depresses productivity and/or survival (Verme 1969), as suggested by the death of the two individuals due to apparent starvation. However, apparent starvation can be attributed to other factors, including underlying health issues such as parasites and disease (Murray et al. 2006), not just sub-optimal nutrition. Additionally, most individuals successfully reared at least one calf during the three study winters, despite being categorized as mildly or moderately nutritionally limited. This discrepancy may be due to incorrect classification of moose nutritional status from body fat estimates. The thresholds of nutritional limitation that we used were developed for elk (Cook et al. 2004) and subsequently applied to moose (Cook et al. 2021b). The authors classified elk with <12% body fat as nutritionally limited because fat levels below this threshold resulted in reduced adult and yearling pregnancy, delayed conception, reduced calf and yearling mass, and reduced probability of survival. However, these fat thresholds may not translate adequately to moose. For example, Shiras moose have a high probability of pregnancy with as little as 6% body fat (Ruprecht et al. 2016) and Alaskan moose with ~10% body fat (Procter et al. 2020 [based on data from Testa & Adams 1998]). According to the Cook et al. (2021b) index, moose with these amounts of body fat would be considered moderately and mildly nutritionally limited, respectively, yet still have high probability of pregnancy. The Northwestern moose studied here had a high pregnancy rate (92%) even when mean body fat was as low as 7.41% in 2021 (see Table 3-1). Pregnancy is linked to maternal condition in moose (Keech et al. 2000), but perhaps other reproductive parameters (not studied here) are even more sensitive to maternal condition, such as twinning (Franzmann & Schwartz 1985, Boer et al. 1992, Gasaway et al. 1992), parturition (i.e., prenatal mortality) (Testa & Adams 1998, Milner et al. 2013), and yearling pregnancy rates (Boer 1992). Unfortunately, no body fat thresholds have been reported for Northwestern moose in relation to these parameters. Thresholds were reported for the Alaskan subspecies (Testa & Adams 1998), but there is likely low applicability given that Alaskan moose are larger and therefore require higher fat levels, as demonstrated above in relation to pregnancy. More research is needed to understand the nutritional status of moose in relation to body fat and to create appropriate thresholds that relate body fat of Northwestern moose in BC to important biological parameters.

Without evidence of the ramifications of nutritional limitation (i.e., depressed pregnancy and calf survival rates), and without knowledge of potential underlying causes of the two cases of apparent starvation, I cannot conclude that nutritional limitation is playing a major role in the population decline in WMU 3-18. With calf survival rates sufficient to support a stable to growing population, it seems unlikely that nutrition alone is limiting the growth of this population. Increasingly hot and dry conditions due to climate change (Spittlehouse 2008) may be affecting moose by causing thermoregulatory stress, decreased forage intake, changed behavioural patterns, and decreased forage quality (see Chapter 2). If nutritional limitation is contributing to this population's decline, it may be through exacerbating the negative impacts of these other stressors (Murray et al. 2006).

Effect of Habitat Use on Moose Condition and Reproduction

The nutritional condition of adult female moose was not related to their habitat use, either cutblocks or recent burns, but rather to year: all moose lost body fat from 2020 to 2021 and all gained body fat from 2021 to 2022. With significant differences in spring and summer weather conditions and plant nutritional quality year-to-year (see Chapter 2), body fat may be related to annual variability in both weather conditions and plant nutritional quality. Spring and summer weather conditions can affect moose condition directly through the cost of thermoregulation (van Beest et al. 2012, Shively et al. 2019) and indirectly through effects on plant nutritional quality (Bø & Hjeljord 1991, Top et al. 2017). This double-fold effect on moose may explain the annual differences in moose condition recorded during our three capture years. Additionally, reduced maternal nutritional condition as a result of hot and dry spring/summer conditions has been associated with reduced calf body mass (Hjeljord & Histøl 1999) and recruitment rates (Monteith et al. 2015). With climate change, spring and summer conditions in the region are expected to become increasingly hot and dry (Spittlehouse 2008), which may lead to more years where moose experience thermal stress, nutritional limitation, and poor calf recruitment rates, potentially resulting in further declines in this population.

I found early winter calf survival was best explained by use of burns in summer, though the importance of this correlation was somewhat questionable (i.e., $P > 0.05$ in 18/20 iterations). Indeed, three of the four most successful individuals (i.e., those that reared the most calves) used burned areas almost exclusively after the 2021 wildfires. Moose used recently burned habitats when they were within or adjacent to their pre-fire summer range, but no individuals made directed movement to exploit a recently burned area that was not already partially within their summer range (Wallin 2023), as described in other areas as well (Gasaway et al. 1989). This trend in increased calf production post-wildfire also has been found in Alaska (Spencer & Hakala 1964). There are several possible explanations for this correlation. Firstly, increased quality of regenerating forage in recently burned areas may have helped adult females to support the high costs of lactation. There often is a pulse in nutrients (e.g., nitrogen, phosphorus, potassium) after wildfires (Fuentes-Ramirez et al. 2008) that can lead to a short-term increase in the nutritional quality of some forage species (MacCracken & Vierek 1990, van Dyke & Darragh 2007, Proffitt et al. 2019). Additionally, fires shift landscapes toward younger successional stages that typically contain more ungulate forage (Proffitt et al. 2016, 2019, Brown et al. 2018). Greater access to high-quality forage may allow moose to invest more in lactation, resulting in the higher early winter calf survival observed in this study. Secondly, higher early winter calf survival may be due to decreased rates of predation in burned areas, where abundant downed woody debris may confer an advantage to moose when evading predators (Geist 2005). However, Ganz et al. (2022) found predation rates on mule deer to be equivalent in burned and unburned areas. Lastly, higher early-winter calf survival could be linked to reduced human harvest due to a motor-vehicle closure of the Tremont Creek wildfire area that was in effect from autumn 2021 through spring 2023 (British Columbia Ministry of Tourism, Arts, Culture and Sport 2023). Though licensed hunting of moose calves is rare in this area (only one antlerless moose has been harvested in WMU 3-18 since 2017 [C. Procter, personal communication, October 2023]), unlicensed hunting does occur in the forms of year-round rights-based harvest by Indigenous peoples and illegal poaching. Although it is challenging to verify, the motor-vehicle closure could have led to a decline in unlicensed and/or illegal calf harvest. Indeed, risk of human harvest increases for moose using areas with high road densities (Mumma & Gillingham 2019). Studies from Ontario and Alaska have reported moose populations increasing after wildfire only when hunting pressure was concurrently low (Bishop & Rausch 1974, Rempel et al. 1997). More research is required to determine why moose using recent burns were more likely to successfully rear a calf if nutrition is not a proximate cause of success.

Limitations

Due to a modest sample size, this study serves as a preliminary examination of the relationship between moose nutritional condition and landscape disturbance. Further study is required to make definitive population-level inferences.

I focused on the link between summer habitat use and early winter nutritional condition, as summer is considered the key time of year for ungulates to build up body reserves (Hjeljord & Histøl 1999, Cook et al. 2004). However, fall and winter nutrition also are important, affecting over-winter fat loss, prenatal mortality, and calf survival (Milner et al. 2013), and could be examined in future research.

Because we did not conduct calf survival surveys during the summer and fall, it was not possible to analyse differences in summer habitat use between individuals with and without calves. However, recent research in central interior BC indicates that moose with and without calves both prioritize foraging over cover and seem not to display significant differences between cutblock use and selection (Francis et al. 2020, Mumma et al. 2021). The lack of information on calf survival also limited our ability to interpret early winter adult female body condition data, as adult females that experienced pre- or perinatal calf mortality would likely be in better condition the following winter than those that reared a calf throughout the summer but lost it prior to winter captures (Cook et al. 2021a).

Management Implications

Despite finding overall poorer plant nutritional quality in cutblocks than forests (Chapter 2), I did not find a link between use of cutblocks in summer and adult female moose condition or reproduction. The lack of correlation between use of cutblocks in summer and subsequent condition and reproduction could point to the fact that increased browse production in cutblocks may compensate for decreased quality, that moose foraged on plant species whose quality is better or equal in cutblocks than forests (e.g., Saskatoon, willows), and/or that moose foraged in the edges of cutblocks, which provide forage of intermediate nutritional quality. Taken together with my results in Chapter 2, this suggests that cutblocks with a relatively high edge:area ratio may provide abundant but intermediate-quality forage for moose, making up for higher-quality forage found in more limited quantities in unlogged forest habitat.

New burns seemed to play a positive role in calf production, highlighting the fact that moose are suited to fire- and disturbance-mediated landscapes that provide a mosaic of habitat types and forest successional stages within natural disturbance regimes (Geist 1971). This preliminary research suggests that projected increases in wildfire frequency in interior BC (Haughian et al. 2012) may benefit moose. Burning (where safe and appropriate) and restoring historical burn regimes may be appropriate management actions, as demonstrated in BC (Goddard 2011) and beyond (Boucher 2003, DuBois 2008, Fredriksson et al. 2023), with potential to increase the low calf recruitment rates documented in some other populations in BC (Procter et al. 2020). Continued monitoring of moose populations in BC following the record-breaking wildfire seasons in recent years (British Columbia Wildfire Service 2023b) also may elucidate this relationship.

Pregnancy and early winter calf survival rates in this study appeared in line with healthy populations and could support a stable to growing population. This points toward adult female survival, rather than calf production, as being the possible mechanism of population decline. Overall, I did not find compelling evidence that poor nutrition was playing a major role in the decline of this population, directly or indirectly, such as through calf production. This points toward other factors being involved in the decline of this population. If nutrition is contributing to this decline, it may be acting in an additive or synergistic manner with other factors such as (but not limited to) harvest of adult females, thermoregulatory stress, and decreased plant nutritional quality as a result of climate change. Further long-term investigation is needed.

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CHAPTER 4: CONCLUSION TO THE THESIS

Summary

The overarching goal of my thesis was to understand whether nutritional limitation stemming from anthropogenic landscape disturbance was a potential driver of a moose population decline in southern interior British Columbia (BC). Specifically, I sought to understand whether logging practices were altering the nutritional quality of plants foraged by moose and whether potential nutritional limitation as a result of logging potentially was affecting moose condition and reproduction. This led me to measure and compare the key nutritional constituents of forage species growing in cutblocks, cutblock edges, and unlogged forests. I then calculated daily digestible protein and energy requirements for lactating adult female moose in summer and determined whether forages provided sufficient nutritional value to support healthy moose. I also tracked early winter body fat, pregnancy, and calf survival of a cohort of adult female moose, assessed whether individuals were nutritionally limited, and determined whether individual use of human disturbance (i.e., logging cutblocks) and natural disturbance (i.e., wildfire) on the landscape impacted their condition and reproduction.

My research produced several key findings: Firstly, I found that most forages provided sufficient digestible energy to support healthy moose, but did not provide sufficient digestible protein, regardless of whether they were from cutblocks, edges, or forests. The four forage species I sampled were generally of poorer nutritional quality in cutblocks than in forests, though this was not the case for all plant species. Despite these differences in plant nutritional quality between cutblocks and forests, I did not find a link between use of cutblocks and condition or reproduction. I did, however, find a positive but weak correlation between use of recently burned habitats and calf survival.

Secondly, all moose (except one individual in one year) had body fat levels indicative of mild to moderate nutritional limitation according to one set of standards (Cook et al. 2021), and two individuals died of apparent starvation. However, pregnancy rates and calf survival rates were high enough within my cohort of study animals to support a stable to growing population, though my sample size was modest, and a more extensive study would be valuable for drawing definitive population-level inferences.

Finally, this study was conducted over the course of two years with differing weather conditions: in 2021 spring and early summer conditions were unusually hot and dry, while in 2022 conditions did not become hotter than average until midsummer. Concurrently, forage nutritional quality varied significantly year to year, with plants being of poorer nutritional quality during the hot and dry growing season of 2021. I also found significant differences in moose body condition between study years: all moose had less body fat in 2021 than in 2022, likely due to a combination of reduced forage quality and increased thermal stress in 2021.

Conclusions

My findings indicated that the digestible protein content of forages was insufficient to support healthy moose and was lower in cutblocks than forests. While some individuals seemed to be nutritionally limited, most individuals successfully reproduced, and early winter calf survival was sufficient to support population growth. Therefore, I conclude that nutritional limitation is not a principal driver in this population's recent decline, though it may be acting in an additive or synergistic manner with other stressors such as unlicensed harvest and thermal stress due to climate change in a landscape heavily disturbed by forestry and wildfire. Ultimately, continued monitoring and investigation will be required to fully understand the drivers of recent and pervasive moose population declines.

Management Recommendations

The principal management recommendations stemming from my findings are:

1) Retaining unlogged forest habitats within managed forests is important for providing higher-quality forage for moose, particularly as quality declines over the summer.
2) Planning cutblocks to maximize edge habitat also will maximize forage quality in an ecotone preferred by moose (Hjeljord et al. 1990).

3) Forecasted increases in wildfire occurrence in interior BC (Haughian et al. 2012) may be favorable for moose populations. Allowing wildfire to maintain a dynamic forest landscape may benefit moose. This approach is used by wildlife managers in North America (Boucher 2003, DuBois 2008, Goddard 2011) and Scandinavia (Fredriksson et al. 2023).

4) The sole index relating moose body fat to nutritional limitation does not seem to apply to moose in this study or to other moose populations in BC (C. Procter, personal communication, August 2023). Moose researchers and managers in BC would benefit from an index developed specifically for Northwestern moose in BC. The index should demonstrate a clear link between nutritional limitation and depressed reproductive rates (e.g., pregnancy, parturition, twinning, calf survival).

5) Wildlife managers in Region 3 would benefit from continued study of this population along with a parallel study of an adjacent management area with a stable or increasing population. The focus should be on understanding whether declining numbers are due to adult female mortality or calf recruitment, effects of nutritional limitation on parturition, twinning, and calf survival, and consideration of other potential drivers of population decline such as unregulated human harvest and climate change.

Suggestions for Future Research

This research focused on four principal forage species preferred by moose. Further research on a larger suite of species would be costly but advantageous, as moose consume a variety of plants and adapt their selection based on the nutritional composition of available plants (Felton et al. 2016, 2021, Spitzer et al. 2023). Additionally, examination of a larger suite of nutritional and antinutritional constituents may reveal other nutritional limitations.

I found digestible protein to be limiting in most samples, and this may be exacerbated if rising temperatures and increasingly dry conditions further decrease plant nutritional quality and/or moose forage intake (Shively et al. 2019). With climate change, years where moose experience challenging thermal and nutritional conditions will become increasingly frequent. More research is required to fully understand the implications of climate change on moose nutrition and foraging.

In this study I used percent ingesta-free body fat as the metric of body condition. While this is a standard metric for assessing overall ungulate condition, fat is the body's energy reserve, while protein is converted to muscle mass (Stephenson et al. 2002). Given that I identified potential protein limitation in forages, that protein reserves are critical for pregnancy and lactation (Allaye-Chan 1991; Tobit et al. 1985), and that moose increasingly catabolize protein when their fat reserves are low (Torbit et al. 1985), future studies should measure loin muscle thickness via ultrasonography as an additional assessment of condition (e.g., Cook et al. 2021). These data may help further elucidate the link between body condition and protein limitation in moose. Indeed, connecting moose body fat to reproductive performance was difficult. I found evidence of nutritional limitation in some individuals, but pregnancy and early winter calf survival rates were not unequivocally indicative of a nutritionally limited population. Further research into other productivity parameters that may be more tightly linked to maternal nutritional condition is required, including studies focusing on parturition, twinning, and calf cause-specific mortality. As well, due to small sample size, my findings on condition, pregnancy, and calf survival should be regarded as preliminary findings. These findings clearly indicate some effects of nutritional limitation, but a larger sample size is required to quantify these effects at the population level.

Lack of clear evidence that maternal nutritional condition reduced productivity leads me to believe that nutritional limitation is not the principal contributing factor in this population's decline. However, sub-optimal nutrition may amplify the detrimental impacts of other potential stressors, including human harvest and climate change. Research into unregulated harvest of adult female moose would elucidate whether population declines are due to decreasing numbers of adult females. Research into the effects of climate change on moose would allow us to understand the extent to which concurrent reductions in forage quality and increases in thermoregulatory stress due to increasingly hot and dry weather conditions are affecting moose.

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APPENDIX A

Information and calculations required to calculate the daily nutritional requirements of adult female Northwestern moose raising a singleton calf in summer.

1. Assume the parturition date. The mean date of parturition for moose in central interior British Columbia is May 21st (Procter et al. 2020). Therefore, this date was used in the calculations**.**

2. Calculate the daily metabolic body weight (MBW) of an adult female Northwestern moose throughout the summer.

a. The average weight of Northwestern cow moose at the onset of lactation is 344 ± 29 kg (Reese & Robbins 1994). Assume the moose are this weight on the date of parturition determined in Step 1.

b. After 4 months, the moose studied by Reese & Robbins (1994) weighed 368 ± 19 kg, meaning that they gained 0.2 kg per day. Add 0.2 kg to the moose mass each day.

c. Calculate the daily metabolic body weight (MBW) of the moose in kg by raising the daily mass in (2b) to the 0.75 power.

3. Calculate the daily dry matter intake (DMI, in g/day) for an adult female Northwestern moose raising a singleton calf.

a) The DMI of two free-ranging Northwestern moose without calves (in g DM/kg MBW) are reported in Figure 1 of Renecker & Hudson (1985). The figure showed DMI values of ~90−110 g/kg MBW/day in late May, ~125−135 g/kg MBW/day in July, and ~75−80 g/kg MBW in October (exact dates not reported). Therefore, values were assumed to be 100 g/kg MBW/day on May 25th, 130 g/kg MBW/day on July 15, and 77.5 g/kg MBW on October 15th, and were assumed to increase/decrease linearly between reported values. Shively et al. (2019)

reported higher spring DMI rates from a larger sample of Alaskan moose. However, the values from Renecker & Hudson (1985) were used in the calculations as Northwestern moose were studied here.

b) Based on an unpublished model by D. Spalinger (provided by L. Shipley), females with singleton calves increase their DMI by 10% over the DMI of an unreproductive female. Moose with twins increase their DMI by 20%. Increase the DMI from (3a) by 10% by dividing by 0.9.

c) Calculate the daily DMI in g/day by multiplying the daily DMI in g/kg MBW (3b) with the MBW (2c).

Calculation of the daily digestible protein requirement of an adult female Northwestern moose raising a singleton calf in the summer:

5. Calculate the daily digestible protein required for milk production for a singleton calf.

a) The daily milk intake of a singleton calf in g/day wet weight is reported in Figure 1 of Reese & Robbins (1994). Based on Figure 1, the following values were used: 3100 g/day at 7 days post-partum, 3900g/day at 17 days, 4760 g/day at 23 days, 4700 g/day at 30 days, 4600 g/day at 40 days, 3250 g/day at 58 days, 2100 g/day at 78 days, 2700 g/day at 98 days, and 1600 g/day at 122 days post-partum. Extrapolate linearly between reported values.

b) The protein in milk (in g/100g) is reported in Figure 2 of Reese & Robbins (1994). Based on Figure 2, the following values were used: 7.9 g/100 g at 5 days post-partum, 7.10 at 10 and 20 days, 7.2 at 25 days, 7.4 at 35 days, 7.5 at 42 days, 7.8 at 50 days, 9.0 at 62 days, 9.1 at 72 days, 8.75 at 82 days, 9.75 at 95 days, and 11.9 g/100 g from 105 days post-partum onward. Extrapolate linearly between reported values.

c) Calculate the daily protein requirement for lactation by multiplying (5a) and (5b).

d) Assume that there is 80% efficiency metabolizing protein from food (Robbins 1983) by dividing (5c) by 0.8.

6. Calculate the daily digestible protein requirement for the adult female to gain 0.2 kg of weight per day.

a) Convert kg to g, assuming that 20% of moose body weight is protein (Robbins 1973) by multiplying by 0.2, and assuming an 80% protein metabolism efficiency (Robbins 1983) by dividing by 0.8.

7. Calculate the daily protein requirement for maintenance.

a) The daily urinary nitrogen (N) excretion in g N/day is reported in Schwartz et al. (1987) as 0.561 g N/kg MBW + 0.056. Calculate the daily urinary N excretion by including the daily MBW calculated in (2c).
b) Convert N to protein by multiplying (7a) by 6.25.
c) The daily excretion of metabolic fecal N (in g N/day) is reported in Schwartz et al. (1987) as 0.458g N/100 g DM. Calculate the daily excretion of metabolic fecal N by multiplying it with the daily DMI in (3c), making sure to convert (3c) from g/day to 100g/day first.
d) Convert N to protein by multiplying (4c) by 6.25.
e) Sum (7b) and (7d) to calculate the total protein cost of maintenance.

8. Calculate the total daily digestible protein requirement by summing the daily requirements for lactation (5d) weight gain (6d) and maintenance (7e).

9. Multiply the daily digestible protein requirement (8) by the daily DMI (3c) to calculate the required digestible protein content of the forages in g/100 g DM.

Calculation of the daily digestible energy requirement of an adult female Northwestern moose raising a singleton calf in the summer:

10. Calculate the daily digestible energy required for milk production for a singleton calf.

a) The daily milk intake of a singleton calf in g/day is reported in Figure 1 of Reese & Robbins (1994). See (5a) for details.

b) The energy in milk in kcal/g is reported in Figure 2 of Reese & Robbins (1994). Based on Figure 2, the following values were used: 1.6 kcal/g at 5 days post-partum, 1.33 at 10 days, 1.30 at 20 days, 1.28 at 25 days, 1.42 at 35 days, 1.34 at 42 days and 50 days, 1.60 at 62 days, 1.45 at 72 days, 1.58 at 82 and 95 days, 1.80 at 105 days, 2.05 at 115 days, and 2.08 kcal/g at 125 days post-partum. Extrapolate linearly between reported values.

c) Calculate the daily energy requirement for lactation by multiplying (10a) and (10b).

d) Assume that there is 70% efficiency converting metabolizable energy to gross milk energy (Blaxter 1962, Reid 1968) by dividing (1c) by 0.7.

e) Assume there is 88.5% efficiency converting digestible energy to metabolizable energy (Schwartz et al. 1988) by dividing (1d) by 0.885.

11. Calculate the daily digestible energy requirement for adult female maintenance and weight gain.

a) The digestible energy intake required to sustain a weight change of 0.2 kg/day is 172.7 kcal/kg MBW/day, as calculated using the equation $Y = -1.230 + 0.00828X$ developed by Schwartz et al. (1988) to express the relationship between daily digestible energy intake and weight change for 9 Alaskan moose between November and April. Calculate the daily digestible energy intake by multiplying 172.7 kcal/kg MBW by the MBW in (2c).

12. Calculate the total daily digestible energy requirement by summing the daily digestible energy requirements for milk production (10e) and maintenance and weight gain (11a).

13. Multiply the daily digestible energy requirement (12) by the daily DMI (3c) to calculate the required digestible energy content of the forages in kcal/g DM.

14. Convert the requirement to kJ/g DM by multiplying (13) by 4.184.

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