

**FORAGING FOR ELEMENTS: MAMMALIAN RESPONSES TO PLANT
STOICHIOMETRY ACROSS SCALES**

By

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ABSTRACT

Energetic demands, nutritional needs, and the scale of foraging collectively influence terrestrial herbivore feeding decisions to meet nitrogen (N) intake requirements. I measured moose (*Alces alces*) selection for distributions of browse N content and biomass at three scales. Additionally, I measured snowshoe hare (*Lepus americanus*) preference for browse N content under varying energetic and nutritional demands using cafeteria experiments. I predicted that both herbivores would select for N content; this selection would be stronger for moose at smaller scales and for hares under greater nutritional demands and weaker for moose at larger scales and for hares under greater energetic demands. Moose responses did not support my scalar predictions, but I uncovered individual-level selection trade-offs. The hare experiments supported my energetic and nutritional demand predictions. Collectively, nutrient availability within terrestrial systems may influence herbivore movement and behaviours, although individuals remain flexible in how they respond to and attain limiting nutrients.

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LIST OF ABBREVIATIONS AND SYMBOLS

Δ AIC – Change in Akiake's Information Criteria

AFL – Agriculture Food Lab

AIC – Akiake Information Criteria

C – Carbon

DBH – Diameter breast height

iSSA – integrated step selection analysis

MCP – Minimum convex polygon

N – Nitrogen

OMP – Old Man's Pond study area

P – Phosphorus

PP – Plum Point study area

PSC – Plant secondary compound

PSM – Plant secondary metabolite

RSA – Resource selection analysis

RSF – Resource selection function

StDM – Stoichiometric distribution model

CHAPTER 1: GENERAL INTRODUCTION

1.1 Herbivory from the elemental perspective

Herbivores are specialised to fuel reproduction and growth with primary producers, converting and assimilating the carbon-heavy (C) food source into their more nitrogenous (N) and phosphorous (P) tissues (Figure 1.1; Elser et al. 2000; Boersma et al. 2008; Rizzuto et al. 2019). To do so, herbivores have digestive adaptations: large flat teeth, rumens, enlarged cecums, and elongated intestines (Barboza et al. 2009). Additionally, they display complex behavioural adaptations and must, with some flexibility, consume large quantities of the mismatched food (Fagan et al. 2002; Sterner and Elser 2002; Parker et al. 2009) while selecting for food of higher N and P compositions, i.e. quality (Figure 1.1; Ball et al. 2000; Schatz and McCauley 2007; Nie et al. 2015). Herbivore food intake represents the removal of plant biomass and thus availability of leaf litter (Hawlena et al. 2012), as well as the productivity of herbivore populations (DeMott et al. 1998; McArt et al. 2009; Felton et al. 2018) and thus resources for predators. Therefore, the flexibility of intake and food choices by herbivores is an ‘ecologically relevant trait’ (Hawlena and Schmitz 2010) that influences productivity at all trophic levels (Schmitz et al. 2018).

1.2 Herbivore feeding preferences

Plants are abundant in most terrestrial ecosystems, but vary in terms of quality at many levels of biological organization; herbivores respond to this variation. For example, seasonally-driven temporal variation in forage quality across landscapes or regions

predicts large herbivore migrations (Hebblewhite et al. 2008). Within an individual plant, herbivores may select certain plant organs and reject others (Bryant and Kuropat 1980). Generalist browsers often prefer some species over others (Rodgers and Sinclair 1997), and within a species, may select for individuals on the basis of age class (Bryant et al. 1985) or even genotype (Laitinen et al. 2002). Studies most often test foraging hypotheses by measuring herbivore feeding across plant species. Less is known regarding how quality variation within a plant species may affect herbivore fitness or forage choice.

In systems with constant external influences such as predation risk, herbivore foraging choices are primarily driven by forage properties. While feeding preferences by herbivores can be explained by various plant chemical components including plant secondary compounds (PSCs; Bryant et al. 1985; Schmitz et al. 1992), fibre (Hodges and Sinclair 2003), sodium (Worker et al. 2015), calcium (Nie et al. 2015), and protein content (a correlate to N; Felton et al. 2009), ecosystems are often N and P-limited (White 1993; Elser et al. 2000) and herbivores are generally found to select for N and P. For example, *Daphnia pulex* forage more in areas with algae of higher P composition (Schatz and McCauley 2007) and N fertilization of forest increases usage by moose (*Alces alces*) and snowshoe hare (*Lepus americanus*; Ball et al. 2000). In fact, terrestrial herbivores are thought to be N-limited along with their ecosystems, and show higher fitness in areas with greater N-availability (e.g. McArt et al. 2009). Measuring herbivore responses to plant elemental compositions, like N and P, quantifies the ecologically relevant trait of feeding choice. Elements are common across trophic levels and between the abiotic-biotic divide (Sturner and Elser 2002). If mammalian herbivores show

interspecific selection on the basis of N and P and intraspecific selection for plants of N and P treatments (e.g. Schmitz et al. 1992), then they should favour, within a single species, those of naturally higher N and P content.

1.3 A consideration for scale

Herbivores make feeding decisions according to the scale of forage selection. Starting at the first order of selection, a species' geographic range, resource selection by individuals refines to the home range level, or second order selection, and within-home range level, or third order selection (Johnson 1980). Herbivores continue to make choices between patches and bites of forage (Bailey et al. 1996). At the finer scales of foraging, a herbivore makes more frequent choices dependent on the information available at the given scale (Senft et al. 1987; Rettie and Messier 2000). It is therefore assumed, that coarser factors that mainly influence forage biomass impact selection at larger scales while finer factors that pertain to forage quality affect selection at smaller extents (Senft et al. 1987; Bailey et al. 1996; van Beest et al. 2010). For example, Wilmshurst et al. (1999) found that wildebeest large-scale movements correspond with an energy-maximizing strategy based on grass height, but at the smaller extent, wildebeest selected areas based on grass greenness and not height. As a result, predictions of herbivore feeding choices must be scale specific, and foraging patterns of a species should be measured at multiple scales. If elemental measures of forage are to aid nutritional ecology and foraging theory, they should have some predictive power at multiple scales.

1.4 A consideration for physiological influences

Within a scale of foraging, herbivores individuals vary in feeding choices as a reflection of physiological processes, needs, and limitations. Most notably, conspecifics can differ in metabolic rate due to their external environment, life stage, season, and body condition (Kooijman 2009). Metabolisms increase in endotherms experiencing temperatures outside their thermal neutral zone (Chappel and Hudson 1978; Sheriff et al. 2009), reproducing mammalian females (Speakman and McQueenie 1996), and animals with larger body masses (Peck et al. 2005; Speakman 2005). As animals feed to maintain bodily functions and production, their feeding behaviours should reflect their energetic demands (Hillebrand et al. 2009; Sperfeld et al. 2017). For example, lactating mice (*Mus musculus*) show 311% higher feeding rates than non-reproducing female mice (Speakman and McQueenie 1996). We should expect that herbivores become less preferential towards plant qualities when feeding under heightened energetic demands because of increased intake requirements limit the herbivore in how selective they can be (Barboza et al. 2009). Increased cortisol production from stress may also increase metabolic rates of animals (DuRant et al. 2007). Predation-induced stress, with metabolic rate the mechanism, is hypothesized to cause an increase in selection for energy-dense, digestible carbohydrates or C by herbivores (D. Hawlena and Schmitz 2010).

Foragers must maintain the intake of various plant components or currencies when feeding (Felton et al. 2018) and if a herbivore experiences a deficit of a particular currency, it should modify its feeding choices to increase the intake of such currency (Barboza et al. 2009; Hillebrand et al. 2009; Wagner et al. 2013). Individuals of one

region or locality can be limited in a given dietary compound more than conspecifics of another location. For example, McArt et al. (2009) found that two regions of Alaska, USA had a 23% difference in available protein for moose and modelled that moose from the region of higher protein availability gained more lean mass over the growing season. System nutrient and mineral availability likely influences the feeding decisions of herbivores (Wagner et al. 2013). Conspecifics likely interact with their plant communities differently based on energetic and dietary demands.

1.5 The boreal system

The boreal system is ideal for testing hypotheses of herbivore intraspecific feeding choices under scalar, energetic, and nutritional constraints using resource elemental measures (C, N, P). The boreal forest has a short growing season, long winters, and low nutrient availability. As the planet's largest terrestrial biome, the boreal covers 11% of Earth's terrestrial surface (Bonan and Shugart 1989) and is responsible for 22% of global forest carbon sinks (Pan et al. 2011). The low ambient temperatures, soil temperatures, and solar angles cause low plant growth rates. Few plant species, particularly trees, can prosper under the restricted growing conditions and low nutrient availability of the boreal, causing low plant diversity (Bonan and Shugart 1989) and likely more intraspecific choice by herbivores.

Herbivores, like the moose and snowshoe hare, respond to the low food quality by selecting plant species, individuals, or patches with higher protein or N concentrations (Ball et al. 2000; Seccombe-Hett and Turkington 2008; Wam et al. 2018). Indeed, N and

protein have been hypothesized to be primary limiting agents for both moose and snowshoe hares (Sinclair and Smith 1984; Schwarts et al. 1987; McArt et al. 2009), and these two species have been subject to many foraging studies or models (Sinclair et al. 1982; Moen et al. 1997; Rodgers and Sinclair 1997). Unlike many boreal herbivores, moose and snowshoe hares do not hibernate during the cold winters to endure the food shortages (Humphries et al. 2017) and summertime foraging must balance the loss of body condition during winter (Whittaker and Thomas 1982; Moen et al. 1997); Moose must maintain high feeding intake rates (Belovsky 1984; Schwarts et al. 1987), which can cause areas of high moose density to become over-browsed (McInnes et al. 1992; Ellis and Leroux 2017). Snowshoe hares have high and variable metabolisms (Sheriff et al. 2009) and carry only a few days' worth of fat and protein reserves, requiring them to make frequent feeding decisions to sustain a body homeostasis (Whittaker and Thomas 1982). Snowshoe hares, like moose, can reduce plant density via foraging but for smaller understory plants or seedlings (Olson and Kielland 2016). The moose and snowshoe hare, who remove plant biomass at different rates are both constrained by food quantity and quality, but moose are particularly limited by intake rate and hares by food composition (Figure 1.1).

1.6 Thesis Overview

In this thesis I test if moose and snowshoe hares exhibit intraspecific selection for forage elemental measures at four different scales. At the landscape, home range, and patch extents, I measure moose selection for white birch (*Betula papyrifera*) quantity C (g/m²), to proxy biomass, and nitrogen composition (%), to proxy quality, achieved using

moose collar data and stoichiometric distribution models (StDMs) which predict plant stoichiometry from remotely sensed landscape variables (Leroux et al. 2017).

Specifically, using moose, I test the hypothesis that large herbivore selection for forage quantity should decrease and selection for forage quality should increase as the scale of foraging refines. At the bite-level, using snowshoe hare cafeteria experiments, I measure snowshoe hare consumption between two offerings of black spruce (*Picea mariana*) of differing N and P compositions. The spruce offerings were from the snowshoe hare trapping grid used to capture study individuals. Here, I also account for traits known to affect the energetic and nutritional demands of mammals. I test the hypotheses that individuals under high energetic demands should be less preferential to forage N and P, while those under higher N and P demands should be more selective for forage N and P. My thesis tests scalar, nutritional, and energetic effects on herbivore diet choice, using the unifying currency of elements, bridging nutritional ecology, or animal behavioural and physiological responses to ecosystem-level processes, and ecological stoichiometry, or the internal regulation by organisms to maintain stoichiometric.

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Figure 1.1. A snowshoe hare (A) and a moose (B) foraging in the boreal forest. Here, as the snowshoe hare, whose body is approximately 11.2% nitrogen (i.e. N; Rizzuto et al. 2019), chooses its bite, it selects the browse of higher nitrogen (N) composition. The moose chooses to forage in a patch with browse of relatively high nitrogen composition, and its feeding decisions balance the carbon and nitrogen losses from protein synthesis, respiration, and excretion.

1.8 Co-authorship statement

Chapter 2 and Chapter 3 of this thesis were co-authored with Shawn J. Leroux, Yolanda F. Wiersma, Travis R. Heckford, Matteo Rizzuto, Isabella C. Richmond, and Eric Vander Wal. I lead the study designs, data analyses, and writing for all chapters in this thesis. S.J. Leroux, Y.F. Wiersma, and E. Vander Wal contributed the data for Chapter 2 and provided guidance for all stages of the thesis. T. Heckford and I.C. Richmond assisted with data collection for Chapter 3. T. Heckford, M. Rizzuto, and I.C. Richmond gave critical feedback on the design, interpretation, and writing for both chapters. Chapter 2 has been submitted for review at *Journal of Animal Ecology* and is formatted for the journal. Chapter 3 will be submitted for review (target journal unknown) upon thesis completion.

CHAPTER 2: QUANTITY-QUALITY TRADE-OFFS REVEALED USING A MULTISCALE TEST FOR HERBIVORE RESOURCE SELECTION ON ELEMENTAL LANDSCAPES

2.1 Abstract:

Herbivores consider the variation of forage qualities (nutritional content and digestibility) as well as quantities (biomass) when foraging. Such selection patterns may change based on the scale of foraging, particularly in the case of ungulates that forage at many scales. To test selection for quality and quantity in free-ranging herbivores across scales, however, we must first develop landscape-wide quantitative estimates of both forage quantity and quality. Stoichiometric distribution models (StDMs) provide an opportunity to address scalar hypotheses because they predict the elemental measures and stoichiometry of resources at landscape extents. Here, we use StDMs to predict elemental measures of understory white birch quality (% nitrogen) and quantity (g carbon/m²) across two boreal landscapes. We analysed GPS collared moose (n = 14) selection for forage quantity and quality at the landscape, home range, and patch extents using both individual and pooled resource selection analyses. Based on existing literature, we predicted that as the spatial extent of foraging decreased from the landscape to the patch, selection for white birch quantity would decrease and selection for quality would increase. Counter to our prediction, pooled-models showed selection for our estimates of quantity and quality to be neutral with low explanatory power and no scalar trends. At the individual-level, however, we found evidence for quality and quantity trade-offs, most notably at the home range scale where resource selection models explain the largest

amount of variation in selection. Furthermore, individuals did not follow the same trade-off tactic, with some preferring forage quantity over quality and vice-versa. Such individual trade-offs show that moose may be flexible in attaining a limiting nutrient. Furthermore, our findings suggest that herbivores may respond to forage elemental compositions and quantities, giving tools like StDMs merit towards animal ecology applications. The integration of StDMs and animal movement data represents a promising avenue for progress in the field of zoogeochemistry.

2.2 Introduction

Finite energy and material within ecosystems forces constraints upon all trophic levels. Heterotrophs are left to optimize their energy intake with strategic foraging and evolved digestive tracts (Werner and Hall 1974; Pyke, Pulliam, & Charnov, 1977). For herbivores, digestion of plant material proves challenging because, while producers consist mostly of carbon-based compounds, consumers consist of proportionally more nitrogenous and phosphorous compounds. Thus, primary consumers must eat relatively large amounts of producer matter to meet their body composition requirements (Barboza, Parker, & Hume, 2009; Fagan et al., 2002; Sterner & Elser, 2002). Additionally, access to plant matter of higher digestibility and assimilation efficiency can contribute to higher animal growth rates, survival, and reproductive outputs (McArt et al., 2009; Parker, Barboza, & Gillingham, 2009; Wam, Felton, Stolter, Nybakken, & Hjeljord, 2018). As a result, herbivores have evolved strategies to forage based on both plant qualities (i.e., digestive efficiency or palatability) and quantities (i.e., biomass or abundance; Parker et al. 2009). However, growing conditions can influence the fine-scaled, nutritional compositions of plants, limiting our ability to measure and map plant quality across landscapes. Large herbivores forage at multiple spatial scales, from the landscape to the bite-level (Johnson, 1980; Senft et al., 1987), and likely respond differently to plant quantities and/or qualities across scales, collectively influencing their ecosystem effects (Estes et al., 2011; Schmitz et al., 2018).

Herbivores display foraging tactics that consider plant qualities along with quantities because both can be limited, but the strategy for food acquisition may depend

on the scale of foraging (Cruz-rivera & Hay, 2000; Hebblewhite, Merrill, & McDermid, 2008; Van der Wal et al., 2000; Wilmshurst, Fryxell, Farm, Sinclair, & Henschel, 1999). In terrestrial landscapes, plant biomasses and nutritional contents may depend on environmental factors such as habitat type (Sardans, Rivas-Ubach, & Peñuelas, 2011), soil nutrients (Fan et al., 2015; Sardans et al., 2011), elevation (Yang, Huang, Zhang, & Cornelissen, 2015), or slope (Leroux et al., 2017), creating a heterogeneous distribution of plant quantities and qualities. When the two forage properties do not positively correlate across a landscape, herbivores should adopt one of multiple strategies: either balancing selection between quantity and quality; or selecting one over the other. An individual's tactic for quantity and quality selection is likely to depend on scale because information available for decision-making increases in resolution with reducing scales of foraging (Rettie & Messier, 2000; Senft et al., 1987). The scalar hypothesis predicts that coarser factors influence larger scaled foraging decisions, and such factors are often those that affect forage quantities, such as climate, water bodies, and plant biomass (Bailey et al., 1996; Wilmshurst et al., 1999). Additionally, finer factors that influence smaller scaled foraging decisions, e.g., patch use or bite choice, are often quality-related indicators, like plant morphology, palatability, nutrient content, and secondary compounds (Bailey et al., 1996; Senft et al., 1987; Verheyden-Tixier et al., 2008; Wilmshurst et al., 1999). Thus, herbivores are likely to show selection for plant quantities at the larger scales of foraging, and are more likely to exhibit selection for plant quality as the scale of foraging reduces (van Beest, Mysterud, Loe, & Milner, 2010).

Testing selection for plant qualities across multiple scales of foraging remains challenging in many systems because measuring plant quality at larger spatial extents may not always be feasible. Plant biomass has been estimated or measured across larger spatial extents in various ecosystems (Fortin, Fryxell, O’Brodovich, & Frandsen, 2003; Lone et al., 2014), often for forestry purposes (Foroughbakhch, Reyes, Alvarado-Vázquez, Hernández-Piñero, & Rocha-Estrada, 2005). Unlike measures of quantity, which use units of mass or abundance, measures of quality are less comparable because they use contents or concentrations of different internal components such as energy (Fryxell, 1991), protein (Felton et al., 2009), fertilization (Ball, Danell, & Sunesson, 2000; Nie et al., 2015), lignin (Fahey & Hussein, 1999), or secondary compounds (Behmer, Simpson, & Raubenheimer, 2009). Meanwhile, Weisberg and Bugmann (2003) highlight the need for an “accurate database of the spatial heterogeneity of available forage of varying quality, over the same fine scales as are modeled” (p. 4) as a way to measure quality in the context of foraging strategies for ungulates. However, due to landscape data limitations, studies remotely measuring ungulate responses to spatial distributions of forage usually default to plant species categorizations as estimates of forage quality and subsequently disregard intraspecific variation in quality (for example van Beest et al. 2010). While using browse species is not an incorrect way to capture quality variation, it limits which foraging scales a study can investigate, findings may not be comparable across systems, and model responses to categorical variables cannot be directly compared to those of continuous variables.

Plant elemental compositions offer the opportunity to describe both interspecific and intraspecific variation of forage quality in a continuous manner. Plant nitrogen content is a common elemental measure to correlate with forage quality because nitrogen is a limited nutrient in terrestrial ecosystems, required for protein synthesis, and needed in higher proportion by animals relative to plants (Fagan et al. 2002; Sterner and Elser 2002). Elements are a base unit for all living organisms, and heterotrophs rearrange element components they consume into compounds they require. Thus, the direct nutritional driver behind foraging may best be observed by measuring selection for nitrogen content rather than composite currencies or nutritional compounds (Felton, Wam, Stolter, Mathisen, & Wallgren, 2018). However, studies which measure herbivore responses to plant nitrogen contents often do so with small-bodied herbivores (Schatz & McCauley, 2007), use smaller scales of observation (Nie et al., 2015), or are otherwise restricted to experimental conditions (Ball et al. 2000; but see Moore et al. 2010, Champagne et al. 2018). Certain technological developments, such as high-resolution airborne imaging spectroscopy, have made landscape-wide mapping of nitrogen content possible, but only in ecosystems where the forage is aerially visible (Schweiger et al. 2015). Recently developed methods, termed Stoichiometric Distribution Models (StDMs; sensu Leroux et al. 2017) present a solution by modeling understory plant elemental quantities and compositions across landscapes, allowing for variation in both forage quantities and qualities to be predicted across landscapes.

Here, we used StDMs to investigate selection strategies of forage quantity and quality, across multiple spatial extents for a large, wide-ranging, understory browsing

mammal. We studied a moose (*Alces alces*) - white birch (*Betula papyrifera*) system on the island of Newfoundland, Canada, and measured individual moose resource selection in relation to understory white birch availability at the landscape, home range, and patch-scales. Our landscape-wide estimates of available forage for white birch quantities and qualities derive from the continuous elemental predictions of the StDMs. Our objective was not to create highly predictive, cross-season moose resource selection models, but to test the relationship between moose habitat selection patterns and distributions of browse in terms of browse elemental predictors for quantity and quality across multiple foraging scales. To do so, we measured moose resource selection during the short temporal window of the early growing season in Newfoundland as this was the temporal window of the StDM predictions. We predicted that if moose show selection for white birch quantity and quality, their selection for quantity would be highest at the landscape extent and decrease when refined to home range and then patch extents, while the reverse would be true for white birch quality selection (van Beest et al., 2010). We also predicted that quantity-quality trade-offs may occur, but the direction of such trade-offs would depend on the scale of foraging; at no scale should there be negative selection for both plant quantity and quality (Figure 2.1). Collectively, this study represents an opportunity to test the foraging strategies of an ungulate species under non-experimental conditions by linking the biogeochemical landscape to herbivore movements.

2.3 Methods

2.3.1 Study Region and Moose Collaring

This study took place on the northern peninsula of the island of Newfoundland, Canada (Figure 2.2). Dominant tree species of this region include black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch, which is the primary forage for moose during the early summer months (Dodds, 1960). We collared 14 adult moose (male = 4; female = 10) in this region between 2011 and 2015 with GPS collars set to take locations every two hours. Each individual was collared for the duration of one year (2011 n=5; 2013 n=1; 2014 n=5; 2015 n=3; Table A1). The 14 moose collars were deployed in two areas approximately 300 km apart within the island of Newfoundland: Plum Point study area (PP; n = 7) and Old Man's Pond (OMP; n = 7; Figure 2.2). Three additional moose were collared in a third study area (Leroux et al., 2017), but we did not use these data because there were too few moose individuals to test our predictions. The boundaries of each study area were delineated using minimum convex polygons (MCPs) at 95% around all of their respective moose fixed locations. MCPs returned total areas of 514 km² and 393 km² for the PP and OMP study areas respectively (Figure 2.2).

2.3.2 Forage quantity and quality measures

We used spatial predictions from StDMs (i.e., Stoichiometric Distribution Models), a method for predicting resource elemental compositions and quantities across a landscape, to represent forage resources in this study (Leroux et al., 2017). We clipped white birch leaves from the browsing heights (0.3-2.0 m) of 1-6 individuals at 10 m radius plots (n = 106) across the Plum Point study area. Sampling was constrained to a

small temporal window (June 30 and July 7 2015) representing green-up time to minimize temporal variation in foliar elemental composition due to senescence. At each plot, we measured densities of three size classes of white birch by height (0.3-0.5 m; 0.51-1 m; 1.01-2 m). We estimated biomass for each age class by measuring standing stocks (all leaves between heights 0.3- 2.0 m) from a sample of trees and then used these estimates to calculate total white birch biomass for each plot (Leroux et al., 2017). Ground-collected samples were then sent to the Agriculture and Food Laboratory at University of Guelph (Guelph, Ontario, Canada) and analysed for carbon, nitrogen, and phosphorus compositions (%). Using the biomass estimates and measured elemental compositions, we calculated elemental quantities (g/m^2) for each plot. Lastly, the carbon, nitrogen, and phosphorous quantities (g/m^2) and compositions (%) of newly developed understory white birch growth (June 1st - July 16th) were fit to six landscape predictors across the two study areas of our moose collar data (Leroux et al., 2017). Landscape predictors included three abiotic features- normalized aspect, slope, and elevation- and three biotic features- landcover, stand height, and dominant tree species (see Table A1 for StDM covariate details). Because our plant data derives from StDMs fit for the specific temporal window of early summer, we subset all collar data to only include fixes from that same temporal window (June 1st to July 16th). There was a mismatch of year between some individual moose GPS collar data and forage data from StDMs (1-4 years, mean = 1.93). The six-explanatory landscape variables that predicted forage elemental measures in the StDMs are fairly static in this system relative to the 4-year window of mismatch. We assume the relative StDM predictions to remain consistent within this 4-

year window (i.e., areas with high quantity of white birch in year t will also have high quantity in year $t+1$), but also assume moose response findings to be conservative given inter-annual climatic variation. Leroux et al. (2017) further explains the details of plant sampling, elemental measure calculations, and model fitting.

We used final StDM spatial predations of reasonably strong fits (R^2). To represent forage quantity, we used StDM predictive surfaces of white birch carbon quantity ($\log \text{g/m}^2$; $R^2 = 0.28$) because carbon is the most abundant element in plant matter. To estimate forage quality, we used StDM predictive surfaces of white birch nitrogen composition (%; $R^2 = 0.31$) and assume nitrogen concentration to positively correlate with browse quality (Ball et al., 2000; Mattson, Jr., 1980; McArt et al., 2009). While this method does not account for plant secondary metabolite (PSM) concentrations, moose have been found to be nitrogen-constrained (McArt et al., 2009). *Betula* species favour using carbon-based PSMs (Palo, 1984), have also been experimentally shown to be nitrogen-limited, and display most PSMs at higher concentrations under greater UV exposure rather than greater nitrogen fertilizer (Keski-Saari, Pusenius, & Julkunen-Tiitto, 2005). Since plants often acquire fibre and lose nutritional content as they gain biomass during the growing season, (Hebblewhite et al., 2008), we also tested for negative correlations (Pearson's r) between our white birch quantities and qualities which could be driven by static, landscape variation in plant age.

2.3.3 Defining the scales of foraging

To test if moose selection for quantity or quality of forage changes depending on the scale of foraging, we examined moose resource selection at the landscape, home

range, and patch extents, or second, third, and 3.5th order selection according to the Johnson (1980) framework. We used the R statistical program for all analyses (version 3.5.1; R Core Team 2018). We designated each study area, either Plum Point or Old Man's Pond, to be the 'landscape' for its moose individuals. We calculated 'home range' extents for each individual with MCPs at 95% around all GPS fixes within the time window of this study (June 1st-July 16th) using the R package "adehabitatHR" (Calenge, 2006). Lastly, we defined our highest resolution of forage landscape data, 30 m x 30 m pixels, to be 'patches', or the immediate area around a sample or GPS fix point. We did not collect plant data in waterbodies, wetlands, roads, etc. and did not use StDMs to predict forage values in these habitats (Leroux et al. 2017). Therefore, we also cleaned moose GPS data to remove points that did not have predicted StDM values, and the same was done for all additional sample points created to test resource selection at each scale. We used two types of resource selection analyses and the same predictive StDM landscape layers to test selection at all three scales (Figure 2.1; Figure A1).

2.3.4 Forage selection: landscape extent

At the landscape, our study's largest spatial extent, foraging decisions include where an animal places its home range (Boyce, 2006; Johnson, 1980). To test if home ranges differ in the availability of forage quantities and qualities compared to the landscape, we used a resource selection function (RSF), a model which compares used and available locations of an organism and can be fit with logistic regression by assuming the exponential function:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)$$

with x_j representing resource variables $j = 1, 2 \dots k$ and β_l representing model coefficients $l = 0, 1 \dots k$ (McLoughlin, Morris, Fortin, Vander Wal, & Contasti, 2010).

We defined available points to be within study areas, or ‘landscapes’ (i.e., PP and OMP), and used points to be within home ranges (Dupke et al. 2017; Figure A1). We sampled available points from study areas randomly at 22 points per km². We sampled using points from home ranges in a uniform grid at 70 points per km², using the “spsample” function in the “sp” R package (Bivand, Pebesma, & Gomez-Rubio, 2013). At each point, we extracted the values for white birch quantity carbon (log g/m²) and nitrogen composition (%) from our predictive StDM landscape layers. We employed an RSF to compare used and available moose points with explanatory variables being carbon quantity and nitrogen composition and their interaction term. The logistic regression was fit, using the “glm” function (family = binomial, link = logit) in the R statistical program for each study area and its respective seven home ranges and once with data from both study areas and all 14 home ranges.

2.3.5 Forage selection: home range extent

Our next, finer-scale of foraging was the home range. At this scale, we sought to investigate if areas used by a moose differ to the availability of forage quantities and qualities of its total home range (Johnson, 1980). To do so, we defined available points to be within home ranges, using the same method completed to sample used points in the landscape-scale analysis. We defined used points to be collar fixes (Dupke et al. 2017; Figure A1). At each point, we extracted the white birch carbon quantity and nitrogen composition measures from our predictive StDM landscape layers. We fit the RSF using

a logistic regression with the ‘glm’ function in the R statistical program for each of the 14-individual moose and once with all individual data from both study areas pooled together. Explanatory variables were carbon quantity and nitrogen composition and their interaction term, like in the landscape scale.

2.3.6 Forage selection: patch extent

The last, and most restricted extent of foraging we investigated was the patch in which foraging decisions include the animal’s choice of a patch (i.e., 30 m x 30 m pixel) over those available at the time of selection (Charnov, 1976). Here, we adopt an integrated step selection analysis (iSSA) to ask if moose select patches of certain forage quantities or qualities over others (Avgar, Potts, Lewis, & Boyce, 2016). The iSSA pairs each used location to a set number of random locations the moose could have viably visited instead based on the distributions of the individual’s total step lengths and turn angles (Avgar et al., 2016). This technique of sampling from the animal’s natural range of movement speeds, or step lengths, and trajectories, or turn angles, allows for a more precise estimation of fine scale resources available to that animal at a given location.

We performed iSSA with the ‘amt’ R package (Signer, Fieberg, & Avgar, 2019). First, we transformed the used fixes into 2-hour steps (straight line distances between consecutive locations). Prior cleaning of the data created some temporal gaps in between GPS fixes, so we eliminated any steps that had a time difference greater than two hours. A gamma distribution of step lengths (the log transformed value represents the scale parameter) and a von Mises distribution of cosine-transformed turn angles were used to describe movement behaviour (speed and directionality respectively) of individuals.

From each start point, 10 available step locations were calculated by randomly extracting step lengths and turn angles from such distributions. We then extracted the white birch carbon quantity and nitrogen composition measures from our predictive StDM landscape layers at all step end locations. Used points were paired to the generated available points in the conditional logistic regressions. Explanatory variables for the model included the quantity carbon values, nitrogen compositions, step lengths, turn angles and all combinations of interaction terms. We fit the conditional logistic regression model, using the ‘clogit’ function in the R ‘survival’ package, for each of the 14-individual moose and once with all individual data from both study areas pooled together (Therneau & Grambsch, 2000).

2.4 Results

2.4.1 Descriptive results

The mean predicted quantity carbon of white birch forage from the PP (514 km²) and OMP (393 km²) study areas were 0.23 g/m² and 0.35 g/m² respectively. The maximum quantity carbon was 4.09 g/m² in PP and 3.53 g/m² in OMP while minimum values were 0.024 g/m² for PP and 0.021 g/m² for OMP. The mean white birch nitrogen concentration in PP was 2.82% and 2.74% in OMP. Maximum nitrogen content values were 3.61% and 3.78% and minimum nitrogen contents were 1.89% and 1.59% for the PP and OMP study areas respectively. The average size of a moose individual’s home range for our study’s time frame (June 1st-July 16th) was 12.36 km² for PP individuals and 11.07 km² for OMP individuals (Table A3).

We used selection coefficients from our resource selection analyses to assess the direction and strength of moose selection for white birch quantities and qualities and pseudo R^2 to assess the strength of our selection analyses. R^2 s from the patch extent iSSAs cannot be directly compared to landscape and home range RSFs because of the different model types used (i.e. conditional logistic regression vs. logistic regression). Positive coefficients represent positive selection for the resource, negative coefficients represent avoidance of a resource, and near-zero coefficients represent neither selection for nor against a resource. Interaction coefficients represent selection trade-offs between quantity and quality with positive interactions representing a preference for forage quantity over quality and negative interactions representing the reverse. Collectively, we found differing directions and magnitudes of selection for birch quantity and quality, with models showing a wide range of explanatory powers depending on the spatial extent (landscape- home range- patch) and sample-level (individual or pooled).

2.4.2 Landscape Extent

Selection coefficients for quantity carbon were -0.02 in PP, and -1.03 in OMP. Selection coefficients for nitrogen composition were -1.00 in PP and 2.01 in OMP. Our RSFs explained 1.6% and 3.2% of the variation for PP and OMP respectively. The pooled model, using data from both study areas had virtually no explanatory power ($R^2 = 0.007$) and selection coefficients for quantity carbon and nitrogen composition were -1.66 and 1.32 respectively (Table 2.1).

2.4.3 Home Range Extent

At the home range-level is where moose individuals showed the strongest selection. Individuals showed a large range of selection for both forage properties, with carbon selection coefficients ranging from -10.8 to 17.0 and nitrogen selection coefficients ranging from -13.4 to 8.6 (Figure 2.3, Table 2.1). Up to 18% of variation was explained in individual models, but some individual models had no explanatory power (pseudo R^2 0.009-0.18; Table 2.1). No individuals negatively selected nor positively selected for both quantity carbon and nitrogen composition; highly positive selection for one component is paired with a negative selection of its counterpart and vice versa (Figure 2.4). For individual models, pseudo R^2 s did not relate to the number of available points for individual RSFs ($t = -0.77$; $p = 0.46$). The pooled-sample model shows weaker selection ($C\beta = 1.84$, $N\beta = -0.88$) and virtually no explanatory power ($R^2 = 0.006$; Table 2.1).

2.4.4 Patch Extent

Selection coefficients from the patch-scale iSSAs ranged from -5.22 to 7.77 and -6.32 to 11.87 for white birch quantity carbon and nitrogen composition respectively (Figure 2.3; Table 2.1; Coefficients for step length, turn angle, and their interactions with white birch carbon and nitrogen in Table A4). Individual models explained from zero to 3.9% of selection (pseudo R^2 ; Table 2.1). Similar to the home range-scale, most individuals did not show simultaneous negative or positive selection for both birch characteristics, but with a somewhat smaller range of coefficient values (Figure 2.4). For individual models, pseudo R^2 s did not significantly relate to the number of available

points for individual RSFs ($t = -1.95$; $p = 0.075$). The pooled-sample model shows little to no selection ($C\beta = 1.11$, $N\beta = -0.42$) and no explanatory power ($R^2 = 0.001$; Table 2.1).

2.4.5 Interaction Coefficients and Comparison of Scales

The large range of individual coefficients for both carbon and nitrogen measures create a lack of trend between scale and quantity-quality selection in the pooled models (Figure 2.3). Within a scale, individual models with the strongest selection trade-offs (interaction β -coefficient) often had higher explanatory power (Figure 2.4). Based on the interaction coefficients (positive values representing selection for quantity in avoidance of quality), trade-off tactics of individuals did not tend to change between the home range and patch extents: carbon-nitrogen interaction coefficients typically converged towards zero with only two individuals switching their trade-off strategy (Figure 2.5). We did not find repeated cases of negative correlations between predicted white birch quantity carbon and nitrogen composition from study areas and home ranges (Pearson's r ; Table A2). These home range white birch correlation values did not have any significant effect on the respective individual model interaction coefficients (linear model weighted by standard error; $t = -0.523$, $p = 0.605$).

2.5 Discussion

Herbivore foraging strategies reflect the physiological challenge of converting carbon-heavy matter into more phosphorous and nitrogenous tissues: the tendency to select for plant compositions of higher N and P or plant quantities (Nie et al., 2015). We tested

moose resource selection of forage nitrogen content and forage abundance at multiple scales using elemental measures of white birch nitrogen composition (%) and quantity carbon (log g/m²) respectively. We found support for our prediction that negative selection for both carbon quantity and nitrogen contents would not occur at any scale, but likewise found no instances of individuals selecting positively for both measures, which we predicted would occur at all scales (Figure 2.4). Unlike findings by van Beest et al. (2010), there was no distinct trend between forage selection strategy and scale (Figure 2.3). Instead we found considerable individual variation: at the home range-scale, individual moose favoured either quantity or quality at the expense of the other, with both trade-off directions expressed at similar magnitudes (Figure 2.4). Such individual variation should not be overlooked given moose have significant effects on plant biomass and productivity (Ellis & Leroux, 2017), and intraspecific diversity in functional traits can influence total ecosystem processes (Raffard, Santoul, Cucherousset, & Blanchet, 2019).

At the home range-scale, we found the strongest selection of white birch nitrogen concentration and biomass (quantity carbon), showing both negative and positive responses for either by individual moose ($R^2 < 0.18$). Consequently, we find evidence that moose display distinct quantity-quality trade-offs within their home ranges (Figure 2.4). Such trade-offs support use of birch nitrogen composition as an estimate of forage quality, as has been done in other studies (Ball et al., 2000; Schweiger et al., 2015). Naturally higher nitrogen contents in browse must increase the digestibility and nutrient acquisitions in the digestively-constrained moose (Belovsky, 1978), so as to offset their

need for prioritizing foraging in areas with high browse abundances. To confirm that trade-offs in forage selection were not due to growing trade-offs within white birch (i.e. as birch grows it becomes less nitrogenous), we tested for correlation between birch carbon quantity and nitrogen composition across each home range and study area. There were few cases of negative correlations between white birch quantity and quality within home ranges, and furthermore, any correlations between white birch StDM predictions did not influence moose selection trade-offs. Possibly, a lack of positive correlation between white birch quantities and nitrogen compositions is sufficient to limit moose and force trade-off foraging strategies. StDMs predict resource elemental compositions, not the allocations of such elements, like PSMs. While nitrogen is most commonly allocated to protein building in plants, tannins can interact with protein- limiting available nitrogen- (McArt et al., 2009), and PSM production by *Betula* can be induced by UV exposure, not necessarily nutrient availability (Keski-Saari et al., 2005). Thus, environmental driven production of PSMs in white birch could add a layer of complexity to our landscapes of quality. This could potentially explain the diversity of individual selection patterns but would require further plant sampling and landscape modelling to properly investigate.

We found no selection responses at the landscape-scale, while patch-scale models produced coefficients slightly more equivocal than the home range models. Contrary to our prediction that the landscape-scale models would result in the highest selection coefficients for birch quantity, neither white birch nitrogen contents nor carbon quantities explained moose home range placement. Other studies have found that moose display

landscape-level selection for forage quantity as predicted, but when using coarser measures of forage availability (Dussault et al., 2005; Herfindal et al., 2009). Though we predicted that nitrogen composition selection coefficients would be highest at the patch-scale, we observed similar individual selection patterns for nitrogen and quantities with less explanatory power, as for the home range models (Figure 2.4). Most individuals maintained their trade-off strategy from the home range to the patch-scale, similar to trade-offs in roe deer (*Capreolus capreolus*) found by Dupke et al. (2017), but the trade-offs become more equivocal at the patch-scale (Figure 2.5). This could imply that once a moose selects an area within a home range to forage, the differences between patches may be less important than maintaining high daily forage intake (Belovsky, 1984; Parker et al., 2009). Moose often over-browse forest habitats in Newfoundland (McLaren, Roberts, Djan-Chekar, & Lewis, 2004), reflecting their hyperabundance. Alternatively, selection may bypass our defined patch-scale, but occur within the patch. A study by Astrom, Lundberg, & Danell (1990) found moose food choice to be better explained at the tree-level than at the stand-level, and Danell, Edenius, & Lundberg (1991) found moose tree handling time to increase with tree size, suggesting tree-level foraging decisions.

Individuals varied the directionality of their quantity and quality selection, overriding any potential sample-wide trend between spatial extent and selection (Figure 2.4). Other studies have found herbivory quantity-quality trade-offs, where all individuals practice a similar trade-off tactic (Durant, Fritz, & Duncan, 2004; Van der Wal et al., 2000; Wilmschurst et al., 1999). We find a unique situation in which individuals display

opposing trade-offs, from prioritizing forage quantity over quality, to equal priority for quality over quantity, and many that select for neither. Detecting opposing strategies would not have been possible had our models not been performed at the individual-level. If moose are indeed plastic in their trade-off strategy, quantity-quality functional responses remain possible (Leclerc et al., 2016); alternatively, if moose individuals are consistent then fitness should be influenced by trade-off decisions (Parker et al., 2009; Wam et al., 2018).

Despite having only two predictor variables, we explained anywhere from 0 to 18% of the variation in individual RSFs within forested areas. Rather than use multiple acting landscape variables, such as forest type or aspect ratio, directly in RSAs to infer foraging strategies (Zweifel-Schielly, Kreuzer, Ewald, & Suter, 2009), we linked these features to plant compositions and biomass first, creating more deterministic, and nutritionally-linked resource selection analyses (RSAs; Leroux et al., 2017). Our intent was not to create highly explanatory RSAs, but rather test how moose select for two specific forage characteristics at multiple scales during a critical window of plant growth in forest patches. Unexplained variation in RSAs could have developed from differences between sexes, study areas, years (Barboza et al., 2009), the effects of carbon-based PSMs (Palo, 1984), or tannin-bound nitrogen (Keski-Saari et al., 2005). Despite these constraints, we still were able to detect moose selection for plant nitrogen and biomass, suggesting that our findings are conservative estimates. As remote sensing accuracy and precision increases globally and landscape plant biogeochemical models increase in predictive power, such RSAs should improve predictability as well. Additionally, we can

link individual, seasonal, and availability-dependent differences (Barboza et al., 2009) in selection of plant carbon and nitrogen to the carbon and nitrogen cycles. Large terrestrial animals are known to have large-scale presence-absence or density-driven effects on plant communities (Estes et al., 2011), yet they are often not incorporated into carbon cycle models (Schmitz et al. 2018). Moose browsing and effects on litter nutritional composition have been shown to negatively impact ecosystem net primary productivity (Ellis & Leroux, 2017; Schmitz et al., 2014). The individuals of this study that chose to forage in areas of higher birch carbon quantities rather than areas of higher nitrogenous birch could be the individuals which have, directly, the largest negative effect on plant productivity (Kolstad et al., 2018). We also interpret our observed trade-off as evidence that moose strive to meet certain nitrogen intake amounts either through browse amounts or nitrogen contents. Feeding trial work has estimated the daily nitrogen requirements for body maintenance in moose to be 0.627 ± 0.073 g/kg BW/day, and daily requirements are to be higher during the reproductive and growing season (Schwartz, Regelin, & Franzmann, 1987). Daily nitrogen intake not only equals the nitrogen removal from primary producers, it also positively correlates to fecal nitrogen content (Howery & Pfister, 1990), which could be integrated into nitrogen cycling models. With moose being a dominant browser across the boreal biome, their foraging behaviours can have broad implications towards boreal carbon and nitrogen cycles.

Connecting ecological theory across scales and systems has remained a problem in ecology, especially in the case of species distributions and food webs (Levin, 1992). Scale presents particular challenges for ungulate foraging, because such species react to

plant distributions from the bite-level to the regional-level, making a case for tools like StDMs that capture the heterogeneity of plant qualities across landscapes (Leroux et al., 2017; Weisberg & Bugmann, 2003). Elements remain one of the common currencies between trophic levels and systems (Sterner and Elser 2002). Therefore, studying food selection with elemental measures aligns with Levin's (1992) assertion that community ecology developments "must revolve around attempts to discover patterns that can be quantified within systems, and compared across systems" (p. 1947). Ungulates can rapidly change plant communities, nutrient cycles, and whole ecosystems through herbivory and fecal deposition (Didion, Kupferschmid, & Bugmann, 2009; Hobbs, 2018). In our study we found that some moose in a population make individually varying trade-offs between both forage quantity and quality, implying that moose are nutritionally limited but flexible in their intake tactics. With the current accessibility of remote sensing data and wildlife monitoring technology, we have the opportunity to make inferences about animal responses to fine-scaled, biogeochemical processes and link these processes to ecosystem models.

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Table 2.1. The number of Used (U) and Available (A) points and summaries (intercepts (Int.), β -coefficients, and standard errors (SE)) and evaluations (pseudo R²) for pooled and individual models measuring moose selection for white birch quantity carbon (Qty C; log g/m²) and nitrogen compositions (% N). The landscape (LN) and within-home range (HR) scales used logistic regressions and conditional logistic regressions were used for the patch (Pt) scale.

Scale	Model	U	A	Int.	Qty C		% N		Qty C x %N		R ²
					β	SE	β	SE	β	SE	
LN	Pooled	8433	20000	-4.74	-1.66	0.17	1.32	0.11	0.55	0.06	0.007
LN	PP	4084	9345	1.61	-0.02	0.26	-1	0.19	-0.06	0.09	0.016
LN	OMP	4349	10655	-6.53	-1.03	0.25	2.01	0.15	0.37	0.09	0.032
HR	Pooled	3242	8433	1.76	1.84	0.31	-0.88	0.2	-0.6	0.11	0.006
HR	PP2	171	1105	2.63	0.29	1.42	-2	1.1	-0.29	0.53	0.026
HR	PP3	310	522	13.79	4.61	1.41	-5.5	0.91	-1.71	0.54	0.18
HR	PP4	230	978	21.05	9.05	2.26	-8.35	2.08	-3.35	0.83	0.012
HR	PP5	124	971	2.74	7.16	2.78	-1.36	1.99	-2.39	0.98	0.083
HR	PP6	210	100	-23.15	-7.46	2.97	8.65	2.34	2.69	1.09	0.076
HR	PP8	67	128	-4.74	-2.55	4.3	1.99	3.02	1.2	1.66	0.04
HR	PP9	240	280	-11.79	-8.41	3.35	4.2	1.99	3.01	1.14	0.048
HR	OMP4	285	1148	-5.73	-0.31	1.3	1.25	0.75	-0.09	0.44	0.028
HR	OMP5	251	531	38.86	17.01	3.67	-13.34	2.46	-5.67	1.28	0.07
HR	OMP7	343	523	-0.92	0.27	1.03	0.11	0.43	-0.19	0.38	0.009
HR	OMP11	267	671	1.86	2.38	1.32	-0.99	0.79	-0.82	0.43	0.009
HR	OMP12	235	371	4.42	7.31	1.96	-1.48	0.91	-2.24	0.63	0.061
HR	OMP13	361	936	-14.64	-3.7	1.45	4.71	1.02	1.24	0.51	0.051
HR	OMP15	148	169	-16.61	-10.8	3.35	5.45	2.21	3.6	1.21	0.123
Pt	Pooled	2140	19242	-	1.11	0.49	-0.14	0.42	-0.32	0.17	0.001
Pt	PP2	90	712	-	7.77	4.712	-1.33	3.59	-2.76	1.65	0.019
Pt	PP3	221	1930	-	4.69	1.83	-1.51	1.92	-1.69	0.7	0.013
Pt	PP4	145	1314	-	-4.09	3.73	4.16	4.45	1.79	1.46	0.009
Pt	PP5	74	649	-	7.49	4.07	1.11	3.8	-2.21	1.38	0.016

Pt	PP6	150	1383	-	-2.4	3.82	11.87	4.06	0.37	1.33	0.022
Pt	PP8	31	225	-	-4.1	7.87	0.21	7.28	1.43	3	0.039
Pt	PP9	160	1470	-	-1.38	3.49	-0.3	3.14	0.55	1.15	0.01
Pt	OMP4	182	1632	-	3.57	2.6	0.54	2.1	-1.17	0.84	0.005
Pt	OMP5	145	1310	-	4.69	4.75	-6.32	4.13	-1.77	1.66	0.006
Pt	OMP7	250	2362	-	-2.14	1.35	-1.97	1.42	0.86	0.48	0.008
Pt	OMP11	167	1505	-	0.45	2.11	1.11	2.1	-0.02	0.64	0.009
Pt	OMP12	152	1305	-	3.45	2.53	-0.81	1.85	-0.93	0.82	0.008
Pt	OMP13	295	2772	-	-0.37	1.7	3.44	1.8	0.26	0.58	0.009
Pt	OMP15	78	673	-	-5.22	4.79	2.63	4.14	1.44	1.78	0.017

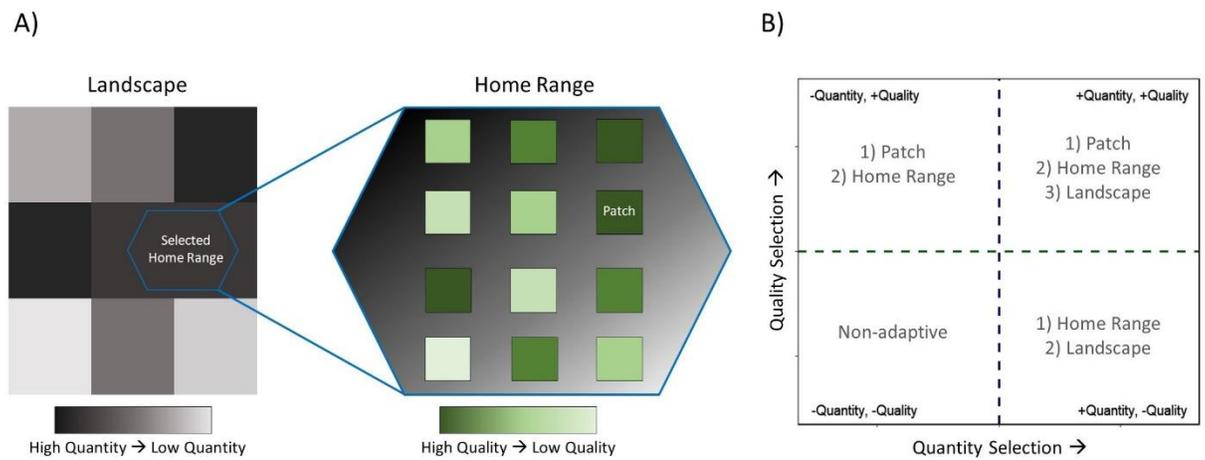


Figure 2.1. A) Conceptual diagram of resource grain from the perspective of different spatial extents. Landscapes are composed of a coarse patchwork of forage quantities, within which are home ranges with a finer-scaled gradient of quantities and patches of forage varying in both quantity and quality. B) According to literature, at the landscape extent, herbivores should most often positively select for quantity, while at the patch extent, they should most often positively select for quality. At the home range extent, either quantity or quality could be selected for. At no scale should moose negatively select for both quantity and quality.

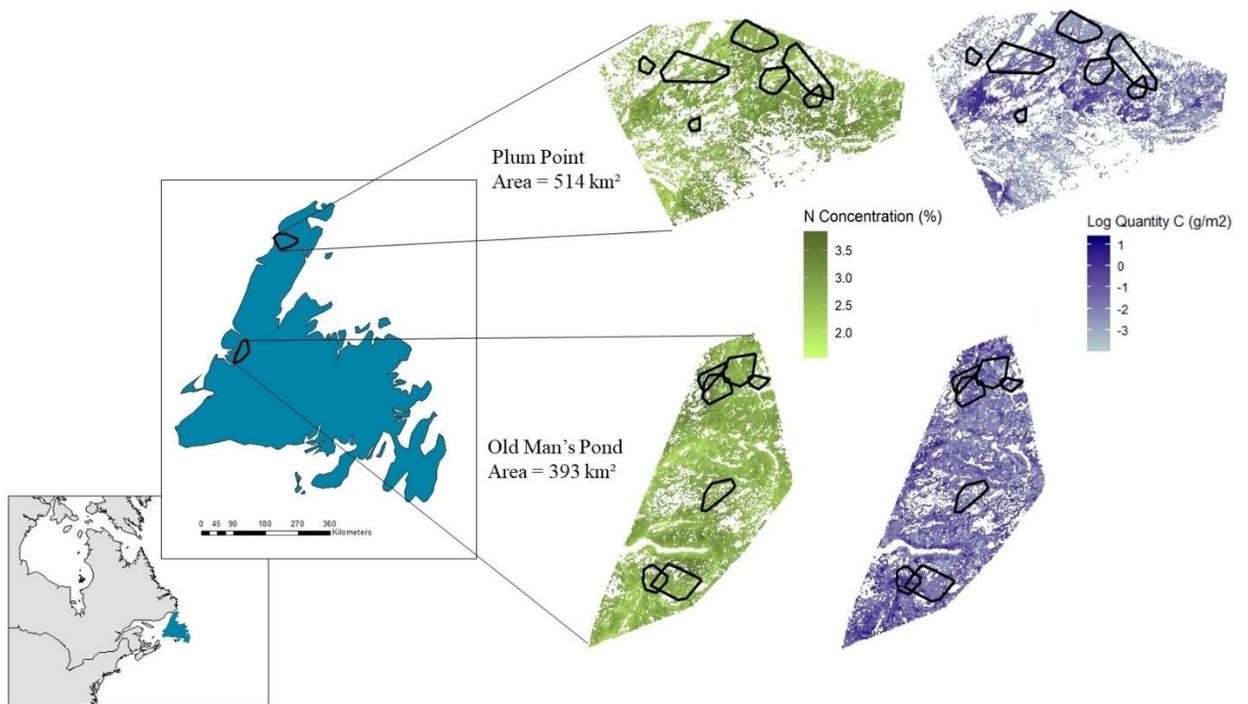


Figure 2.2. The island of Newfoundland in relation to eastern North America, with the boundaries of our study areas shown. Within each study area, we show their stoichiometric distribution model outputs for white birch forage nitrogen concentrations and carbon quantities and the MCPs of each study area's study moose home ranges. White areas are areas where we have no inference for certain habitat types like wetlands or water bodies.

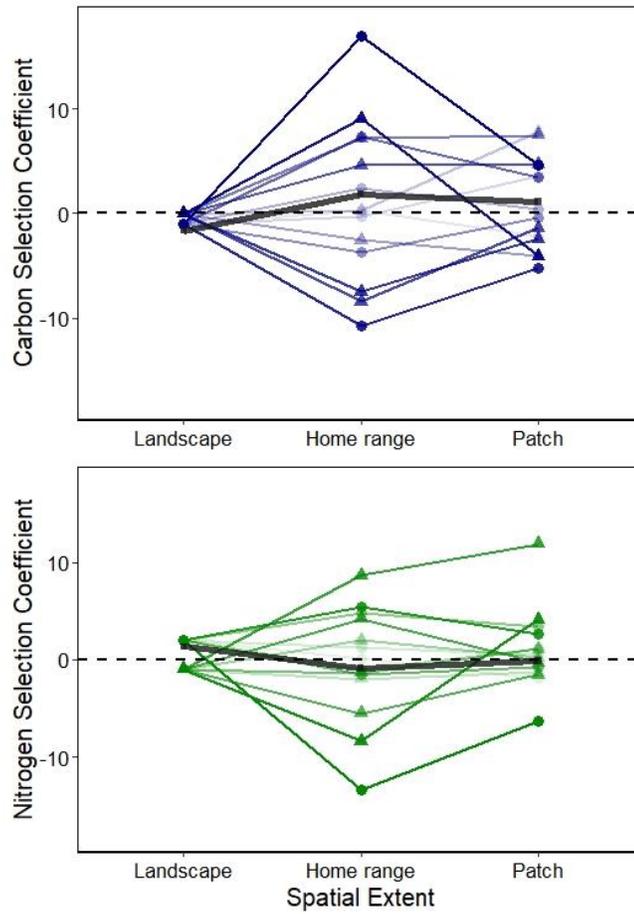


Figure 2.3. Selection coefficients, positive coefficients representing positive resource selection, for white birch carbon quantities ($\log \text{g/m}^2$) and nitrogen compositions (%) from all three scales of foraging modelled. Individuals' coefficients are linked between the patch and home-range scales, and to the coefficient values of their respective study areas (PP=triangles, OMP=circles) with lines shaded by the absolute mean of quantity carbon and nitrogen composition coefficients from the individual's home range-scale models ($|\text{C}\beta + \text{N}\beta|/2$). Darker shades represent individuals whose coefficients were, on average, further from zero at the home range-scale. The black line in each panel shows the coefficients from models using all individuals pooled.

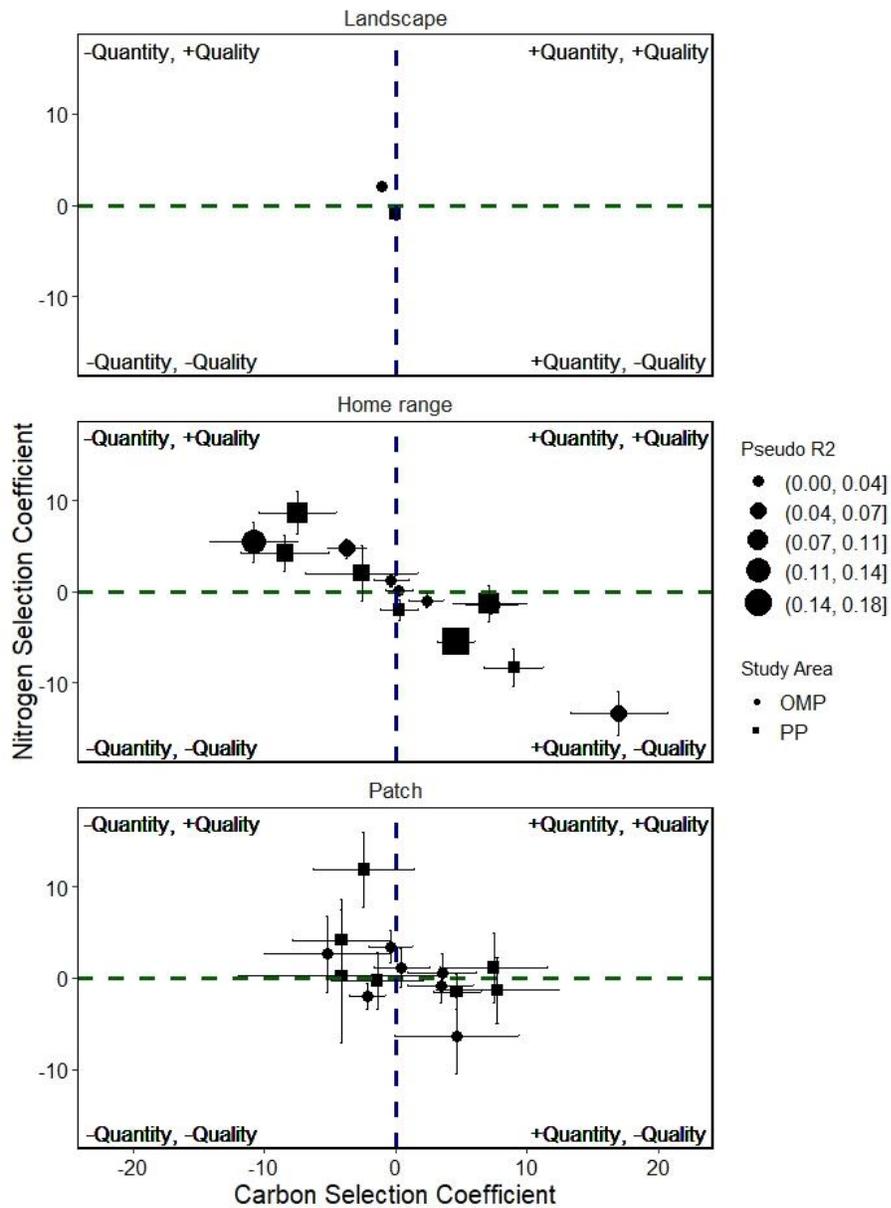


Figure 2.4. Selection coefficients with standard errors for white birch carbon quantity and white birch nitrogen composition from all scales of foraging modelled in this study, landscape, home range, and patch, plotted against one another. Axis scales are equal across panels, coefficients are scaled in size by their pseudo R^2 , and individuals are distinguished by their study area.

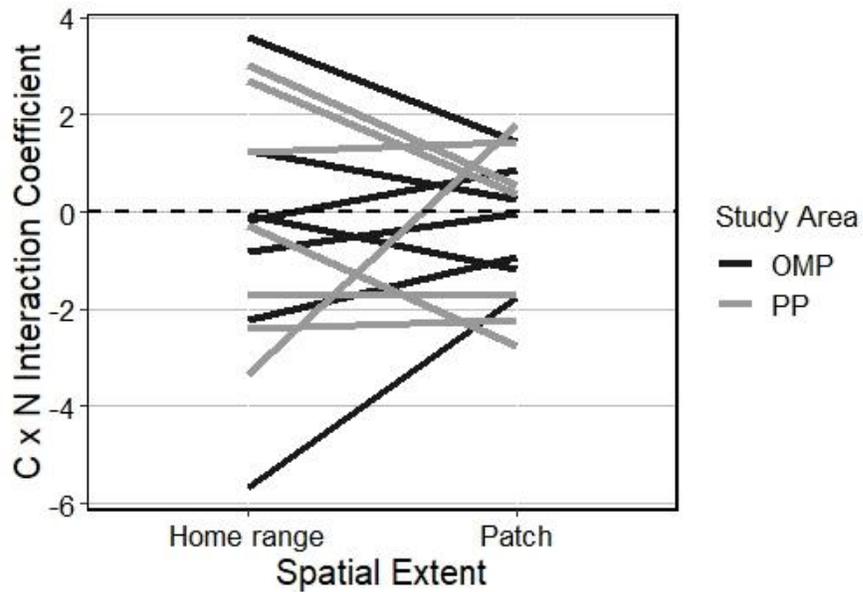


Figure 2.5. White birch quantity carbon and nitrogen composition interaction coefficients from home range (RSFs) and patch (iSSAs) individual moose selection models. Selection coefficients are linked between scales by individual and shaded by study area. Positive CxN coefficients represent individuals who selected positively for quantity carbon and negatively for nitrogen compositions, while negative CxN coefficients represent the opposite scenario.

CHAPTER 3: SNOWSHOE HARE INTRASPECIFIC FORAGE CHOICE UNDER ENERGETIC AND NUTRIENT CONSTRAINTS

3.1 Abstract

Herbivores should prefer browse of higher nitrogen (N) and phosphorus (P) contents, but energetic and nutritional constraints may affect feeding choices. Here, we test the prediction that snowshoe hares (*Lepus americanus*) prefer black spruce (*Picea mariana*) of higher N and P compositions, and that this preference would be dampened in individuals with heightened energetic demands, and greater in individuals with heightened nutrient demands. We measured black spruce N and P contents at 36 locations across a 500 m x 500 m snowshoe hare live-trapping grid on the island of Newfoundland, and found a moderately strong correlation between N and P compositions ($r = 0.66$). We then offered two choices of spruce to hare individuals from the trapping during the autumn of 2018, from areas with highest (N = 1.3; P = 0.74) and lowest (N = 0.19; P = 0.11) N and P compositions in 24-hour cafeteria-style experiments ($n = 22$). We proxied energetic demands with coat colour (%) and low ambient temperature ($^{\circ}\text{C}$), and nutritional demands with the spruce N and P from individual origins on the trapping grid. We ran nine competing models that tested energetic and nutritional influences on total consumption and preference. Hares slightly preferred feeding on high-ranked spruce, as predicted ($p < 0.1$). Less insulative coats increased consumption rates and reduced preference for high ranked spruce. Colder ambient temperatures correlated with a preference for low rank spruce ($p < 0.05$), but not consumption rate ($p = 0.77$). Hares from areas of the grid with low spruce N, or low N availability, were more selective

towards high ranked spruce ($p < 0.05$), meanwhile origin P had no effect ($p = 0.18$).

Collectively, we find support for all three of our predictions, linking foraging ecology to energetic and nutrient demands under an ecological stoichiometry framework.

3.2 Introduction

Herbivory is a process whereby primary consumers transform carbon-heavy primary producer matter into nitrogenous- and phosphorous-rich animal matter (Elser et al. 2000; Boersma et al. 2008; González et al. 2018). Under this notion, the adaptive herbivory strategy should be to prefer plants of higher nitrogen (N) and phosphorus (P) content. Indeed, food quality has been found to impact herbivore growth and fitness (DeMott et al. 1998; McArt et al. 2009; Parker et al. 2009; Felton et al. 2018). *Daphnia pulex* show preference to forage of lower C:P ratios (Schatz and McCauley 2007), giant pandas (*Ailuropoda melanoleuca*) match their seasonal migrations with changes in N, P, and calcium contents in bamboo across the landscape (Nie et al. 2015), and ungulates browse more in areas with plants of higher nitrogen contents (Ball et al. 2000; Schweiger et al. 2015; Chapter 2). While selection for elemental nutrients is observed in mammalian herbivores, it is most often only used to explain preferences across species, age classes, or distinct plant parts. Less often are experimental designs used to investigate the potential differences in selection over smaller ranges of quality, such as natural variation within a single species (Chapter 3).

Plant species are now recognized to be plastic in their elemental compositions in response to microclimates and growing conditions (Sternner and Elser 2002). Soil elemental composition has been found to strongly correlate with tree foliar elemental compositions (Fan et al. 2015). Further, a new tool called Stoichiometric Distribution Models (StDMs) has been developed to predict intraspecific elemental variation of understory forage across a landscape based on multiple remotely sensed environmental

and geographical covariates such as slope, elevation, and landcover (Leroux et al. 2017). With biogeographical features found to influence plant elemental compositions, a given browse species may vary in nutrient content at the scale of herbivore species, population, and individual ranges. If herbivores are to show preferences when offered variation in nutritional contents across species, then they should also be able to show intraspecific preference for nutritional content within a plant species with variable elemental composition. Such a response may be strongest toward a highly plastic plant species that shows similar amounts of nutritional variation to that across multiple species. Intraspecific selection should also be strong when foraging within a low-quality species because choosing poorly poses a 'higher risk'. Intraspecific selection likely becomes exaggerated within systems of low plant diversity and nutrient availability; as herbivores navigate a community of few, lower-quality browse species, they should make more within-species foraging decisions.

Intraspecific preferences are not constant, however; energetic and nutritional states influence animal feeding behaviours. Through consumption, animals must acquire enough energy for body maintenance and production (Hillebrand et al. 2009; Sperfeld et al. 2017), but energy requirements change with environmental conditions, life stages, seasons, and body conditions (Kooijman 2009). For example, endothermic animals that do not hibernate nor migrate lower their metabolisms during winter to reduce food intake requirements and survive the winter food shortages (Chappel and Hudson 1978; Moen 1978). These animals do so by growing insulative winter pelage to reduce heat loss (Sheriff et al. 2009) or by reducing daily energy expenditure (Humphries et al. 2005).

Additionally, metabolisms rise when ambient temperatures range outside the endotherm's thermal neutral zone (Chappel and Hudson 1978; Hillebrand et al. 2009; Sheriff et al. 2009). Animals have thus evolved flexible food intake rates in response to temporally variable energetic demands. For example, lactating mice (*Mus musculus*) have 203% higher energy demands than non-reproducing females, and throughout the lactation period have up to 311% higher consumption rates than non-lactating females (Speakman and McQueenie 1996). Because plant digestible carbohydrates are a quick source of energy and consuming large quantities of forage requires more time, herbivores under high energetic demands should be less selective for plant N and P and more selective for digestible carbohydrates or carbon in general (Barboza et al. 2009). Contrarily, when a consumer's demand for a particular 'currency' is greater than the supply or availability, it should be more selective for that given currency (Barboza et al. 2009; Hillebrand et al. 2009; Wagner et al. 2013). For instance, a common deficiency among herbivores is sodium, so many herbivores seek out salt deposits (Worker et al. 2015). Additionally, herbivores that are fed an unnaturally high protein diets may become fibre limited and select more fibrous forage (Hodges and Sinclair 2003). Broadening this framework: herbivores originating from habitats of low N and P availability are likely to be more nutritionally limited and thus more selective for plants N and P than conspecifics from habitats of high N and P availability (Wagner et al. 2013).

Ecological characteristics of the boreal forest merit the testing of intraspecific selection by herbivores on the elemental level within its systems. The boreal forest, one of the planet's largest biomes, has relatively low plant diversity and is nutritionally

limited compared to warmer climates. The widespread and cyclical keystone herbivore of the North American boreal, the snowshoe hare (*Lepus americanus*), is consumed by the majority of predators in all seasons (Humphries et al. 2017; Krebs et al. 2018). Instead of relying on shelter or hibernation (Humphries et al. 2017), to survive winter, hares grow dense coats every autumn and reduce activity to lower energetic requirements (Sheriff et al. 2009). Hares with winter coats have been found to have lower resting metabolic rates across a wide range of ambient temperatures (-20 to 10 °C; Sheriff et al. 2009). Within a population, individuals can differ in when they begin growing winter pelts (Zimova et al. 2016), so on a given day, individuals with different levels of insulation will experience the same ambient temperatures. In general, the snowshoe hare has a high and variable metabolism with low body fat storage (Sheriff et al. 2009), making it a very energetically sensitive consumer (Whittaker and Thomas 1982). Hares are also nutritionally limited and found to subsidise their diets with geophagy (Worker et al. 2015) and even carnivory (Peers et al. 2018). Over recent decades the hare has been subject to dietary studies attempting to investigate the chemical basis of their food choices (Sinclair and Smith 1984; Ellsworth et al. 2013).

Frequent investigations have shown the general preference ranking of browse species for hares (Bryant and Kuropat 1980; Rodgers and Sinclair 1997). These preferences are often attributed to hare selection for protein and energy content (Rodgers and Sinclair 1997; Ellsworth et al. 2013), and avoidance of secondary metabolites (Bryant et al. 1985). However, findings on snowshoe hare diet selection can be more complex. In multiple cases, feeding strategies appear to balance intake rates of fibre and

protein (Hodges and Sinclair 2003) or protein and secondary compounds (Schmitz et al. 1992), and findings on avoidance of secondary compounds confound one another (Sinclair and Smith 1984; Bryant et al. 1985). Sinclair and Smith (1984) originally speculated that the inconsistent results across snowshoe hare feeding studies were perhaps due to specific differences in defence chemicals across “species, growth stages, or even individuals”. Investigating the preference of snowshoe hare feeding within a single browse species could potentially clarify drivers of interspecific choice. Hares prefer browse of older age classes when selecting from one species (Bryant et al. 1985), and reject certain plant parts such as the green foliar buds of white birch (*Betula papyrifera*), green alder (*Alnus viridis*), and balsam poplar (*Populus balsamifera*; Bryant and Kuropat 1980). While these are cases of intraspecific preferences by snowshoe hares, preference for intraspecific nutritional variation due to natural growing conditions remains underexplored. Laitinen et al. (2002) is one example in which 5 clones of *Betula pendula* were grown in two distinct habitats — mineral and peat soil — then offered to mountain hares (*Lepus timidus*), a congeneric of the snowshoe hare. Peat-grown birches had more resin than mineral-grown individuals, but hare preference was mostly explained by clone or genotype. Effects of growing conditions may be stronger in lower-quality browse species and should be validated with nutritional measures of browse.

Here, we investigate the consumption choices of snowshoe hares for naturally-occurring elemental variation in a single, low-quality, browse species in Newfoundland, Canada. We measured the elemental nutrient compositions (N and P) of black spruce (*Picea mariana*), a low-quality (i.e., high relative foliar C:N) but abundant browse, across

a snowshoe hare trapping grid. Then, we conducted cafeteria style experiments on individual hares during a 3-week period autumn season under naturally varying ambient temperatures. Hares were in the process of growing winter coats, with some more delayed than others. We provided two choices of spruce from areas on our grid with spruce of highest or lowest N and P compositions. For each cafeteria experiment, we measured the hare's consumption rates of both spruce offerings, stage of winter coat development, the low ambient temperature it was exposed to, and the spruce N and P compositions from its origin area. We used this experiment and the known biology of the snowshoe hare to test three hypotheses:

H1. The Intraspecific Choice Hypothesis: within a plant species, herbivores prefer individuals with higher compositions of limiting elements.

H2. The Energetic Demand Hypothesis: heightened energetic demands increase an herbivore's daily intake requirement and demand for digestible carbon, reducing its display of predictions by H1.

H3. The Nutrient Demand Hypothesis: heightened nutrient demands increase an herbivore's display of predictions by H1.

We predicted that hares would generally prefer black spruce of higher quality, or N and P (H1). Hares with less-developed winter coats (Sheriff et al. 2009) or those experiencing colder temperatures (Sinclair et al. 1982) would consume more total spruce and show a lower preference for spruce N and P (H2; Barboza et al. 2009), while hares whose 'origins' or home ranges on the grid with lower spruce N and P compositions would

show a stronger preference for spruce N and P (H3; Hillebrand et al. 2009; Wagner et al. 2013).

3.3 Methods

3.3.1 Trapping grid and plant-snowshoe hare sampling

We carried out this work on a snowshoe hare trapping grid located on the eastern coast of the island of Newfoundland, Canada. During October and November, the seasonal window of this study, the area experiences daily mean temperatures of 7.4°C (SD = 1.4) and 2.3°C (SD = 1.3) and an average monthly precipitation of 93.1 mm and 80.9 mm respectively (Environment Canada 2019). Our trapping grid is in a forest with seeded and now mature white spruce (*Picea glauca*), and naturally occurring black spruce (*Picea mariana*) and white birch (*Betula papyrifera*). The trapping grid was 500 m by 500 m and contained 50 tomahawk traps arranged approximately 75 m apart on six transects with traps spaced 55 and 37 m apart at the ends of transects to connect the trapping lines (Figure 3.1). Between late-June and early-August of 2017, we sampled black spruce, the most abundant browse species on the grid, from an 11.3 m radius around each trap location. To control for effects of age class on elemental compositions, we only sampled from black spruce that were 0-2 m in height. Starting in the NW corner of the sample radius, we moved clockwise and collected the foliar and leaf-stem material of one individual per intercardinal direction (NW, NE, SE, and SW), until we had collected an approximate wet weight of 10-20 grams, and froze samples at -20°C until elemental analysis. In addition, we measured two habitat variables at each trap location: the

diameter breast height (DBH) of five dominant trees and the canopy closure of each intercardinal direction using a spherical crown densiometer. In October of 2018, prior to our experiments, we trapped the entire grid twice to create a sample of known hare individuals and then proceeded to trap portions of the grid to capture hares for cafeteria experiments. Throughout all trapping, we gave hares unique ear tags upon first capture and recorded the trap location for every individual capture to learn the geographic origin of individuals. We recorded the weight (nearest 20 g), sex, right hind foot measure (mm), age class (adult or juvenile; according to guidelines by Keith et al. 1968) for every individual capture.

3.3.2 Spruce elemental analysis

Here, we defined black spruce quality as nitrogen (N) and phosphorus (P) compositions (%). Black spruce samples (~10 g each) from our trapping grid were processed by the Agriculture Food Lab (AFL) at the University of Guelph. Nitrogen compositions were determined using an Elementar Vario Macro Cube, and phosphorus compositions were determined using a microwave acid digestion CEM MARSxpress microwave system and brought to volume using Nanopure water. The clear extract supernatant was further diluted by 10 to accurately fall within calibration range and reduce high level analyte concentration entering the inductively coupled plasma mass spectrometry detector (ICP-MS).

3.3.3 Cafeteria Offerings

Using the results from AFL, we regressed N and P compositions to canopy cover and DBH to validate that spatial variation in spruce N and P could be explained by habitat features characteristic of plant growing conditions. For cafeteria offerings, we aimed to clip from multiple, adjacent trap locations of black spruce of highest and lowest quality to increase the likelihood that other trees not originally sampled in these areas would show similar trends. Because spruce N and P compositions did not perfectly correlate across the grid ($r = 0.66$; Figure 3.1) we used N as our primary predictor of quality given it is regularly considered the limiting element of terrestrial systems (White 1993). For our final clipping locations, we chose three adjacent sampled trap locations that had the highest and lowest spruce N compositions according to the lab analyses (Figure 3.1).

During the fall of 2018 we harvested black spruce from within 18 m of the six sample locations as offerings for cafeteria experiments. We clipped twigs (< 0.3 m from terminal end) from low branches (< 1.5 m) of adult trees (> 2 m). We clipped from adult trees instead of trees under 2 m because otherwise we would exhaust available browse to clip and adult spruce are more palatable to hares. For example, a diet of strictly juvenile white spruce (*Picea glauca*), a congeneric of black spruce, causes hares to lose weight at nearly double the rate than a diet of adult white spruce (Rodgers and Sinclair 1997). We assumed adult trees would have similar relative nutritional rankings as the juveniles (< 2 m) originally sampled (i.e. areas with higher N compositions in juveniles are also areas with higher N compositions in adults). Spruce from the three trap locations of highest N composition were categorized as the ‘high nutritional rank’ offering, while spruce from

the three trap locations of lowest N composition were categorized as the ‘low nutritional rank’ offering. We bagged spruce from each clipping location separately and then mixed bags together thoroughly by nutritional rank. From mixed bags, we subsampled 17 wet grams from different branches throughout the bag and then sent these to AFL for the same lab analysis as done on original samples to confirm nutrient ranking (see Appendix C for results and discussion on subsampling). Spruce clippings were kept refrigerated at 0-5°C for the duration of the study. To select final browse for cafeteria experiments we eliminated any twigs or parts of twigs more than 5 mm in diameter or devoid of needles, and ensured all twigs were less than or equal to 10 cm in length to fit inside feeding bins. We repeated the clipping and subsampling process when cafeteria experiments exhausted the spruce offerings.

3.3.4 Cafeteria Experiments

All details of animal handling and experimentation were approved by Memorial University’s animal use ethics committee (AUP 18-02-EV). During November of 2018, we kept individual hares from our trapping grid temporarily captive for 24 hours in enclosures 100 cm wide, 90 cm high, and 120 cm deep. We placed enclosures in a forested area on the trapping grid at least 10 meters apart from one another. Enclosures had roofs to protect hares from precipitation and control for vertical cover or predation risk, a secured box for shelter, a water pail, and two baskets, one per side, for spruce offerings. We paired each enclosure with a camera trap, triggered by movement (30 second delays) to later ensure that hares used the entire enclosure and did not display a preference to a certain side. We had six enclosures total, and because a night in between

experimental days was needed to capture new study individuals, we could run a maximum of 6 cafeteria experiments per 48 hours.

To capture individuals for experiments, we set approximately 16 traps on two transects overnight (< 12 hours) with bait of apple, alfalfa cubes, and timothy feed. Access to high-protein timothy has been found to lower hare preference for protein or N and increase their preference for fibre (Hodges and Sinclair 2003). Thus, if the high-protein timothy that hares fed on during capture did have an effect on our cafeteria experiments, literature suggests it would not favour our predictions. We rotated the use of our trap lines to minimize repeated trapping of the same individuals. Upon checking traps, we weighed each hare, reserving only those greater than 1300 g in mass for experiments (Keith et al. 1968). If individuals from the most recent cafeteria experiments (< 4 nights prior) were caught, they were considered ineligible for that day's experiments and released. Hares from cafeteria experiments conducted more than four nights prior, if caught, had to show recovery from experimentally-induced weight loss (within 5% of original weight), a common repercussion of single species feeding (Rodgers and Sinclair 1997), to be eligible. We retained up to six eligible hares and transported them to the enclosures. The final recordings for each individual before experiment start were ID, sex, coat colour (% of total pelt that was white), and total mass to the nearest 20 g.

Individual hares were put into our enclosures containing water ad libitum and approximately 130.0 g piles of both the high- and low-nutritional content spruce samples in secured baskets on opposite sides, assigned randomly, of the enclosure (1 m apart). We noted the exact experiment start time and left hares alone in their enclosures. Camera

traps recorded ambient air temperature throughout the experiments ($^{\circ}\text{C}$). After 24 hours, we removed hares from their enclosures, terminating the experiments, and noted the exact end time. Hares were temporarily kept post-experiment to recover by feeding on timothy pellets and apple. We then weighed hares to the nearest 20 g, fitted each with a VHF collar to monitor survival, and returned them to the site of their capture. Post release of hares, we collected and weighed the remaining twigs to the nearest 0.1 g from each spruce offering.

3.3.5 Statistical analyses

Before experiments, we measured the starting mass (s) of each spruce pile in cafeteria experiments and post experiments, we measured remaining mass (r) of each pile. We calculated the total consumption ($T_i = s - r$) of the two ranks of spruce offered as either h for the high nutrient (T_h) or l for low nutrient (T_l). All statistical tests had the response variable of total consumption of a pile T , the binary explanatory variable of spruce rank to indicate if total consumption was T_h or T_l and test the Intraspecific Choice Hypothesis, and the Experiment ID as a random variable to pair consumption of the two spruce choices within an experiment. Additional variables used to test the Energetic Demand Hypothesis included the coat colour (% white pelt) of the individual and the low ambient temperature ($^{\circ}\text{C}$) during the experiment. To proxy nutritional states of hares and test the Nutrient Demand Hypothesis, we calculated 'origin' N and P values for each individual by averaging the mean N and P values for all trap locations where the individual was caught during the study period (October-November). To ensure the trap locations which were not originally sampled (no spruce < 2 m) had spruce elemental estimates, we

interpolated results from sampled locations across the grid using ArcGIS Spatial Analyst (Childs 2004). We tested for correlations (Pearson's r) between the energetic variables, coat colour and temperature, and the nutrient variables, origin N and origin P, to confirm that tests for each hypothesis were independent and not impacted by our trapping patterns, e.g., we trapped hares from areas with lowest origin N on the warmest days.

We conducted all data cleaning and statistical analyses in the R statistical program (Version 3.5.1; Team 2018). We compared nine linear mixed models with second-order Akaike Information Criterion (AICc) using the 'aictab' function from the AICcmodavg R package (Mazerolle 2017). The models we compared included the Base (spruce rank only) as a direct test of the Intraspecific Choice Hypothesis, the Energetic (coat colour and low temperature) as a test of the Energetic Demand Hypothesis, and the Nutrient (origin N and P) as a test of the Nutrient Demand Hypothesis. In addition, we ran models for each variable independently, Coat Colour (coat colour), Temperature (low temperature), Nitrogen (origin N) and Phosphorus (origin P) to test each component of the hypotheses separately as well as a Full model with all competing variables and the intercept only or Null model (Table 3.1).

3.4. Results

3.4.1 Trapping Grid Elemental and Habitat Measures

Of the 50 sampling locations on our trapping grid, 36 had black spruce present. From this sample, the mean nitrogen concentration was $1.01 \pm 0.18\%$ and the mean phosphorus concentration was $0.14 \pm 0.036\%$. The maximum N and P compositions were 1.41 % and

0.20 % respectively, while minimum N and P compositions were 0.68% and 0.09% respectively. N and P compositions had a Pearson's correlation coefficient of 0.66 and, when regressed (P response to N) against one another, showed a significant relationship (t-value = 5.08 ± 0.025 , $p > 0.001$; Figure 3.1). The mean canopy closure and DBH for all 50 trap locations were $77.84 \pm 28.05\%$ and 9.16 ± 2.28 cm respectively. Combined, canopy closure and DBH explained 35.5% of the grid's spruce N variation and 25.1% of spruce P variation (multiple R^2), with canopy closure having a significant effect towards both (N t-value = 3.094, $p < 0.01$; P t-value = 3.041, $p = 0.0046$) and DBH being insignificant towards both (N t-value = 0.931, $p < 0.01$; P t-value = -0.402, $p = 0.69$; Figure B1). The sites where we clipped high-nutrient ranked spruce for cafeteria experiments originally showed N compositions ranging from 1.17% – 1.39%, and P compositions from 0.169% – 0.197%. Sites where we clipped low-nutrient ranked spruce showed N compositions ranging from 0.71 % – 0.76 %, and P compositions from 0.101 % – 0.113 % (Figure 3.1).

3.4.2 Captive Cafeteria Experiments

We conducted a total of 22 cafeteria experiments from November 5th to November 20th of 2018 on 20 individuals (M = 7; F = 13), two of which were tested twice. Low temperatures during experiments ranged from -4°C to 2°C . There were no meaningful correlations ($-0.16 < r < 0.19$) between energetic variables and nutritional variables, implying our trapping patterns did not affect the independence of our hypothesis tests. Camera trap records of each experiment showed that hares regularly used all areas of the enclosures and ate primarily during the dark hours (18:00- 06:00). The side of spruce

rank piles, relative to enclosure entrance, did not show to have an influence on hare consumption ($t = -1.048$, $p = 0.31$). All hares appeared to sort through spruce piles, spreading twigs around within a 0.25 m radius of the baskets, when feeding. We also observed that hares tended to reject the last 3-5 mm of spruce terminal ends, as these tips of twigs frequently remained post experiment. Hares ate on average 127.8 g (SD = 32.0) of spruce total during experiments, 69.2 g (SD = 23.3) from high ranked spruce and 58.6 g (SD = 20.3) from low ranked spruce.

When testing which models best explained total consumption using AICc comparisons, we found the top ranked models to be the Nitrogen model followed by the Coat Colour ($\Delta\text{AICc} = 0.970$) and Energetic ($\Delta\text{AICc} = 0.973$) models, which explained 23%, 21%, and 30% of feeding variation respectively (Marginal R^2 ; Table 2). The models with a ΔAICc greater than 2.00 and less than 4.00, in order of increasing ΔAICc , were the Temperature, Base, Full, and Null models (Table 3.2). The Nutrient and Phosphorus models received less support according to AICc comparison ($\Delta\text{AICc} > 4$). Hares appear to slightly, but not significantly prefer higher ranked spruce over lower ranked spruce (Base model; $\beta = 10.67 \pm 6.19$, $p < 0.10$), with rank alone explaining 6% (marginal R^2) of feeding variation, but the Base model was not a top-ranked model (Table 3.2; Figure 3.3). Coat colour, or percent winter pelt, was negatively correlated with total consumption of a spruce offering (Coat Colour model; Coat $\beta = -31.11 \pm 13.15$, $p < 0.05$; Table 3.3; Figure 3.4). The interaction between coat colour and spruce rank was positive (Coat Colour model; $\beta = 11.18 \pm 19.50$), but insignificant ($p = 0.57$) implying no effect on spruce choice. Low temperature did not have a significant effect on total consumption of spruce

offerings (Energetic model; $\beta = -0.3.22 \pm 2.32$), but it did positively correlated with a hare's preference for high ranked spruce (Energetic model; Temp*Rank $\beta = 8.03 \pm 3.21$, $p < 0.05$; Table 3.3; Figure 3.5). The top ranked, Nitrogen model, found origin N to negatively correlate with preference for high ranked spruce (N*Rank $\beta = -146.73 \pm 60.74$ $p < 0.05$; Table 3.3; Figure 3.5). All covariates combined in the Full model collectively had an R^2 of 0.47, but this model was not top ranked. The Nutrient and Phosphorus models failed to rank above the Null model (Table 3.2; Table B1).

3.5 Discussion

When faced with a choice, herbivores should browse the most digestible and high-quality food. While many studies confirm this notion, they do so by measuring consumer responses to variation between plant species (Sinclair and Smith 1984), parts (Bryant and Kuropat 1980), or age classes (Bryant et al. 1985). Studying intraspecific choice can inform the mechanisms behind interspecific choice as well as management practices, like single species seeding for forest regeneration (Heroy et al. 2018). During the autumn of 2018 in eastern Newfoundland, Canada, we tested if snowshoe hares could differentiate between black spruce with different nutrient compositions, or the Intraspecific Choice Hypothesis, using individual cafeteria-style experiments. Specifically, we measured and mapped N and P compositions for black spruce across our hare trapping grid and offered spruce from areas of highest and lowest N and P in cafeteria experiments. We also tested if heightened energetic demands would increase hare consumption rates and dampen intraspecific preference, and if, conversely, heightened nutrient demands would increase intraspecific preference. Our findings support the Intraspecific Choice Hypothesis

predictions because hares consumed more spruce of the higher nutritional rank. We found partial support for the Energetic Demand Hypothesis: winter coat development negatively correlated with total spruce consumption and reduced preference, and temperature positively correlated to preference for high ranked spruce. We also found support for the Nutrient Demand Hypothesis: origin N content negatively correlated with preference for high ranked spruce. Our study integrates ecological stoichiometry with foraging ecology, testing energetic and nutrient constraints on plant-herbivore interactions (Sperfeld et al. 2017).

When offered two options of black spruce, hares preferred amounts of those clipped from areas of the grid with higher N and P compositions, supporting the predictions of the Intraspecific Choice Hypothesis (Figure 3.3). Spruce rank alone explained some variation of feeding (marginal $R^2 = 0.06$; Base model), but not as much as models that incorporated energetic and nutritional variables in addition. These other models continue to find an effect of spruce rank, but also when interacting with energetic (i.e., temperature) and nutritional (i.e., origin N) covariates. Evidence of intraspecific browse preferences have been observed in other herbivores. Lambs (*Ovis aries*) prefer aspen (*Populus tremuloides*) of higher protein content from natural conditions in feeding trials (Heroy et al. 2018). Even a species thought to only use assimilation and respiration processes to maintain stoichiometric homeostasis, *Daphnia pulex*, seek out patches of lower C:P within a single algal species (Schatz and McCauley 2007). In the case of the snowshoe hare, we find intraspecific selection for quality and further, that this preference may be plastic and affected by energetic and nutritional demands.

We found support for all aspects of the Energetic Demand Hypothesis when considering winter coat development as a proxy for energy requirements, and partial support when considering ambient temperature with the mechanism unknown. The first part of the Energetic Demands Hypothesis posits that higher energetic needs translates to higher intake rates by the herbivore; for this we found partial support. Ambient temperature did not affect consumption rates as predicted (Sinclair et al. 1982), while pelage did. Specifically, our findings predict that hares with 50% more winter coat will eat approximately 31.1 g less total spruce per day (Figure 3.4; Coat model). We propose that one potential mechanism of this finding could be metabolic change. When experiencing temperatures near or around freezing (-4 to 4 °C), hares with fully developed winter coats have lower resting metabolic rates than those with fall pelage (Sheriff et al. 2009). While Sheriff et al. (2009) uncovered this binary metabolic difference, the relationship between coat colour and metabolism may be continuous according to our results, if feeding rate indicates metabolic rate. While winter pelage is an adaptation to high seasonality, temperature did not have a significant relationship to total daily intake of spruce, implying temperature did not affect energetic requirements. Sinclair et al. (1982) found this relationship between temperature and daily intake by hares using a temperature range of -20°C to 10°C and a very high-quality feed (20% crude protein). We suspect our range of ambient low temperatures (-4°C to 2°C) was too narrow and our food was too low-quality (4.25% - 8.81% crude protein; N×6.25; Mariotti et al. 2008) to find a similar effect.

Part two of the Energetic Demand Hypothesis states that energetically driven higher intake rates require more time feeding and lowers the herbivore's selective ability to be choosy. Findings from the Energetic, Coat, and Temperature models collectively support for the second component of the Energetic Demand Hypothesis. We found no meaningful interaction between coat colour and rank, but do not receive this as counter support of the hypothesis because, unlike in other models, rank was no longer significant when accounting for coat colour. Only accepting a negative interaction between coat colour and rank as support for the Energetic Demand Hypothesis would risk making a type II error. The hypothesis also predicts that higher energetic demands increase consumer requirements for energy and digestible carbon. We did find a negative interaction between temperature and rank (Figure 3.5), implying hares experiencing colder temperatures preferred low ranked spruce. Here, higher intake requirements must not be the mechanism of this effect, as we originally predicted, because temperature had no effect on total consumption. The mechanism may be a higher requirement for digestible carbon, and thus an appeared avoidance of protein or nitrogen (Hawlana and Schmitz 2010; Sperfeld et al. 2017).

We predicted, by the Nutrient Demand Hypothesis, that hares from areas with low N and P availability would display a stronger preference for the high ranked spruce; effects of origin N supported this prediction (Figure 3.5). The Nitrogen Model was the top ranked model according to AICc comparison and explained 23% of feeding variation. Lack of correlations between origin N and the energetic covariates negates the possibility that this effect of origin N was due to correlated energetic variables. Despite correlation

between spruce N and P across the trapping grid ($r = 0.66$), we found hares from areas with spruce lower in N had greater preference for high ranked spruce, but origin P had no effect on spruce preference. We see two primary, non-exclusive explanations for this difference. The first being that spruce N may be a better indicator of general growing conditions for other plant species that are available to hares, and thus a better predictor of nutrient availability. We did find evidence for this explanation when testing if the habitat covariates that incorporated other tree species, DBH and canopy closure, could explain black spruce N and P compositions across the grid. Together, DBH and canopy closure explained 10% more variation of spruce N than spruce P. The second potential explanation is that terrestrial systems are historically understood to be more limited by N than P (White 1993) and this notion may extend to the system's herbivores, like the snowshoe hare, making N availability a better predictor of terrestrial herbivore nutrient deficiency (McArt et al. 2009). There exist many other drivers of nutritional limits on herbivores, such as seasons, disturbances, and drought, and therefore there are many other contexts to test between N and P limitations in terrestrial, free-ranging herbivores. Collectively, we find evidence that the nutrient availability within an herbivore's home range may be limiting enough as to affect foraging strategies; a herbivore of one habitat quality may select plants and nutrients differently than its conspecific from another habitat.

Combined, spruce rank, coat colour, temperature, origin N, and origin P explained 47% of snowshoe hare feeding responses during cafeteria experiments. We suspect that there was substantial variation within spruce rank due to inter and intraindividual

differences which may account for a large portion of the feeding variation. Within individuals, plants allocate more N and P to their leaves than stems (Tang et al. 2018; Zhang et al. 2018), but we could not control for exact ratios of leaf to stem tissue. Laitinen et al. (2002), which tested hare preference for clones of *Betula pendula*, found tree genotype to explain much variation of feeding. Genotype may affect allocation of secondary compounds (Laitinen et al. 2002), interacting with nutrient contents, but most variation of secondary compound allocation and its effects is studied under an interspecific contexts (Sinclair and Smith 1984; Schmitz et al. 1992; Rodgers and Sinclair 1997). Experimental manipulation of plants to create intraspecific quality treatments would likely reduce feeding variability, but be less representative of natural conditions.

If herbivores display intraspecific feeding preferences, then variation of quality within a plant species may be significant enough to affect herbivore fitness (Parker et al. 2009; Wam et al. 2018). We find support for all three of our hypotheses, and mainly that snowshoe hares may be sensitive to the natural gradients of plant intraspecific quality across areas as small as their home ranges. The availability of nitrogen, not phosphorus, within home ranges may also influence individual nutrient demands and feeding choices—evidence that terrestrial herbivores are ultimately nitrogen-limited (White 1993). Lastly, herbivores are not only nutritionally constrained because heightened energetic demands increased feeding rates and dampened preferences. Individuals that expend more energy interact with plant communities differently. Collectively, this study posits the links between herbivore metabolisms, nutritional states, and feeding patterns, explained under the unifying, ecological stoichiometry framework.

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Table 3.1. All the linear mixed models (paired by experiment) compared with AICs to explain the total grams consumed from a spruce offering per 24-hour cafeteria experiment (22 experiments, 44 observations). Bolded models incorporate all fixed effects relative to each hypothesis.

Model Name	Fixed Effects
Null	None
Base	Rank
Coat Colour	Coat*Rank
Temperature	Temp*Rank
Energetic	Coat*Rank + Temp*Rank
Nitrogen	Origin N*Rank
Phosphorus	Origin P*Rank
Nutrient	Origin N*Rank + Origin P*Rank
Full	Coat*Rank + Temp*Rank + Origin N*Rank + Origin P*Rank

Table 3.2. AICc comparisons of linear mixed models (paired by experiment) predicting snowshoe hare consumption of black spruce pile when offered in pairs, of high and low nutrient rank, during cafeteria experiments (n = 44). All models incorporate spruce pile nutrient rank as a fixed effect. Models ranked within 2 Δ AICc of the top model are bolded.

Model	K	AICc	Δ AICc	AICc weight	Log Likelihood
Nitrogen	6	400.138	0.00	0.307	-192.934
Coat Colour	6	401.107	0.970	0.189	-193.419
Energetic	8	401.111	0.973	0.188	-190.498
Temperature	6	402.980	2.842	0.074	-194.355
Base	4	403.012	2.874	0.073	-196.993
Full	12	403.130	2.992	0.069	-184.533
Null	3	403.372	3.235	0.061	-198.386
Nutrient	8	405.516	5.378	0.021	-192.701
Phosphorus	6	405.7697	5.559	0.019	-195.713

Table 3.3. Coefficients, standard errors, and marginal R²s of the top five AICc-ranked linear mixed models for black spruce consumption in order of AICc rank. The models are linear mixed models paired by experiment and all incorporate spruce pile nutrient rank as a fixed effect.

Model	Rank (R)	Coat	Temp	N	Coat*R	Temp*R	N*R	R²
Nitrogen	154.64*** (59.85)	- -	- -	12.40 (45.86)	- -	- -	-146.73** (60.74)	0.23
Coat Colour	6.09 (9.64)	-31.12** (13.15)	- -	- -	11.18 (19.50)	- -	- -	0.21
Energetic	7.31 (8.85)	-38.01*** (13.28)	-3.22 (2.32)	- -	28.36 (18.38)	8.03** (3.22)	- -	0.31
Temp	17*** (6.56)	- -	-0.73 (2.36)	- -	- -	6.17** (3.14)	- -	0.17
Base	10.67* (6.19)	- -	- -	- -	- -	- -	- -	0.06

*p<0.1; **p<0.05; ***p<0.01

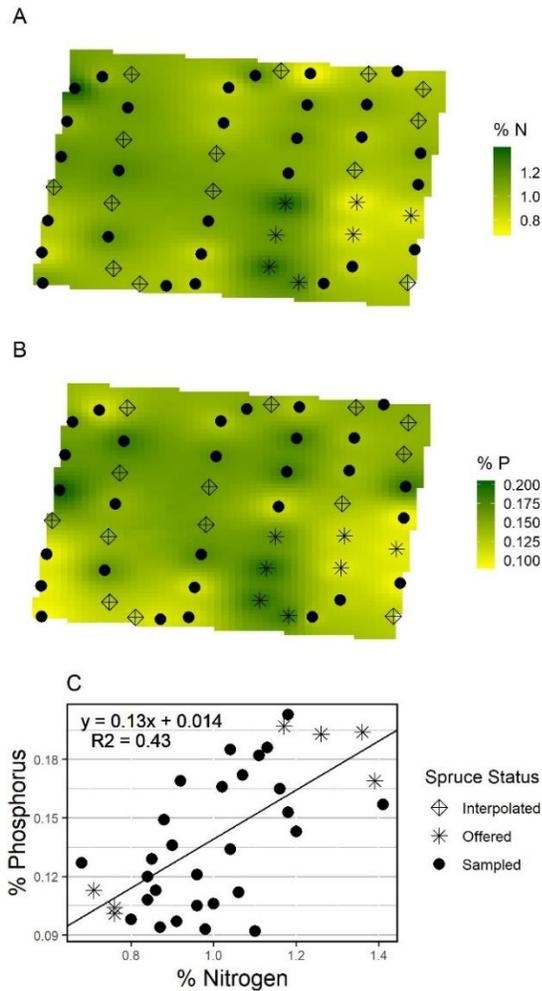


Figure 3.1. Interpolated maps of the trapping grid’s black spruce A) nitrogen and B) phosphorus compositions. Each sample location also represents a snowshoe hare trap. Spruce was sampled during the summer of 2017 for N and P analysis at sites where the species was present (circles and stars) and these results were then used to interpolate the whole grid and give values to locations which did not have spruce within their sample plots (crosses). Areas of highest and lowest nitrogen compositions were offered (stars) in cafeteria experiments during the fall of 2018. Spruce N and P compositions from sampled locations plotted against one another, with their linear relationship shown (C).

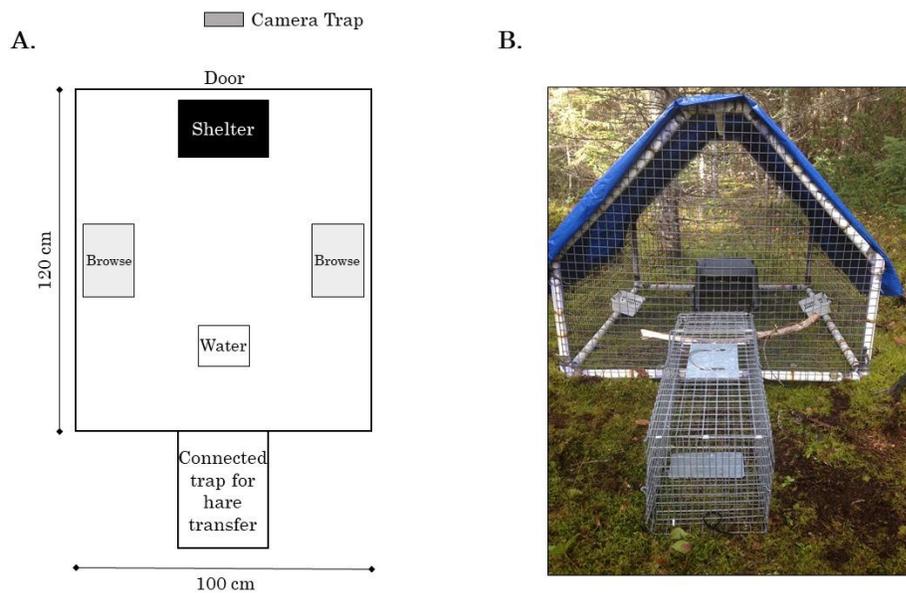


Figure 3.2. Overhead diagram (A) and photograph (B) of a cafeteria enclosure.

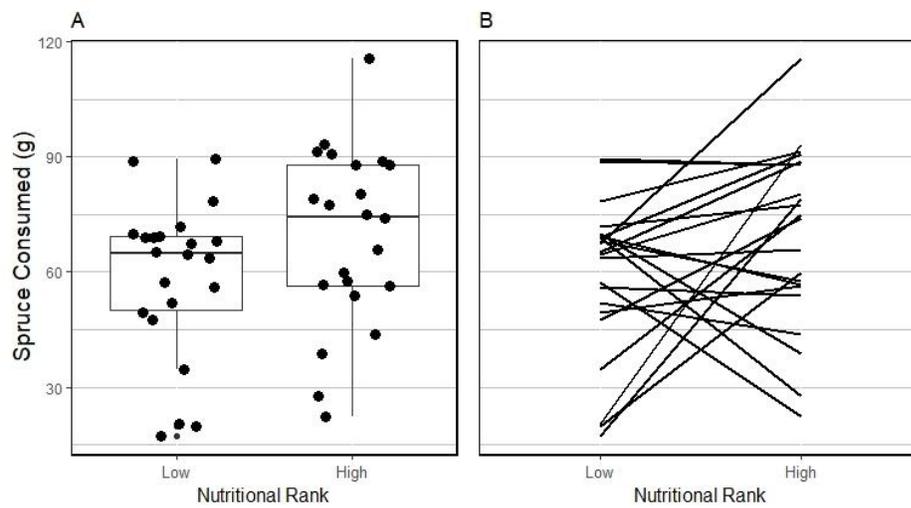


Figure 3.3. A) Overall trend of snowshoe consumption (g) of browse piles (44 observations) when offered two nutritional ranks of black spruce during 24-hour cafeteria experiments (2018; n = 22) and B) the trends of individual experiments pairing offered spruce ranks.

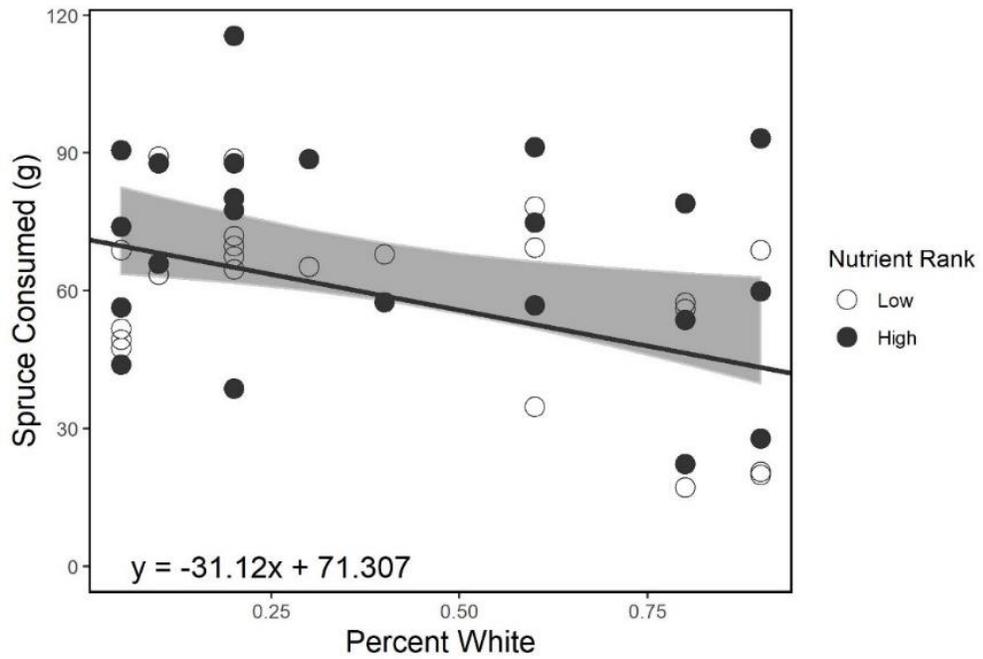


Figure 3.4. The mass (g) of black spruce consumed from each spruce offering by individual snowshoe hares during 24-hour, autumn-timed (2018), captive cafeteria experiments (n = 22) in relation to the coat colour (% white) of the hare. Marginal $R^2 = 0.19$. Equation of the linear relationship and 0.95 confidence interval (grey band) are shown.

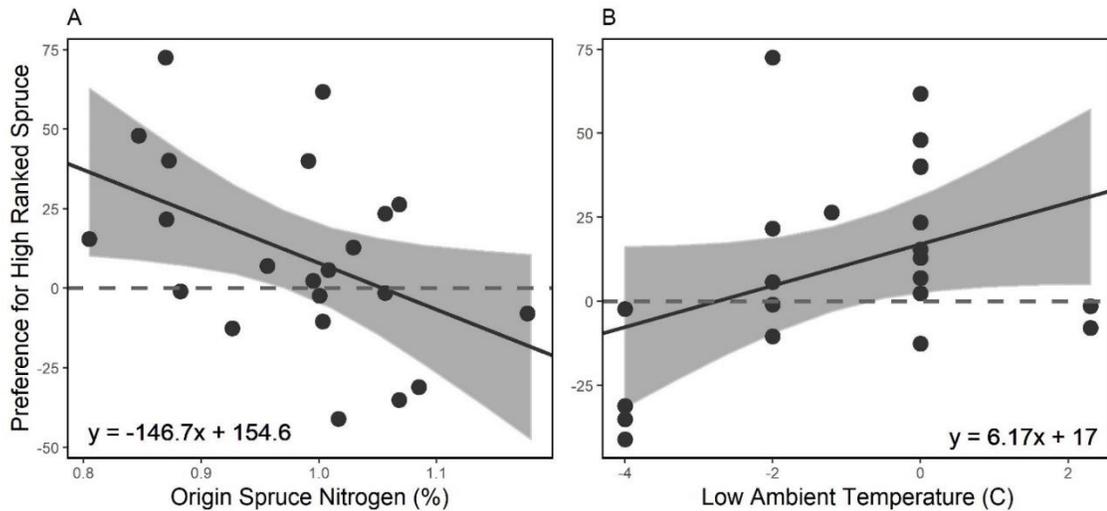


Figure 3.5. Snowshoe hares preference for high ranked spruce (g; calculated by: high rank consumption – low rank consumption) during 24-hour cafeteria experiments (n = 22) in relation to spruce N compositions of a hare’s origin area (A) and the low ambient temperature during experiment (B). Preference was calculated to visualize the interaction coefficients between Origin N and Rank (A) and Low Temperature and Rank (B) in the Nitrogen and Temperature models. The lines representing no preference between spruce ranks (dashed) and linear regressions between preference and explanatory variables (solid) are shown. $R^2 = 0.21$ (A) and 0.15 (B). Equations of each linear regression and 0.95 confidence intervals are shown.

CHAPTER 4: SUMMARY AND CONCLUSIONS

4.1 Background

Herbivory represents energy and nutrients removed from living materials of primary producers and made available to consumers, influencing productivity at all trophic levels (Elser et al. 2000; Boersma et al. 2008; González et al. 2018). Nutritional ecology links herbivore behaviour and physiology with ecosystem-level processes (Simpson and Raubenheimer 2012). Nutritional Geometry (hereafter NG; Raubenheimer et al. 2009) and Ecological Stoichiometry (hereafter ES; Sterner and Elser 2002) are some of the frameworks developed to help nutritional ecology unify scale, time, and the various levels of biological organization. NG studies foraging as an organism's intake regulation of multiple currencies in order to maintain a nutritional homeostasis (Raubenheimer et al. 2012). ES generally focuses on the internal regulation by organisms to maintain stoichiometric homeostasis or body carbon (C), nitrogen (N), and phosphorus (P) compositions (Sterner and Elser 2002). These frameworks have been considered to help unify nutritional ecology and make it more “nutritionally, organismally, and ecologically explicit” (Raubenheimer et al. 2009). According to Raubenheimer et al. 2009, a framework is nutritionally explicit if it identifies the roles and interactions of food components, is organismally explicit if it explains the physiology, morphology, and life history of the herbivore, and is ecologically explicit if it uncovers the effects of animal phenotypes on ecological communities. Here, I discuss the value of borrowing from ES – elemental currencies – and integrating them with NG in the context of terrestrial herbivory.

NG and ES are suitable to describe and predict herbivory processes because they consider multiple currencies (Raubenheimer et al. 2009). Plants are generally less digestible, more chemically defended, and variable in elemental composition compared to animal tissue (Elser et al. 2000). Herbivores must navigate varying food qualities, balance the intake of amino acids dissimilar to their own, consume appropriate amounts of fibre, and avoid plant secondary compounds (PSCs; Barboza et al. 2009; Felton et al. 2018). The various composites within plant matter collectively affect its quality to an herbivore, and food quality influences herbivore fitness (Parker et al. 2009; Wam et al. 2018). Thus, it is critical that a framework for herbivore nutritional ecology incorporate multiple currencies, like NS and ES do, in order to be nutritionally explicit. The framework must also be ecologically explicit because as the ‘trophic bottleneck’ (Elser et al. 2000; Boersma et al. 2008; González et al. 2018), herbivore actions cascade in both trophic directions. NG and ES contrast here, with NG typically focusing on the organismal level, and ES on currency flows between system and trophic levels (Cherif et al. 2017; Sperfeld et al. 2017). Distinct to ES, also, is the use of elemental currencies, which are common between organisms, species, trophic levels, and systems (Sturner and Elser 2002).

4.2 In Defence of Elemental Currencies

Elemental currencies, despite being simple, do represent some herbivore nutritional requirements. A common association is N and protein. ‘Crude protein’ content has historically been proxied by measuring N and multiplying it by the Jones conversion factor of 6.25 (Mariotti et al. 2008). This has become a justified estimate for plant crude

protein because N from other compounds including nucleic acids, nitrates, and phospholipids, are often assumed to be negligible in plants. However, this conversion factor can cause protein estimates to have a 15 to 20% error (Mariotti et al. 2008) and does not account for diversity and quality of amino acids (Barboza et al. 2009). Given these constraints, many foraging studies still use crude protein as an estimate for plant quality (Felton et al. 2009; Ellsworth et al. 2013; Heroy et al. 2018). Studying foraging in terms of crude protein can decouple the link between foraging decisions and ecosystem N for readers unfamiliar with the Jones conversion factor while not being an accurate assessment of amino acid concentrations in food. Terrestrial systems have long been understood to be N limited (White 1993), and this limitation is reflected in terrestrial herbivores (McArt et al. 2009; Chapter 2).

More complex is the use of C as a nutritional indicator. C compositions of food should correlate with Gross Energy content, the measure of all C oxidized when burned inside a bomb calorimeter (Barboza et al. 2009). However, C content, nor Gross Energy, does not differentiate between carbohydrate sources within food, which have particularly large implications for herbivore nutrition (Raubenheimer et al. 2009). Starch, the storage carbohydrate in plants, is a polysaccharide composed of alpha-oriented glucose. It is digestible to animals. The polysaccharide of alpha-glucose's isomer, beta-glucose, is cellulose, the structural carbohydrate in plants. Unlike starch, animal enzymes cannot digest cellulose, and thus, it is elemental orientations that determine the nutritional value of a large percentage of plant matter. Herein lies the major strength of NG compared to ES: a consideration for molecular properties. To be more encompassing of C nutritional

properties, some ES studies and theory differentiate between digestible C and non-digestible C (Felton et al. 2009; Hawlena and Schmitz 2010). This may be the best compromise between making ES more nutritionally explicit while maintaining the common currency of elements.

While elemental measures cannot represent every aspect of nutrition in plant resources, they allow ES to be ecologically explicit—arguably its biggest strength. Elements are the common currency across trophic levels, and so the ES framework has been used to link otherwise un-coupled processes (Sturner and Elser 2002). For example, predation-induced stress on herbivores has been found to influence their feeding and digestive patterns, linking predator activity to plant and detritivore productivity via physiological processes (Hawlena and Schmitz 2010; Hawlena et al. 2012; Leroux and Schmitz 2015).

Lastly, herbivore elemental intakes may be linked to universal internal physiological processes, such as protein synthesis and respiration. The Growth Rate Hypothesis states that growing organisms have lower C:P ratios due to the abundance of P-dense ribosomes required for protein synthesis (Elser et al. 1996). ES and NG notions of homeostasis have also been integrated with the Dynamic Energy Budget (DEB; Kooijman 2009), which models how organisms use N and C for many scales of physiological processes in response to body maintenance and production demands (Sperfeld et al. 2017). This integrative approach has potential to link animal nutrition to ecosystem functioning. I tested the feeding responses of snowshoe hares (*Lepus americanus*) and found that under greater energetic demand, hares increased food intake

and become less discriminating about plant N and P contents (Energetic Demand Hypothesis; Chapter 3). Further, I concluded that the nutritional state of hares, proxied by the N availability of their origin habitat, affects their preferential to N and P contents (Nutrient Demand Hypothesis; Chapter 3). In a collaboration during my MSc, we found that snowshoe hares also vary in their body composition, but the drivers and implications of such variation are yet to be determined (Rizzuto et al. 2019). Herbivores individuals vary in both stoichiometric foraging decisions and body stoichiometry, with a potential driver being nutritional and energetic states (Hillebrand et al. 2009; D. Hawlena and Schmitz 2010). I conclude, based on my work on the snowshoe hare that herbivores conspecifics may interact with plant communities when under varying energetic and nutritional demands.

4.3 Scale

In addition to being nutritionally, organismally, and ecologically explicit, I offer that a unifying framework of nutritional ecology must explain feeding patterns at many scales (Levin 1992). Foraging is traditionally described as orders of selection, with first-order selection being the geographical range of a species, second-order being the home ranges within landscapes, and third-order being selection within home ranges (Johnson 1980). These orders of selection refine, further, to the choices between different patches and bites (Bailey et al. 1996). The ecological impacts of herbivory depend on the scale of forage selection. For example, the bite a browser chooses to eat will affect the total biomass removed from a plant individual (Vivas et al. 1991), affecting that plant's fitness, and therefore the natural selection of the plant population with repetition of this

particular choice (Table 4.1). Alternatively, at the regional scale, herbivore population migration in relation to food availability (Hebblewhite et al. 2008) influences the types and amounts of nutrients moved across the region (Moore et al. 2007; Doughty et al. 2016). Criteria for forage selection are hypothesized to vary by foraging scale too (Table 4.1). Coarser-scale factors like climate, plant biomasses, and water availability, should influence the foraging at larger extents, while finer-scale factors like plant quality (Senft et al. 1987) should influence the smaller extents of foraging. A framework must offer means to capture this complexity of influences.

Herbivores exhibit responses to elemental compositions while foraging at the bite and patch scales. Using cafeteria experiments, a method of providing multiple foods with known properties to a consumer, I found snowshoe hares to differentiate between varying N and P levels within a single browse at the bite-level (Chapter 3). The results have implications at larger scales because the browse choices came from the natural variation of a species across the home ranges of my sample population. If hares respond to N and P at the bite-level, then N and P should affect their daily movements and home ranges. Similarly, Ball et al. (2000) fertilized forest stands (50×50 m) with N and found hares (*Lepus timidus*) and moose (*Alces alces*) to use and forage in the treated plots more than control plots, suggesting that terrestrial herbivores respond to N and P at the patch-level.

Studying the nutritional ecology of free-ranging herbivores proves more challenging at the home range and landscape extents, but methodological developments using the ES offer promising solutions. Most field studies on large herbivore foraging at home range and landscape extents first measure responses to categorical landcover data,

such as habitat type, then link the responses to strategies of nutritional gain through inference (Zweifel-Schielly et al. 2009; van Beest et al. 2010). Improving nutritional inferences from movement of large herbivores requires continuous landscape layers of plant qualities (Weisberg and Bugmann 2003). Elemental landscapes can fill this need, and animals have been found to respond to them. For example, Nie et al. 2015 studied the foraging of the giant panda (*Ailuropoda melanoleuca*) with ground collected elemental measures of bamboo and was able to attribute panda range shifts to intake of calcium, P, and N. I compared moose foraging strategies at three different spatial scales, aided by continuous elemental resource landscapes predicted by Stoichiometric Distribution Models (StDMs; *sensu* Leroux et al. 2017). I found that just two elemental measures of white birch explained from none to 18% of individual moose within-home range selection; elemental landscapes are applicable to movement and foraging ecology (Chapter 2). Continuous nutritional landscapes can be achieved by methods other than StDMs. In ecosystems where forage is aerially visible, high-resolution airborne imaging spectroscopy can map plant nitrogen contents (Schweiger et al. 2015). StDMs have the advantage of using ground collected plant samples (Leroux et al. 2017), making them a viable option in forested landscapes and be consumer-specific by measuring specific plant parts. Collectively, the ES framework provides means to study nutritional ecology of herbivores from the bite to the landscape-level.

4.4 More than elemental ratios

Elemental currencies can be measured in various units, and so the ES framework allows for a small set of currencies to test a variety of foraging hypotheses. Traditionally, ES has

focused on how the variation of organismal elemental ratios, particularly C:N, C:P and N:P ratios explains ecosystem functioning and dynamics (Sterner and Elser 2002). Aside from ratios, we can describe plant resources as elemental quantities (e.g. grams) or concentrations (%), each representing the resource differently. Elemental quantities and concentrations are the two components used to calculate elemental ratios. For instance, quantity C can equate total energy within a space (Barboza et al. 2009), while N composition often represents plant quality (Ball et al. 2000; Van der Wal et al. 2000; Moore et al. 2010; Champagne et al. 2018) because it correlates with protein content (Mariotti et al. 2008). Elemental compositions pose opportunity to answer foraging ecology questions, while elemental quantities have broad implications in areas of nutritional ecology, energetics, and ecosystem ecology, but neither alone adequately can address the impacts of PSCs made by plants to deter herbivory.

Elemental compositions may offer a more precise estimate of plant quality than elemental ratios under certain circumstances. N compositions do not necessarily correlate with C:N ratios because both C, in its many forms, and N contribute to a plant's C:N ratio (Jasienski and Bazzaz 1999). I tested assumptions of ungulate selection for plant quantities and qualities across scales (Chapter 2). I used StDM outputs of white birch C quantities (g/m^2) as a proxy for forage biomass. By using N composition (%), instead of C:N ratios, as my estimate for birch quality, I was able to directly compare moose selection for independent measures of quantity and quality and uncover divergent, individual quantity-quality trade-offs. Such trade-offs show that while plants are variable in a limited resource, like N, their consumers may be plastic in how they attain the

resource. In this case, some moose prioritise foraging in areas with greater concentrations of N, while some prioritize areas of high forage biomass.

The daily intake of C, N and P by herbivores represents both their requirements for body homeostasis and what is removed from plant communities. Herbivores consume plants of varying C and N content, digest and assimilate what is required for their body maintenance and production, and return some portion of C and N back into their environment via respiration and excretion (Sperfeld et al. 2017). Thus, measuring herbivore resource intake in terms of elemental quantities links not only behaviours to metabolic requirements, but also ecosystem nutrient cycling. Daily elemental requirements can be estimated using feeding trials, in which an animal is provided food of a known elemental composition and its daily intake rate is measured. Feeding trials can control for environmental effects such as temperature, seasons, and reproductive stage, and determine homeostasis requirements at various energetic and nutrient states (Sperfeld et al. 2017). If hares feed to attain a certain amount of the limited N in their environment (White 1993), then results of my 3rd chapter find hares on average require 1.28 g of N per captive day during autumn. During this season, snowshoe hares grow winter coats as an evolved strategy for reducing their metabolism in the winter (Sheriff et al. 2009), but timing of winter coat growth varies within a population. I found that, on a given day, hares with fully developed winter coats on average require 62.24 g less spruce per day than hares with no winter pelage, or 0.62 g less N. At larger extents, when we cannot measure intake rate but rather resource selection by an animal, patches of plant elemental quantities can represent the total available resource. Landscapes of resource

elemental quantities could eventually be incorporated into carrying capacity estimates and wildlife density predictions (Leroux et al. 2017). Measuring how herbivores move through patches of resource elemental quantities could help predict herbivore impacts on zoogeochemistry and how herbivores move elements across and within ecosystems (Schmitz et al. 2018).

Some may argue that elemental currencies cannot proxy plant quality because they lack consideration for plant chemical defences. There are numerous examples of herbivore selection against PSCs (Felton et al. 2018; Heroy et al. 2018; Wam et al. 2018). PSCs take many forms and can have negative effects on herbivores unequipped with detoxification mechanisms (Freeland and Janzen 1974). Furthermore, PSC concentrations can change according to growing conditions, like UV radiation (Keski-Saari et al. 2005), so herbivores should avoid PSCs not just by interspecific selection, but intraspecific selection as well (Laitinen et al. 2002). ES based foraging studies cannot infer responses to PSCs because elemental composition analyses do not differentiate between sources of elements. At most, we can assume if PSCs are overwhelmingly carbon-based compounds (e.g. phenols (Worker et al. 2015) or tannins (Wam et al. 2018)), like in plants in systems of low-nutrient availability (Bryant et al. 1982), then C:N ratios should negatively correlate with quality. However, making this assumption prevents any inference on PSC consumption or selection. Moreover, some species produce nitrogen containing PSCs such as toxic “uncommon” amino acids (Freeland and Janzen 1974; Bell 1976), or non-protein amino acids (Huang et al. 2011). Even more frustrating is tannin-bound N, in

which tannins do not consist of N but reduce the absorption rate of plant protein post-consumption (Sinclair et al. 1988; McArt et al. 2009).

I propose that the ES framework must expand its currency to adequately address PSCs in herbivore foraging ecology contexts. In systems where plants either produce N-containing PSCs or N-binding tannins, a potential solution would be to categorize N contents as either available (i.e., protein) or non-available N (i.e., tannin-bound; Felton et al. 2009). The ratio of available N to non-available N would therefore correlate with quality and account for PSCs. This solution maintains the ecological explicitness of elemental currencies, but would require more precise chemical analyses of plants than PSCs or N alone. A second solution, though less ecologically explicit, is to measure N:PSC ratios of plants. This method could recycle data from studies that measured herbivore responses to N (or protein) and PSCs. The idea of N:PSC ratios is not new. Schmitz et al. (1992) tested optimal foraging predictions that the effectiveness of PSCs is conditional on a plant's nutritional content. These predictions assume that herbivores maximize nutrient intake and that PSCs are not necessarily toxic but reduce the digestibility of proteins. Schmitz et al. (1992) offered snowshoe hares the option of the defended *Populus balsamifera* and the less defended *Salix glauca* under various manipulations and found the defences of *P. balsamifera* to be less effective when of higher nutrient content. Since then, many studies have uncovered cases of herbivores balancing nutrient and PSC intake, but do not make predictions or measure in terms of N:PSC ratios explicitly (Rodgers and Sinclair 1997; Seccombe-Hett and Turkington 2008). For example, Behmer et al. (2009) found that when a food had lower protein

content, locusts (*Locusta migratoria*) were deterred more by the presence of tannins. Overall, there is substantial evidence that N:PSC ratios can represent plant quality and that herbivores aim to maintain a minimum N:PSC intake.

4.5 Conclusion

Herbivores regulate the intake of key nutrients, fibre, energy, and toxins to maintain body homeostasis under varying physiological demands and their foraging behaviours reflect this continuous regulation. The feeding choices and intakes of herbivores contribute to the functioning of ecosystems, determining what nutrients is removed from primary producers and moved up trophic levels. Integrating elemental currencies and notions of ES with herbivore foraging creates direct links between animal behaviours, physiological pathways, and homeostasis with ecosystem nutrient cycles. Elemental currencies can be represented as ratios, quantities, and compositions, offering a diverse set of tools to measure food availability and quality. While elemental currencies cannot explain all aspects of terrestrial herbivory, they can be expanded on to include effects of carbohydrate varieties and PSCs. I highlight that any unifying framework for nutritional ecology must also describe feeding processes at multiple scales of foraging— a strength of ES and elemental currencies.

My work demonstrates, at multiple scales, that mammalian herbivores respond to plant stoichiometry. From the landscape to the patch, I measured moose resource selection across elemental landscapes using StDMs (Chapter 2), and, at the bite-level, snowshoe hare preferences for plant elemental quality using cafeteria experiments

(Chapter 3). Both studies found herbivores to select for limited elemental nutrients, but variably. Moose appear to make individual quantity-quality trade-offs when selecting for white birch within their home ranges, with some prioritizing quality over quantity and vice-versa. Snowshoe hares overall prefer black spruce of higher nutritional content. This preference is exaggerated in hares originating from low-quality localities, or those with higher nutritional demands, and reduced in hares bearing less insulative coats and experiencing lower temperatures, or those with higher energetic demands. Moose remove formidable amounts of browse from plants daily (Schmitz et al. 2014; Ellis and Leroux 2017), and snowshoe hare densities largely influence predator abundances (Humphries et al. 2017; Krebs et al. 2018); both species are key players in boreal functioning, thus their fitness and feeding habits are too.

My thesis contributes to the growing ES-nutritional ecology framework by providing evidence that herbivores do respond to elemental currencies of forage, both compositions and quantities, from the home range to the bite level, and that some feeding variation can be explained by the elemental availabilities within individual home ranges and energetic demands. Herbivores are stoichiometrically constrained, but remain flexible in how they attain a limiting element. Overall, ES and its notions can and have contributed to unifying nutritional ecology of terrestrial herbivores across scales while being ‘nutritionally, organismally, and ecologically explicit’.

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Table 4.1. As the scale of foraging increases from the bite to the landscape or region, a herbivore makes fewer decisions per unit of time and considers forage quantity or biomass more and forage qualities less, reflected in the selection criteria associated with each scale. At larger scales of selection, herbivores act on larger levels of plant biological organization. Therefore, the ecological impacts from herbivore foraging depend on scale. In addition, factors influencing herbivore feeding choices are not consistent across scales. To test hypotheses regarding such mechanisms, we must measure forage components and herbivore responses at multiple scales, but no method can accommodate all scales.

Scale	Selection Criteria	Level of Plant Selection	Ecological Impacts	Herbivore Influences	Methods
Bite	N, P, PSCs, Size	Organ, Individual	Plant natural selection	Homeostasis, Metabolism, Life stage	Feeding trials, Cafeteria experiments
Patch	N, P, PSCs, Biomass	Population	Abundances, Community, Reproduction	Daily Intake, Life stage, Forage selection, Predation risk	Direct Observation, Browse surveys, iSSAs*, Patch treatment, StDMs*
Home range	Biomass, N, P, Habitat, Topography, Water	Community	Succession, Productivity, Nutrient movement	Intake rate, Predation risk, Movement rate	RSFs*, StDMs*, Airborne imaging spectroscopy
Landscape or Region	Climate, Water, Biomass, NDVI	Ecosystem, Biome	Species distributions, Nutrient cycling	Intake rate, Migration, Reproduction	RSFs*, StDMs*, Airborne imaging spectroscopy

*Acronyms: iSSA = Integrated step selection analysis; StDM = Stoichiometric distribution model; RSF = Resource selection function.

APPENDIX A. CHAPTER 2 SUPPLEMENTARY FIGURES AND TABLES

A.1 Supplementary Tables

Table A1. Explanatory covariates used in the stoichiometric distribution models to predict the white birch quantity carbon and nitrogen composition values, the type of data each covariate provided, and the description of each covariate's calculation or categories.

Predictor Variable	Data Type	Description/Categories
Normalised aspect	Continuous	Direction of slope
Slope	Continuous	Tangent of surface angle to horizontal
Elevation	Continuous	Height above sea level
Landcover	Categorical	2 categories: Coniferous and other (deciduous or mixed wood)
Stand Height	Categorical	4 categories: 0-6.5m; 6.6-9.5m; 9.6-12.5m; 12.6-21.5m.
Dominant Tree Species	Categorical	3 categories: 75% balsam fir; 50-75% balsam fir with remainder black spruce and/or white birch; 50-75 black spruce or white spruce with remainder balsam fir white birch, or tamarack.

Table A2. Descriptive statistics (means, medians, standard deviations), and the correlation (Pearson's r) for white birch carbon quantity (log g/m²) and nitrogen composition (%), from each designated study area and home range. For every moose individual, we provide its sex and collar year.

MCP	Sex	Year	Area (km ²)	Quantity Carbon			% Nitrogen			C x N correlation
				Mean	Median	SD	Mean	Median	SD	Pearson's r
PP and OMP	-	-	907	-1.65	-1.67	0.89	2.78	-1.67	0.28	-0.01
PP	-	-	514	-1.92	-2.19	0.89	2.82	-2.19	0.27	0.11
OMP	-	-	393	-1.41	-1.53	0.82	2.74	-1.53	0.28	-0.04
PP2	F	2013	26.27	-1.7	-1.7	0.72	2.77	2.73	0.28	0.03
PP3	M	2011	10.64	-1.87	-1.89	0.7	2.66	2.68	0.29	-0.37
PP4	F	2011	16.28	-2.46	-2.59	0.5	2.78	2.79	0.15	-0.16
PP5	F	2011	22.97	-2.27	-2.31	0.63	2.71	2.72	0.23	0.49
PP6	F	2015	2.12	-1.99	-2.22	0.72	2.63	2.67	0.18	0.59
PP8	F	2011	3.13	-2.08	-2.24	0.7	2.61	2.63	0.15	0.09
PP9	M	2011	5.13	-1.82	-1.65	0.7	3	3	0.14	0.12
OMP4	F	2014	20.28	-1.37	-1.57	0.61	2.79	2.8	0.27	0.13
OMP5	F	2015	10.69	-1.79	-1.76	0.54	2.85	2.86	0.13	0.43
OMP7	M	2014	9.18	-0.8	-0.82	0.83	2.75	2.77	0.26	0.13
OMP11	F	2014	12.06	-1.34	-1.31	0.66	3.04	2.98	0.26	-0.44

OMP12	F	2014	6.68	-1.19	-1.37	0.66	3.03	3	0.26	-0.28
OMP13	F	2015	15.08	-1.74	-1.71	0.96	2.82	2.82	0.18	-0.08
OMP15	M	2014	3.51	-1.36	-1.44	0.83	2.68	2.71	0.19	0.08

Table A3. Summaries (β -coefficients and standard errors) of additional terms in the patch-scale integrated step selection functions which are fit with conditional logistic regressions. Terms include step lengths (SL), turn angles (TA), and their interactions between the other, and with carbon quantities (C), nitrogen concentrations (N). For each moose individual we also provide its mean step length (SL; meters) and mean turn angle (TA; degrees) from used steps.

ID			SL		TA		C x SL		N x SL		C x TA		N x TA		SL x TA		
	SL	TA	R ²	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Pooled	189.14	0.81	0.001	0.22	0.18	-0.8	0.35	-0.04	0.02	-0.11	0.06	0.09	0.04	0.28	0.12	0.04	0.02
PP2	187.32	14.64	0.019	0.98	0.9	-0.23	2.16	-0.14	0.15	-0.49	0.33	0	0.33	-0.15	0.78	0.19	0.11
PP3	199.48	-1.95	0.013	0.92	0.59	-1.72	1.11	-0.06	0.12	-0.39	0.29	0.6	0.21	1.16	0.51	-0.04	0.08
PP4	247.88	2.6	0.009	-1.27	1.12	0.37	2.53	-0.11	0.18	0.34	0.43	0.55	0.41	0.65	0.99	-0.13	0.08
PP5	227.14	-14.82	0.016	2.02	1.86	0.8	3.63	-0.23	0.16	-0.8	0.64	-0.33	0.29	-0.67	1.16	0.12	0.13
PP6	61.79	-18.45	0.022	6.41	2.31	9.85	3.81	0.15	0.16	-2.24	0.75	0.91	0.26	-2.85	1.21	-0.18	0.11

PP8	177.39	18.05	0.039	0.32	2.99	12.48	5.97	0.15	0.19	0.07	1.15	-0.14	0.41	-4.44	2.15	-0.21	0.19
PP9	126.3	5.72	0.01	0.21	1.67	-3.02	2.73	0.01	0.07	-0.08	0.55	0.1	0.12	1	0.89	0.09	0.09
OMP4	224.63	4.78	0.005	1	0.79	-2.56	1.78	-0.04	0.13	-0.38	0.27	0.2	0.26	0.85	0.59	0.08	0.07
OMP5	198.72	-2.28	0.006	-0.72	1.5	-3.25	2.8	0.1	0.16	0.32	0.49	-0.43	0.26	0.86	0.94	-0.01	0.09
OMP7	231.82	9.8	0.008	-0.6	0.66	-1.58	1.34	-0.03	0.07	0.21	0.24	0.26	0.13	0.47	0.47	0.13	0.07
OMP11	287.33	-5.62	0.009	-0.02	0.82	-5.55	1.66	-0.07	0.13	-0.03	0.3	0.01	0.24	1.68	0.57	0.09	0.09
OMP12	117.77	1.45	0.008	0.05	0.98	3.23	1.77	-0.04	0.1	-0.03	0.33	0.05	0.19	-1	0.59	-0.02	0.08
OMP13	209.32	-12.63	0.009	0.77	0.72	-3.29	1.44	-0.09	0.05	-0.34	0.24	0.15	0.09	1.15	0.47	0.08	0.06
OMP15	151.04	9.99	0.017	-0.29	1.15	-1.11	2.37	0.12	0.2	0.18	0.42	0.41	0.36	0.66	0.89	-0.01	0.12

A.2 Supplementary Figures

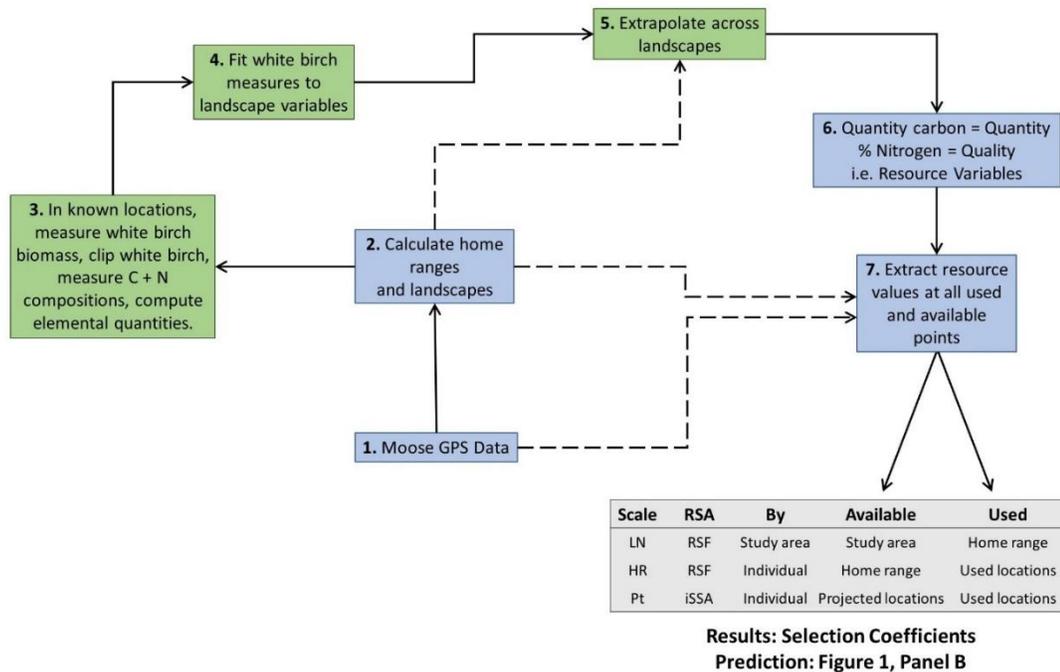


Figure A1. A diagram mapping the analysis pathway to testing the predictions of Figure 1, Panel B, using collar data and Stoichiometric Distribution Models (StDMs). Green boxes represent StDM steps. Blue boxes represent steps that created the data which were directly incorporated into the resource selection analyses (RSAs). Solid lines represent the sequence of direct steps in the total analysis, and dashed lines represent non-sequential input of steps. We used moose GPS data to calculate home ranges and landscapes, from within we sampled forage for stoichiometric measurements to then model and extrapolate across the respective landscapes. The forage measures for quantity and quality are extracted from GPS data and GPS data derived spatial extents (i.e. landscapes or home ranges) and locations (i.e. projected locations). Lastly, we ran models using appropriate data for each scale of foraging.

APPENDIX B CHAPTER 3 SUPPLEMENTARY FIGURES AND TABLES

B.1 Supplementary Tables

Table B1. Results from linear mixed models which ranked below the top ranked models ($\Delta AIC > 2$; see table 3.3 for top ranked models). Models attempt to predict snowshoe hare consumption of black spruce when offered in pairs of high and low nutrient rank during cafeteria experiments (n = 44).

Covariate	Null	Phosphorus	Nutrient	Full
Rank	-	63.17* (36.33)	156.37** (60.88)	148.71*** (51.84)
Coat	-	-	-	-37.61*** (11.67)
Temp	-	-	-	-3.34 (2.07)
Origin N	-	-	-5.17 (63.53)	-4.76 (53.28)
Origin P	-	88.86 (200.52)	103.66 (261.04)	67.43 (223.29)
Coat*Rank	-	-	-	25.78 (15.79)
Temp*Rank	-	-	-	8.17*** (2.80)
Origin N*Rank	-	-	-155.75* (84.60)	-132.35* (72.11)
Origin P*Rank	-	-392.53 (267.98)	53.19 (347.64)	-77.28 (302.21)
Constant	63.91*** (3.33)	46.69* (27.18)	49.78 (45.72)	66.18* (38.30)
Marg. R ²	0.00	0.11	0.23	0.47
Cond. R ²	0.01	0.21	0.31	0.52

*p<0.1; **p<0.05; ***p<0.01

B.2 Supplementary Figures

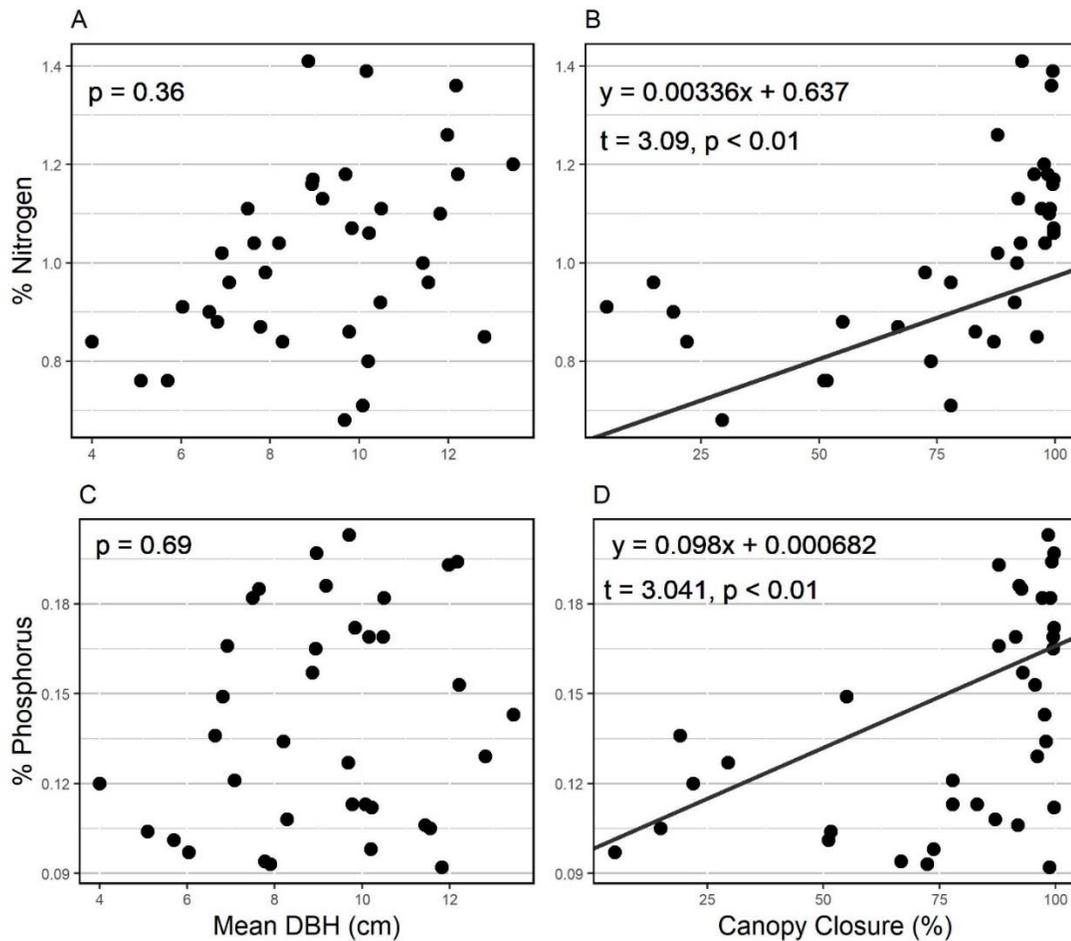


Figure B1. Black spruce N (A and B) and P (C and D) compositions sampled at 36 sites across the trapping grid plotted against site mean tree Diameter Breast Height (DBH; A and C) and canopy closure (B and C). Linear regressions are shown for the significant effect, canopy closure, for both N and P compositions. Collectively, DBH and canopy closure explained 36.0% and 25.1% of spruce N and P variation respectively.

APPENDIX C CHAPTER 3 SPRUCE OFFERING SUBSAMPLING

C.1 Subsampling

During the summer of 2017 black spruce (*Picea mariana*) was sampled at every trap location on our trapping grid with black spruce < 2 m and analysed samples for N and P composition (see methods). From this analysis, we designated 3 areas as being ‘high nutritionally ranked’ (highest %N and %P) or ‘low nutritionally ranked’ (lowest %N and %P). During the fall of 2018, we clipped black spruce (*Picea mariana*) from all six locations, and pooled clippings across locations into bags according to presumed nutritional rank. These ranks of spruce then became the two offerings for snowshoe hare cafeteria experiments (n = 22). We tested whether clippings taken for autumn cafeteria experiments followed similar trends to the original summertime samples. To do this, we subsampled approximately 17 wet grams from each bag of pooled spruce (n = 11), and sent samples to the Agriculture Food Lab (AFL) at the University of Guelph for elemental analysis (see methods).

C.2 Predictions

We anticipated that autumn subsamples would have lower and more variable N and P compositions than original summer sampling because plants become more lignified and C-heavy throughout the growing season. We predicted that the subsamples would maintain the trend of original rank- subsamples from of high rank area clippings would have higher N and P than subsamples from low rank area clippings.

C.3 Results

The median C, N, and P compositions for predicted high ranked spruce subsamples were 52.23% (SD = 0.42), 0.98% (SD = 0.073), and 0.11% (SD = 0.017) respectively (S1). For predicted low ranked spruce, we measured C, N and P compositions of 52.52% (SD = 0.51), 0.99% (SD = 0.026), and 0.099% (SD = 0.018) respectively (S1). Predicted ranks were not significantly different in C ($p = 0.77$), N ($p = 0.93$), or P ($p = 0.16$) compositions. N and P compositions of subsamples did correlate ($r = 0.69$; S2). Compared to original samples from the summer of 2017, for which we based rank designations, the autumn subsamples did not show as much variation in N and P compositions- subsamples did not have as high nor as low N and P compositions as originally high-ranked or low-ranked samples (S3).

C.4 Discussion

Despite strong evidence that hares selected preferentially for high-N and P browse over low N and P browse in the cafeteria experiments, truthing our rank categories with subsampling was inconclusive. We cannot be certain why subsampling did not show the expected rank-trend, but we think the most likely explanation is a methodological one. Original summer sampling took approximately 10-20 g of newly grown browse from multiple juvenile (< 2 m) trees within plots to control for variation from tree and branch age. To clip enough spruce for autumn-timed cafeteria experiments, we clipped > 1000 g of browse at a time and subsampled after we pooled and mixed clippings. This could have caused subsamples to be from fewer individual trees than original sampling and

inter-individual effects as adult trees have more browse and likely more variability in browse quality.

After we reviewed the subsample results, we decided to test how frequently a subsample would yield high-rank spruce that was indeed higher in N and P. We randomly drew a high and a low ranked subsample 100 times using the sample function in base R and calculated the percentage of times the high-ranked subsample was higher in N and higher in P than the low-ranked subsample. We repeated this process 100 times and then created a distribution of percentages of times the subsamples were correctly ranked (S4). On average 45.97, 44.74, and 9.29% of the random draws yielded high-ranked subsamples that were higher, lower, and equal in P compositions than the low-ranked subsample respectively. Similarly, on average 45.02, 45.41, and 9.57% of the random draws yielded high-ranked subsamples that were higher, lower, and equal in N compositions than the low-ranked subsamples respectively. The 97.5th percentiles of the distribution of frequencies that yielded correctly assigned spruce ranks were 54.4% by way of N results, and 55.5% by P results (S4). In comparison, hares consumed more from the high ranked spruce in 59% of cafeteria experiments (S4) and much of the variation in their choice was explained by additional energetic and nutritional factors. If the subsamples were representative of cafeteria experiment offerings and hares selected for N and P compositions in accordance, our results were very improbably (< 1%). Therefore, we believe the subsamples were not representative of the cafeteria offerings.

We do not think the subsample results are evidence that the assignments of quality rank in cafeteria experiments were incorrect, but rather that both ranks

encapsulated a large range of quality and results of the Intraspecific Choice Hypothesis; ultimately indicating that our findings are likely conservative. Indeed, rank only explained 6% of preference. In the future, this variation can be described better by taking more subsamples from cafeteria offerings.

C.5 Supplementary Figures

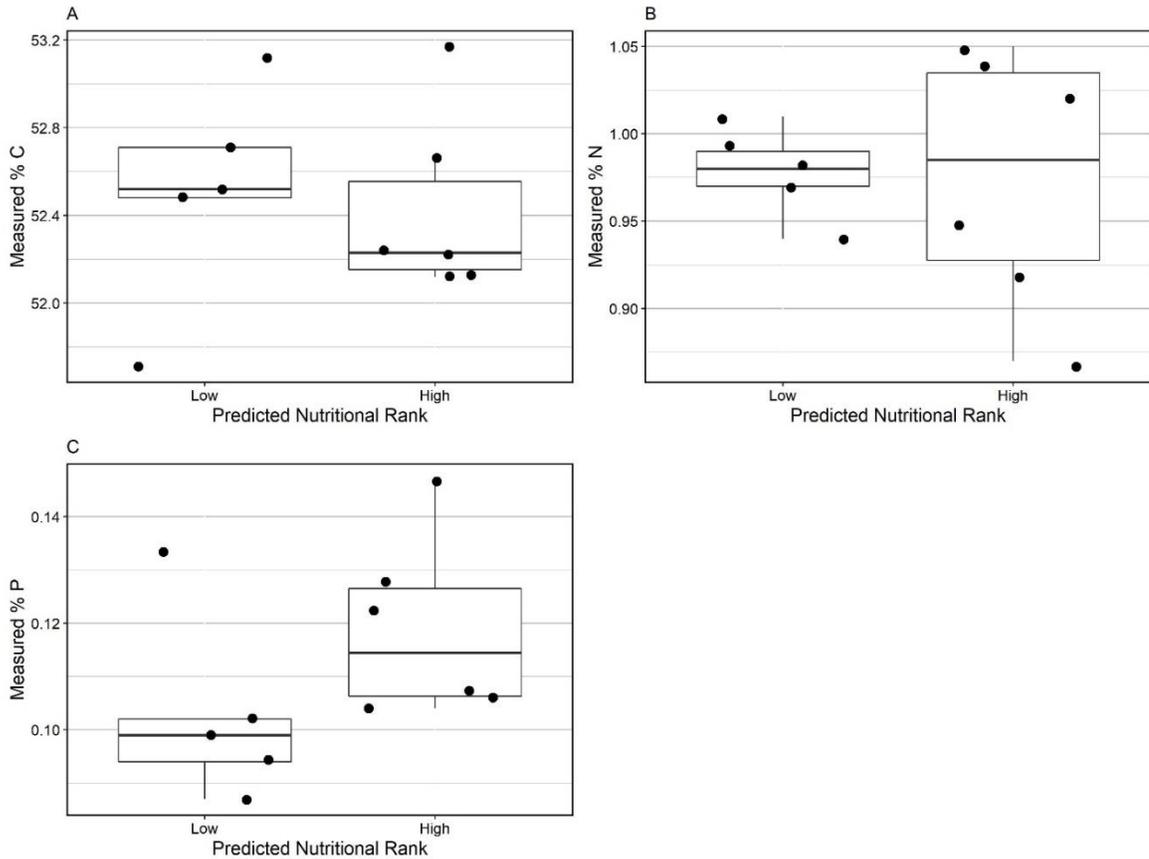


Figure C1. Carbon (A), Nitrogen (B), and Phosphorus (C) compositions of subsamples ($n = 11$) of black spruce (*Picea Mariana*) offerings for snowshoe hare cafeteria experiments during the autumn of 2018. Spruce offerings were clipped from areas of the trapping grid where original sampling from the summer of 2017 found either high N and P (high nutritional rank) or low N and P (low nutritional rank). We predicted that fall offerings would show a similar trend to the summer samples and that spruce from high ranked areas would have higher N and P compositions, and lower C compositions, than low ranked areas.

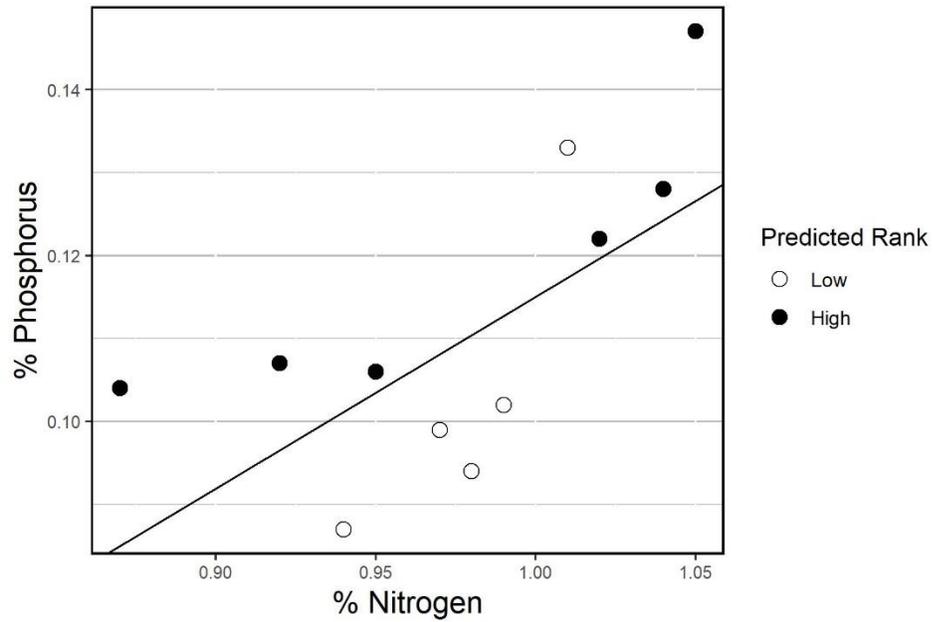


Figure C2. P versus N compositions of subsamples (n = 11) of black spruce (*Picea mariana*) offerings in snowshoe hare cafeteria experiments during the autumn of 2018. Subsample N and P compositions correlated ($r = 0.69$). When plotted against each other with the linear regression shown, high rank subsamples (solid), fell above the line of best fit (lower N:P), while low rank subsamples (open) mostly fell below (higher N:P).

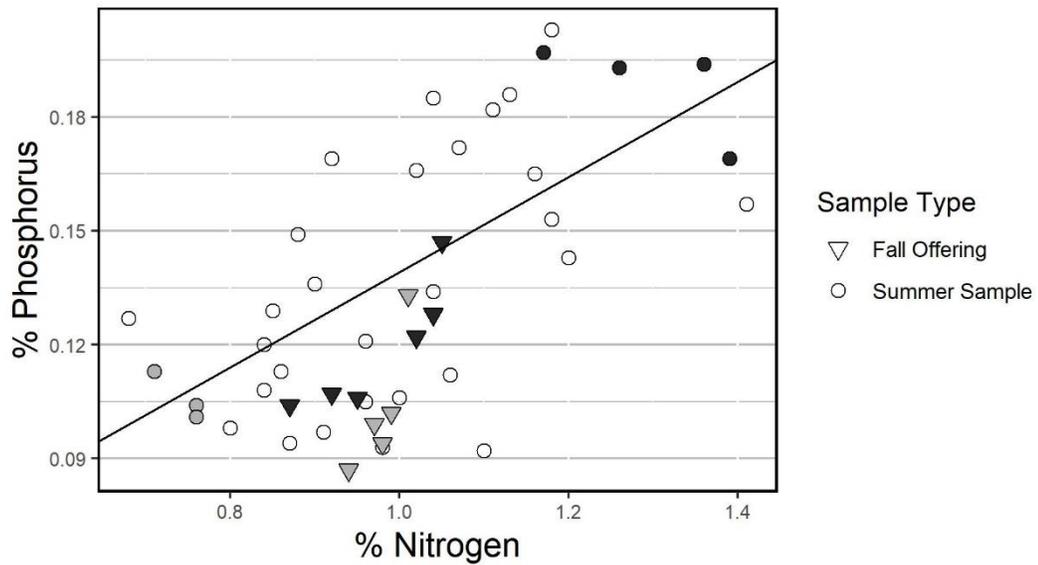


Figure C3. The original measures of black spruce (*Picea Mariana*) N and P compositions across the trapping grid (Figure 2 panel C) from sampling during the summer of 2017 (n = 36; circles) for which we choose areas of highest N and P (dark shade) and lowest N and P (light shade) to supply the ‘high nutritional rank’ and ‘low nutritional rank’ spruce respectively in cafeteria experiments during the autumn of 2018. N and P compositions of subsamples from offerings from the autumn of 2018 for experiments are also shown (n = 11; triangles). The shade of subsample values indicates whether it was taken from clippings of the ‘high rank’ areas (dark) or ‘low rank’ areas (light).

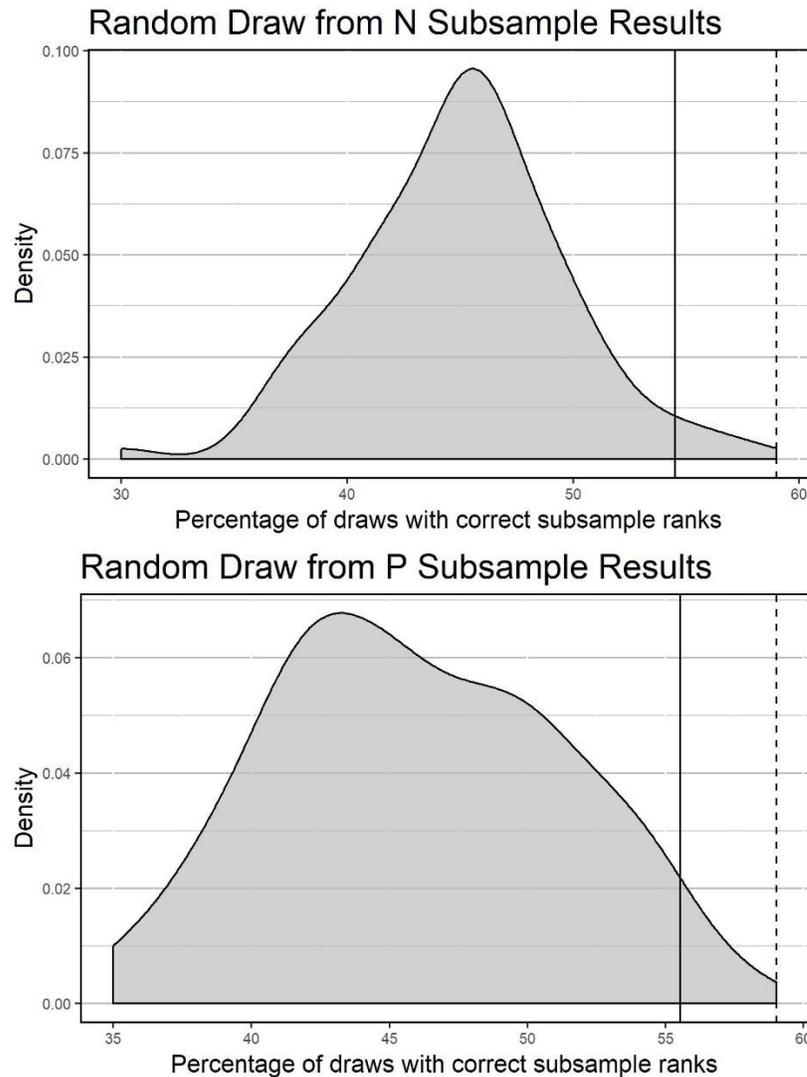


Figure C4. Results from 100 sets of 100 random draws of pairs of a high and low-ranked spruce subsample. From each draw set, we calculated the percentage of times in which the high-ranked subsample was indeed higher in N or P and then plotted the densities of this distribution across all 100 sets. Solid lines represent the 97.5 percentiles of each distribution and dashed lines represent the percentage of cafeteria experiments using spruce offerings that supplied the subsamples in which hares consumed more of the high-ranked spruce (59%).