University of Alberta

GETTING TO THE ROOT OF THE MATTER: GRIZZLY BEARS AND ALPINE SWEETEVTCH IN WEST-CENTRAL ALBERTA, CANADA

by

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DEDICATION

In dedication to my parents Brian and Karen.

ABSTRACT

Wildlife habitat selection is influenced by gender, offspring-dependency, resource availability, and spatiotemporal variation in resource nutrition. In consideration of these factors, this thesis examines alpine sweetvetch (*Hedysarum alpinum*) root and its relationship to grizzly bears (*Ursus arctos*) in west-central Alberta, Canada.

I observed sexually segregated, offspring-dependent functional responses in selection for sweetvetch habitat that was further affected by inter-annual patterns in spring climate (*i.e.*, Pacific Decadal Oscillation). Selection patterns suggested that habitat segregation was due to differences in nutritional requirements between sexes and offspring predation risk. Nutritional analyses of roots indicated that temporal patterns in protein content were influenced by spatial variations in temperature and soil. This spatiotemporal heterogeneity benefits grizzly bears by prolonging the availability of nutritious roots, and may explain why sweetvetch habitats in the mountains were relied upon throughout the spring and how bears could rely on a root digging (habitat) strategy.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

In order to understand the behaviour and ecology of grizzly bears (*Ursus arctos*), it is essential to first understand their diet (McLellan and Hovey 1995). To understand the diet of grizzly bears, you must also have an understanding of their anatomy. Two defining characteristics of grizzly bears are their long curved claws and large ‘hump’ which figures prominently above their shoulders. Together these attributes may be considered adaptations to digging (Herrero 1978; Craighead and Mitchell 1982), and are thought to allow grizzly bears to excavate for underground foods such as, small mammals, roots, and insects, behaviour which differentiates them from black bears (*Ursus americanus*; Herrero 1978).

Roots and bulbs of plants are important food resources for grizzly bears in many areas of North America. In the Yellowstone ecosystem, grizzly bears commonly dig biscuit root (*Lomatium cous*) and yampahs (*Perideridia gairdneri*; Mattson et al. 1991; Mattson 1997), as well as pondweed (*Potamogeton* spp.)and sweet-cicely roots (*Osmorhiza* spp.; Mattson et al. 2004). The bulbs of glacier lilies (*Erythronium grandiflorum*) are commonly dug by grizzly bears in Glacier National Park, Montana (Tardiff and Stanford 1998), as well as in south-western Alberta and south-eastern British Columbia (Personal Observation; McLellan and Hovey 1995). North of the USA-Canada border, grizzly bears commonly dig sweetvetch (*Hedysarum* spp.; Fabaceae) roots, which are uncommon in the US Rockies (Mattson 1997). Sweetvetch roots are typically consumed during the spring and fall, although sometimes also eaten during the active growing season, especially during periods of low berry production (Pearson 1975; Murie 1981; Hamer and Herrero 1987; Hamer et al. 1991; Munro et al. 2006). In west-central Alberta, the principal root excavated and consumed by grizzly bears is alpine sweetvetch (*Hedysarum alpinum*; Munro et al. 2006).

Alpine sweetvetch, also known as pink sweetvetch, bear root, Eskimo potato, and liquorice root, is a circumpolar perennial plant that is widely distributed in northern parts of North America, being found throughout the western boreal forest, aspen parkland, Canadian Rocky Mountains and Foothills, as well as across the arctic tundra (Hamer 1985; Hamer and Herrero 1987; Johnson et al. 1995; McLellan and Hovey 1995; Treadwell and Clausen 2008). In Alberta, alpine sweetvetch is typically found in meadows, open moist woods, slopes, and disturbed areas, and can be found at both high and low elevations (Johnson et al. 1995; Munro et al. 2006; Nielsen et al. 2010). Alpine sweetvetch flowers are pollinated by insects, with pollination by bumble bees (*Bombus flavifrons*) and honey bees (*Apis* spp.) commonly reported (Bassendowski et al. 1989; McGuire 1993).

Alpine sweetvetch has an edible taproot and was traditionally consumed by Native Americans (Holloway and Alexander 1990; Moerman 1998; Johnson et al. 1995; Treadwell and Clausen 2008). Roots can be eaten raw, boiled, baked, or fried, and are harvested in the fall through to spring, when the root is considered to be the most palatable and nutritious (Johnson et al. 1995). During the summer the root becomes dry and woody and is therefore not consumed (Johnson et al.

1995). This is typical of many short stature perennial plants, where above ground spring growth is dependent on resources that have been translocated to roots the previous winter (Clark 1977). The above ground vegetative growth of alpine sweetvetch is also consumed by other animals, including black bears (Kendall 1986), and large ungulates such as American bison (*Bison bison*), Dall's sheep (*Ovis dalli*), caribou (*Rangifer tarandus*), and moose (*Alces alces*; Gucker 2007).

Similar to humans, grizzly bears typically consume alpine sweetvetch roots during pre- and post-flowering stages when it is most nutritious (Hamer and Herrero 1987). The availability of these nutritious roots at a time when resources are relatively scarce make alpine sweetvetch a critical resource for many bears during spring after den-emergence and in late fall before den entry (Hamer and Herrero 1987; Munro et al. 2006). However, some bears excavate roots for consumption throughout the summer, especially at high elevations (Hamer and Herrero 1987; Munro et al. 2006).

In west-central Alberta, alpine sweetvetch roots can be found from the lower elevation mountain and foothills habitats to higher elevation alpine meadows. Seasonal use of alpine sweetvetch by bears in west-central Alberta is typical of other regions in the Canadian Rocky Mountains, including the Flathead River drainage in south-eastern British Columbia, Waterton National Park, Banff National Park, and Kananaskis country, where yellow sweetvetch (*Hedysarum sulpherescens*) also occurs (McCrory and Herrero 1981; Holcroft and Herrero 1984; McLellan and Hovey 1995). Yet, despite the importance of alpine sweetvetch to grizzly bears in many regions, relatively little is known about this resource.

Objectives

This thesis investigates alpine sweetvetch and its relationship to grizzly bears in west-central Alberta, Canada. The study took place within the Foothills Research Institute's core study area near the town of Hinton and south along the foothills and eastern slopes of the Canadian Rocky Mountains (see Chapters 2 and 3 for specific study area maps). This thesis contains four chapters and one appendix, including the general introduction and conclusion, and was written in accordance to University of Alberta guidelines for a paper format thesis. Formatting is consistent throughout the manuscript, with references formatted according to the journal Oecologia (Springer). A brief description of chapters following the general introduction (Chapter 1) is included below.

In Chapter 2, I examine the selection of alpine sweetvetch patches in a mountainous (subalpine and alpine) portion of the study area. Specifically, I try to elucidate whether grizzly bears display a functional response in selection for alpine sweetvetch habitat and whether selection varies between bears of different sex-dependency classes (*i.e.*, males, solitary females, and females with dependent offspring of different age classes). I also examine temporal factors that influence grizzly bear selection of alpine sweetvetch patches, including inter-annual variation in weather via teleconnections in North Pacific Ocean climate variability, and intra-seasonal variation. In Chapter 3, I evaluate how spatial variation in environmental factors influences temporal variation in the nutritional quality of alpine sweetvetch roots, and whether this spatio-temporal variation has the potential to benefit grizzly bears by prolonging the period they can access more nutritious roots. After the presentation of the two data chapters, I present a general discussion of the thesis in Chapter 4. Finally, Appendix A provides a summary of nutritional and digestibility estimates for grizzly bear food items. These estimates are to be used in future regional grizzly bear habitat modelling projects within the Foothills Research Institute Grizzly Bear Program, as well other suitable applications, with the intention of eventually being submitted for publication as a separate article in peer-reviewed literature.

It truly is an honour and privilege to be allowed the opportunity to study the grizzly bear for my M.Sc. thesis. It is my hope that in addition to increasing our knowledge of the dynamic relationship between alpine sweetvetch and grizzly bears, that the nutritional work herein will ultimately aid in the understanding, conservation, and management of grizzly bears both within the study region and beyond.

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CHAPTER 2

GETTING TO THE ROOT OF THE MATTER: SEXUAL SEGREGATION AND FUNCTIONAL RESPONSES IN HABITAT SELECTION OF GRIZZLY BEARS

1. INTRODUCTION

Habitat models based on radio telemetry and/or field survey data are often used by ecologists to gain insight into the patterns and processes that influence wildlife. Frequently the purpose of such models is to study habitat use and selection in order to understand spatial patterns that influence the behaviour of species. Habitat selection is inferred through the relative use of some habitats disproportionate to other habitats, and can take place at several spatial scales (Johnson 1980; Aebischer et al. 1993). Quantifying habitat selection is often achieved by relating proportional habitat use relative to proportional habitat availability within an animal's home range (Johnson 1980; Manley et al. 2002). A major criticism of this approach is the assumption that habitat use is directly proportional to habitat availability (Mysterud and Ims 1998). Studies have since shown that functional responses in habitat use and selection (*i.e.*, the use or selection of a habitat that differs dependent upon the availability of that habitat) occur across a range of taxa including gray squirrels (*Sciurus carolinensis*) and ring-necked pheasants (*Phasianus colchicus*; Mysterud and Ims 1998), tropical birds (Gillies and St. Clair 2010), grizzly (*Ursus arctos*; Gillies et al. 2006) and polar (*U. maritimus*; Mauritzen et al. 2003) bears. For example, a functional response may occur when an animal shows strong selection for a scarce but necessary resource, yet demonstrating avoidance for the same resource when abundant. Yet another type of functional response may occur when a habitat specialist increases their selection for a preferred resource as it becomes more abundant. This form of a functional response has been observed in forest-specializing barred antshrikes (*Thamnophilus doliatus*) and rufous-naped wrens (*Campylorhynchus rufinucha*), whereby they increase their selection for forest habitats as forests availability increases (Gillies and St. Clair 2010). If functional responses are ignored when present, the strength of habitat selection will likely be attenuated and the relationships between habitats and animal selection misinterpreted. For instance, selection for a habitat can change (*e.g.*, from avoidance to selection) dependent upon availability despite use remaining constant.

Another important consideration in resource selection modelling is sexual segregation of habitats due to sexual dimorphism (Gordon et al. 2004). Male-biased sexual dimorphism is common in both herbivorous and carnivorous mammals (Isaac 2005). The body size or foraging selection hypotheses (Main et al. 1996; Ruckstuhl and Neuhaus 2002; Rode et el. 2006) predicts that sexual segregation can occur when males select for habitats that maximize their foraging opportunities. Because of their larger size, males experience higher nutritional costs during periods of low resource availability, which can result in nutritionally driven sexual segregation of habitats where dominant males exclude or deter subdominant animals from higher quality resources (Mooring et al. 2005; Rode et al. 2006). Female reproductive status can also affect habitat segregation. The reproductive strategy-predation risk hypothesis predicts that females will select habitats that minimize the risk of predation to dependent offspring (Main et al. 1996; Bleich et al. 1997; Ruckstuhl and Neuhaus 2002; Rode et al. 2006). Whereas herbivores would be minimizing risk of predation by predators, risk of predation for carnivores often includes infanticide by conspecific adult males (Swenson et al. 1997; Dahle and Swenson 2003; McLellan 2005; White 2005). Due to differences in nutritional requirements between larger-bodied males and smaller-bodied females, the smaller-bodied females can successfully occupy lower quality habitats, thereby avoiding resource competition with adult males while at the same time lowering predation risk to dependent offspring (Rode et al. 2006). However, among some dimorphic ungulate species, habitat segregation can occur due to the additional demands for protein and energy experienced by lactating females that subsequently requires them to select areas with high quality forage, while large males select habitats that allow for a high intake of intermediate quality forage (Barboza and Bowyer 2000). Therefore, sexual segregation of habitat use can result from nutritional constraints imposed by sexual dimorphism as well as differing reproductive strategies between the sexes (Rode et al. 2006).

Temporal variability in the availability of resources can also affect resource selection (Wiens et al. 2008). This is because seasonality in resource abundance, nutritional quality, and phenology can cause shifts in diet, and therefore, habitat selection of animals (Boyce et al. 2002; Nielsen et al. 2002;

Munro et al. 2006). Habitat generalists that rely on a variety of seasonal foods are likely to be more responsive to seasonal changes in resources than habitat specialists that tend to rely on a single resource. For example, the African bush elephant (*Loxodonta africana*) is widely distributed across southern Africa using habitats depending on the seasonal availability of widely dispersed food resources (Codron et al. 2011). Conversely, habitat specialists such as koala (*Phascolarctos cinereus*), which rely on the leaves of eucalypt (*Eucalyptus* spp.) trees as a food source, have relatively small home ranges and select for habitats with high proportions of these trees (Rhodes et al. 2005).

The grizzly bear is a sexually dimorphic generalist omnivore that utilizes a variety of habitats and relies on a wide variety of seasonally available food resources (Hamer and Herrero 1987; McLellan and Hovey 1995; Mattson et al. 2004; Munro et al. 2006; Edwards et al. 2010). In west-central Alberta, Canada, grizzly bears often rely on the roots of alpine sweetvetch (*Hedysarum alpinum*) in spring after den emergence and in fall before den entry due to the scarcity of other food resources and its high nutritional quality during this time (Hamer and Herrero 1987; Munro et al. 2006). While bears in this region that occupy both foothills and mountain environments consume sweetvetch roots, root digging is especially prevalent in subalpine and alpine habitats (Munro et al. 2006). As spring progresses, bears tend to rely less upon sweetvetch roots as young grasses and forbs emerge and as the nutritional quality of roots decline (Hamer and Herrero 1987; McLellan and Hovey 1995; Munro et al. 2006).

Pronounced sexual dimorphism in grizzly bears means that adult male bears are more limited than females by the abundance and quality of food resources in gaining body mass (Welch et al. 1997; Rode and Robbins 2000; Rode et al. 2001). As a result, habitat segregation in grizzly bears may occur due to differences in dietary requirements which require adult males to eat meat to sustain their body mass, while females can subsist on completely vegetarian diets (Jacoby et al. 1999; Rode et al. 2001; Rode et al. 2006). In addition to dietary differences, habitat use by female bears, and particularly those with cubs, is affected by the presence or absence of adult males (Ben-David et al. 2004; Rode et al. 2006). In Alaska, females with cubs avoided habitats with adult males, while solitary females did not, which suggested that predator avoidance in combination with differing reproductive strategies influenced sexual segregation of habitats (Rode et al. 2006). This may be due to an increased risk of infanticide, which has been observed in bears (Olson 1993; Derocher and Wiig 1999; Miller et al. 2003).

Lactating female grizzly bears also experience nutritional costs associated with lactation (Farley & Robbins 1995, Hilderbrand et al. 2000), which is considered the most costly productive process in mammals (Thompson 1992, Robbins 1993). On the Kenai Peninsula, Alaska, females with cubs-of-the-year had the lowest lean body mass in spring after den emergence of any female reproductive class, followed by females with yearlings Hilderbrand et al. (2000). In addition, the nutritional requirements of females with offspring increase after den emergence due to increased protein content of milk, increased protein demands of fast growing cubs, and an increase in the protein metabolism of the non-fasting mother (Farley & Robbins 1995). In the fall, females with cubs-of-the-year and yearlings have approximately the same amount of lean mass as solitary females, but lower body mass, which is attributed to females with cubs utilizing lower quality habitats, or feeding during poorer time periods, in order to avoid cub predation by male bears (Hilderbrand et al. 2000). Therefore, the greater nutritional requirements of large male bears may be more important than female responses in determining habitat selection in grizzly bears (Rode et al. 2006).

In this paper, I explore functional responses, sexual habitat segregation, and seasonal and inter-annual variation in the selection of alpine sweetvetch patches by grizzly bears in subalpine and alpine regions of west-central Alberta, Canada during spring. I hypothesize that: (1) grizzly bears will display a functional response in selection of alpine sweetvetch patches. I predict that selection for patches will decrease as the proportion of available patches increases; however, I do not discount the presence of root digging specialists that increase their selection for alpine sweetvetch patches as the proportion available increases. Diet specialization related to food availability has been observed in grizzly bears as well as other species (Urton and Hobson 2005; Loudon et al. 2007; Edwards et al. 2010). For example, dietary specialization among wolves (*Canis lupus*) has been attributed to differences in food availability within home ranges (Urton and Hobson 2005), while prey availability and foraging ability result in diet specialization in grizzly bears of the Mackenzie Delta (Edwards et al. 2010). I also hypothesize that: (2) there will be differences in selection for alpine sweetvetch patches between male and solitary female bears due to differences in metabolic and nutritional requirements, where we would expect males to select less for sweetvetch patches, especially late in the spring, as they would be selecting for habitats higher in animal protein. I still expect, however, that male bears will use roots in spring because of the relative scarcity of food resources at this time. This may result in: (3) habitat segregation between males and females with dependent young where females avoid predation by adult males.

I also consider temporal factors that influence grizzly bear selection of sweetvetch patches, where I expect that (4): inter-annual variation in weather as measured by a major climate driver in the Canadian Rocky Mountains, the Pacific Decadal Oscillation (PDO), will influence the selection of alpine sweetvetch patches. I predict that warmer years will result in a decrease in selection due to earlier onset of the growing season (and more suitable growing conditions) thereby increasing the availability of alternate resources. I also hypothesize that: (5) the PDO will influence inter-seasonal use where warmer years will see bears selecting for patches earlier than colder years due to both an earlier growing season and date of den emergence.

2. STUDY AREA

I delineated a 1,317 km^2 study area from grizzly bear home ranges along the eastern slopes of the Rocky Mountains in west-central Alberta (53^{o}15’N, 117^{o}30’W), which includes Whitehorse Wildland Provincial Park, the Cardinal Divide, crown lands near Ruby Lake south of the Cardinal Divide, and the adjacent Southesk region of south-eastern Jasper National Park (Figure 2-1). The study area is within both subalpine and alpine subregions with elevation ranging from 1,338 m to 3,084 m. Forests within the study area consist of spruce (*Picea englemanni* × *glauca*), lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*), with alpine meadows and rock outcrops occurring at higher elevations. Alpine meadows (> 1,700 m) in the region occur as herbaceous areas where clusters of trees (< 20% crown closure) are interspersed with forbs, grasses, and sedges (Nielsen et al. 2004).

There is a relatively low density of ungulates in the study area (Munro et al. 2006), which includes moose *Alces alces*, elk *Cervus elaphus*, white-tailed deer *Odocoileus virginianus*, mule deer *O. hemionus*, and bighorn sheep *Ovis canadensis*. Small mammals in the study area include hoary marmot *Marmota caligata* and Columbian ground squirrel *Spermophilus columbianus*. Large carnivores common to the study area include American black bear *U. americanus*, cougar *Puma concolor*, and wolf.

3. METHODS

3.1 Proportion use, proportion available, and selection ratios for alpine sweetvetch habitat

I used GPS telemetry data for 14 bears (Table 2-1) collected by the Foothills Research Institute Grizzly Bear Program from 1999 to 2008 to delineate multi-annual 100% minimum convex polygon (MCP) home ranges which varied in size from 94 to 940 km^2. Bears were captured and collared using techniques following Cattet et al. (2003), and were fitted with either a Televilt GPS-Symplex or an ATS (Advanced Telemetry Systems) GPS radiocollar programmed to acquire positional fixes between every 1 to 4 hours. Telemetry locations were restricted to the subalpine and alpine zones using Alberta Natural Subregions classifications (Alberta Sustainable Resource Development, Alberta Environment, Alberta Community Development and Agriculture and Agri-Food Canada 2005). I used a spatial model of alpine sweetvetch habitat from Nielsen et al. (2010) to calculate the proportion of available (a_i) patches (pixels) within each bear's home range by summing the sweetvetch pixels (160-m^2 resolution) within a home range and dividing this by the total number of home range pixels. As such, I investigated grizzly bear selection for alpine sweetvetch at the patch (third order) scale (Johnson 1980). Proportion available was different for each bear and ranged from 0.12 – 0.40 of their total home range. To account for variation in habitat use, nutritional quality associated with sweetvetch phenology, and bear diets as spring progressed (Hamer and Herrero 1987; McLellan and Hovey 1995; Nielsen et al. 2002; 2003; Munro et al. 2006), I stratified habitat use (where use was defined as a telemetry location within a patch; Arthur et al. 1996) into bi-weekly categories from late April to early July to correspond with the spring use of alpine sweetvetch in the area (Munro et al. 2006). Spring bi-weekly use of alpine sweetvetch habitat was then quantified for each bear and bi-weekly period as a proportion of each bear's GPS telemetry locations using the formula:

$$u_i = n_i / \sum n \qquad (2\text{-}1)$$

where u_i was the bi-weekly proportion use of home range sweetvetch habitat, n_i was the number of telemetry locations within alpine sweetvetch habitat for that period, and $\sum n$ was the total number of telemetry locations collected during that same period. Bi-weekly selection ratios ($w_{(x)}$) were then estimated for individual bears based on proportion use and available sweetvetch habitat following Manly et al. (2002):

$$w_{(x)} = u_i / a_i \qquad (2\text{-}2)$$

where u_i was the bi-weekly proportion use of home range sweetvetch habitat and a_i was the proportion of available sweetvetch habitat based on the MCP home range estimates.

Selection ratios, $w_{(x)}$, utilized a *design III* approach where the unit of replication was considered to be the animal, thereby accounting for autocorrelation and/or psuedoreplication (Thomas & Taylor 1990).

3.2 Habitat selection model

To examine factors affecting the spring habitat selection ($w_{(x)}$) of grizzly bears in subalpine and alpine regions of west-central Alberta, I evaluated support for a series of *a priori* candidate models. Factors hypothesized to influence the spring selection of alpine sweetvetch patches included: availability of habitat, sex and offspring dependency class, inter-annual variation in seasonal climates, and intra-seasonal variation in habitat use and resource availability based on bi-weekly period (Table 2-2).

I used proportion available (AV) of sweetvetch habitat within a home range and a non-linear (quadratic) form of proportion available (AV^2) to evaluate whether selection of alpine sweetvetch patches by grizzly bears differed dependent upon availability (*i.e.*, displayed a functional response). Support for a linear relationship between selection, $w_{(x)}$, and AV would suggest that they are directly proportional to each other (*i.e.*, no functional response). Support for the non-linear quadratic form of proportion availability (AV^2) over the linear form would suggest that selection varies dependent upon the proportion of habitat available which would indicate a functional response.

To assess whether spring selection of alpine sweetvetch patches in the subalpine and alpine differed among sex and offspring dependency classes, I created categorical dummy variables for females with cubs of the year (F_{COY}), females with yearling cubs (F_{1YR}), and solitary females (F_{SOL}). Because there were only two bi-weekly observations for a female bear with two year old cubs, and no observed female bears with > 2 year old dependent offspring, those sex and offspring dependency classes were not considered. As well, a class for subadult bears was not created due to small sample size. I also created a dummy variable called F_{OTHER} that included both solitary females and females with yearlings, therefore allowing us to test whether sex and offspring dependency differences in habitat selection were primarily related to changes associated with females with cubs of the year. In all habitat selection analyses, male bears were used as the reference (indicator) category. Differences are therefore relative to habitat selection in male bears.

To account for inter-annual variation in weather I used the PDO for both the winter (November to April) and springtime (May to July) for each year of observation. The PDO is a pattern of climate variability for the North Pacific Ocean that shifts phases on inter-decadal time scales with additional inter-annual variation (Mantua et al. 1997; Zhang et al. 1997; Whitfield 2010). During a warm (positive) PDO phase, sea surfaces in the central and western Pacific Ocean cool while the sea surface along the west coast of North America warms. The reverse happens during a negative phase in the PDO. These PDO phases influence local terrestrial climates in the north-western and central parts of North America via teleconnections (Mantua et al. 1997; Zhang et al. 1997; Whitfield 2010). For example, during a positive PDO phase temperatures in western North America increase, which results in lower snow accumulation and earlier spring melt (Selkowitz et al. 2002; Whitfield et al. 2010). Variation in April snowpack in north-western USA and south-western Canada has been linked to the PDO more strongly than in any other region (McCabe and Dettinger 2002). Research has also shown PDO teleconnections influence local precipitation (Whitfield et al. 2010) and terrestrial hydrology (Selkowitz et al. 2002) in these regions, as well as the ecology of salmon (*Oncorhynchus* spp.) and marine ecosystem productivity off the coast of British Columbia and Alaska (Mantua et al. 1997; Hare and Mantua 2000).

To account for intra-seasonal variation in resource use and availability, perhaps due to phenological and thus nutritional stages of sweetvetch roots as well as the availability of other food resources, I included bi-weekly period (WEEK) in both linear and non-linear (WEEK^2) forms as a variable to describe within season variability.

Candidate models included univariate models, simple multivariate models without interactions, and multivariate models with interaction terms believed to be relevant to the use and selection of alpine sweetvetch patches (Table 2-3). I used linear mixed models to fit relationships between habitat selection in bears and hypothesized factors using the *lmer* function in the *lme4* package for the program R (R Core Development team 2009). Candidate models were ranked for support using Akaike information criterion (AIC; Burnham and Anderson 2002) for small samples sizes (AIC_c). Using AIC_c values, I selected a confidence set of candidate models that were within 10% of the top model weight. This is comparable to the minimum cut off point for evaluating strength of evidence as suggested by Royall (1997). I included a random effect for individuals in order to account for individual variation among bears (Gillies et al. 2006). Candidate models were made in duplicate, one including a random intercept for each bear (1|BEAR) and the second model a random slope and intercept (VARIABLE|BEAR). However, as models containing only a random intercept consistently outperformed most models incorporating both a random slope and intercept (lower AIC_c weights), I report here only on models containing a random intercept unless otherwise noted. Model averaged parameter estimates were calculated from the confidence set of models by weighting parameter estimates from each model using the AIC_c weight and summing them (Burnham and Anderson 2002).

4. RESULTS

4.1 Grizzly bear selection of alpine sweetvetch

Grizzly bears displayed sexually segregated, offspring dependent functional responses in alpine sweetvetch habitat selection (Table 2-4; 2-5; Figure 2-2). During the spring both males and solitary females were predicted to select for alpine sweetvetch habitat at all levels of availability (selection ratios > 1) in subalpine and alpine regions, yet at varying intensities (Figure 2-2). Solitary females selected for alpine sweetvetch patches the most, followed by males (Figure 2-2). All sex-dependency classes were predicted to select for alpine sweetvetch habitats at low levels of availability, with selection decreasing as availability increased (Figure 2-2). Females with yearlings initially select for alpine sweetvetch patches similar to males at very low levels of availability, but their selection decreases more rapidly than male bears and eventually results in avoidance (selection ratio < 1) of patches at approximately 0.21 proportion available (Figure 2-2). Females with cubs-of-the-year show the lowest selection for alpine sweetvetch patches at low availability, and they begin to avoid patches at approximately 0.17 proportion available habitat (Figure 2-2). Selection for sweetvetch habitat increases again after the proportion of available habitat increases past approximately 0.25 for females with cubs-of-the-year, 0.28 for males, 0.32 for solitary females, and 0.33 for females with yearlings (Figure 2-2). Females with cubs-of-the-year once again start selecting for alpine sweetvetch patches at approximately 0.34 proportion available habitat (Figure 2-2). While females with yearling cubs also increase their selection for alpine sweetvetch patches at higher availability, they continue to show avoidance for the habitat (Figure 2-2). At higher proportions of available sweetvetch habitat, solitary females and males select less than they do at very low levels of availability, while selection by females with cubs of the year is similar at both high and low levels (Figure 2-2). At the highest proportion of available sweetvetch habitat, selection by male grizzly bears is predicted to be nearly that of solitary females (Figure 2-2).

Inter-annual variation in selection for alpine sweetvetch patches due to major climate differences was also supported, with the May-July PDO having a negative effect on selection for all sex and offspring dependency classes (Table 2-5). In years with higher springtime PDO, decreases in selection of sweetvetch habitat were noted (Table 2-5). Conversely, habitat selection for sweetvetch habitat increased during years with negative PDO (Table 2-5). We found no support for intra-seasonal (WEEK variable) trends in the spring selection of alpine sweetvetch patches by grizzly bears (Table 2-4).

5. DISCUSSION

Grizzly bear selection for alpine sweetvetch patches in alpine and subalpine habitats of west-central Alberta was not proportional to availability, as bears displayed a functional response in which selection for sweetvetch patches was greatest when the habitat was either relatively rare or abundant. When the proportion of alpine sweetvetch available in a home range was low, selection for sweetvetch patches was the strongest (with the exception of females with cubs of the year which selected similarly at both low and high levels). This supports the contention that a critically important resource will be selected for most when scarce. I would expect this for sweetvetch patches given the scarcity of other foods in mountainous habitats during the spring (Munro et al. 2006). As sweetvetch patches became more abundant, selection decreased in intensity. This decline was not consistent among bears, as selection for sweetvetch habitat increased when most abundant, suggesting that bears living within landscapes dominated by sweetvetch habitat may adopt a dominant root digging strategy where they specialize their diets to alpine sweetvetch. However, as sweetvetch habitats in the subalpine and alpine are likely to contain other food items (*e.g.*, forbs, grasses, and small mammals), especially later in the spring, it may be that bears specialize their diets to food available within sweetvetch habitats including, but not limited to, alpine sweetvetch roots. This pattern was not limited solely to smaller-bodied female bears, as male bears also adopted a root digging habitat selection strategy when alpine sweetvetch was abundant. This highlights the importance of alpine sweetvetch habitats as a spring resource of grizzly bears, given male bears need a greater amount of meat to support their larger mass (Jacoby et al. 1999; Rode et al. 2001). I would also expect that years in which springtime neonate ungulates are less abundant, particularly in the alpine mountain environments where ungulate densities are lower (Munro et al. 2006), greater use of alpine sweetvetch patches by male bears would be observed. Perhaps when ungulates occur at low enough densities, root digging becomes common for both males and females.

Grizzly bear selection for alpine sweetvetch habitats differed by sex and offspring dependency class. Solitary female bears selected for alpine sweetvetch patches more than male bears, suggesting that habitat segregation occurs due to differences in dietary requirements. Because males require more protein in their diet to increase body mass, we would expect them to select for more habitats containing animal prey; however, it is possible that animal prey, such as small mammals, birds, and ungulates (Munro et al. 2006), are also available to bears within alpine sweetvetch habitat. Females in contrast are better able to utilize alternate food sources than males and can, in some situations, subsist on entirely vegetarian diets (Jacoby et al. 1999; Rode et al. 2001).

Weaker selection for alpine sweetvetch patches by males relative to solitary females, but not females with dependent offspring (sexually-segregated habitat selection), suggests that predator avoidance may affect habitat selection for females with dependent offspring. However, we recognize that female bears with offspring face predation risks from other species in the study region (*e.g.*, wolf, cougar, and American black bear), and their habitat selection is likely a complex balance between offspring safety and food acquisition. In addition, limitations in mobility may affect habitat selection for females with dependent offspring, especially females with cubs-of-the-year. Lower selection by lactating females with dependent offspring may also be due to an increased need for not only protein, but also a more balanced amino acid intake than they can obtain from plants; however, we would still expect females with offspring to avoid high quality habitats when male bears are present despite their increased nutritional requirements (Hilderbrand et al. 2000). This is in contrast to dimorphic ungulate species in which females occupy sites with higher quality forage, while males occupy sites that allow for high forage intake (Barboza & Bowyer 2000, Oehlers et al. 2011).

That solitary females are not excluded by males may also be due to the spring mating period, which occurs from mid-May to the end of July in west-central Alberta, a time when associations between male and female bears occur at higher frequencies (Stenhouse et al. 2005). Male bears may select for alpine sweetvetch patches not only to gain access to the food resource, but also to gain access to oestrous. This suggests that more research involving the effect of breeding season behaviour on habitat selection is required, because such behaviour likely influences the movement and positioning of grizzly bears (Stenhouse et al. 2005)..

Inter-annual variation in climate also affected the selection of alpine sweetvetch patches by grizzly bears in west-central Alberta. In years in which the spring (May-July) PDO was positive, and therefore years with warmer temperatures, lower snow packs, and earlier growing seasons, selection of sweetvetch patches was lower. This reduction of sweetvetch habitat selection may be due to the earlier onset of spring growing season which may help speed the transition and increase the availability and abundance of alternate food resources, such as horsetails, graminoids, forbs, and sedges (Munro et al. 2006). Conversely, increase in the selection for alpine sweetvetch patches during cooler years would likely be due to the reduced availability and abundance of alternate plant food resources. The abundance of winterkilled ungulates may also be higher during negative PDO years, however, it may not be enough for, or available to, bears in mountainous environments to offset the selection for alpine sweetvetch habitats (Munro et al. 2006). It may be that during cooler years, ungulates tend to inhabit lower elevation areas, whereas warmer years may see higher ungulate densities in the mountains thereby offering bears a potential alternative to roots.

I expected PDO to interact with the bi-weekly period of spring where years with higher PDO would result in earlier spring melts and onset of growing season, and therefore an earlier start to the spring den-emergence and the root digging season. I found, however, no support for this hypothesis. I also found no support for the bi-weekly period of spring affecting the selection of alpine sweetvetch habitats, which suggests that in subalpine and alpine mountainous regions, alpine sweetvetch roots (and/or habitats) are relied upon throughout the spring season. This is in contrast to warmer, adjacent foothills environments where bears tend to consume less sweetvetch in favour of green vegetation as spring advances (Munro et al. 2006). The prolonged use of sweetvetch habitats in the mountains may be due to wider variability in environmental factors that influence both the nutritional quality and phenology of alpine sweetvetch. Given greater differences in elevations and slope-aspect relationships, bears may be able to extend the availability of nutritious roots (Hamer and Herrero 1987). Such spatial and temporal variation may be the key reason why bears in mountainous environments can adopt a root digging foraging strategy.

One limitation of our study is that we used alpine sweetvetch habitats defined by presence/absence as a measure of habitat quality. We recognize that more explicit measures of patch quality that include estimates of such things as abundance, nutritional quality, and/or phenology, are needed to improve our analyses of selection (Nielsen et al. 2010); however, such estimates are not available to us at this time. While we used PDO as inter-annual variable to account for differences in snow conditions, start of green-up, and growing season conditions, we did not account for a PDO lag effect which may have shown the influence of previous growing season conditions on the spring selection of grizzly bears.

This study demonstrates that grizzly bears select for sweetvetch habitat differently depending on springtime climate (PDO), availability of habitat, and sex and offspring dependency status. Future research should consider how phenology and nutritional quality of sweetvetch roots vary between mountain and foothill environments and whether local variation in terrain conditions (*e.g.*, elevation, slope, aspect) lengthens the availability of sweetvetch roots.

Table 2-1. Number of GPS telemetry locations, sex, and dependent young of grizzly bears used to examine the selection of alpine sweetvetch patches in subalpine and alpine environments of west-central Alberta. Dependent young classes include solitary females (F_{SOL}), females with cubs of the year (F_{COY}), and females with yearlings (F_{1YR}). Females can have more than one dependency class because observations were taken over multiple years.

Bear ID	No. of GPS locations	Sex	Dependent Young
G1	252	M	
G3	677	F	F_{SOL}, F_{1YR}
G4	566	F	F_{SOL}, F_{COY}
G6	258	M	
G8	1699	M	
G10	117	F	F_{SOL}, F_{COY}
G16	286	F	F_{SOL}, F_{COY}, F_{1YR}
G23	134	F	F_{SOL}, F_{COY}
G27	82	F	F_{SOL}
G28	1023	F	F_{SOL}, F_{COY}, F_{1YR}
G29	24	M	
G35	190	F	F_{SOL}
G43	80	M	
G44	223	M	
Total	5611		

Table 2-2. Hypothesized factors, variable names, and abbreviations of variables used in candidate models.

Hypothesized factor	Variable names (predictor variables)	Abbreviation
Functional response	Proportion available	AV
	Proportion available^2 (non-linear quadratic)	AV^2
Sex & offspring dependency	Female with cubs of the year	F_{COY}
	Female with yearlings	F_{1YR}
	Solitary females	F_{SOL}
	Solitary females + females with yearlings	F_{OTHER}
Inter-annual variation	November - April Pacific Decadal Oscillation	PDO_{Winter}
	May - July Pacific Decadal Oscillation	PDO_{Spring}
Intra-seasonal variation	Bi-weekly period	WEEK
	Bi-weekly period^2 (non-linear quadratic)	$WEEK^2$

Table 2-3. Candidate model hypotheses and model structure used to examine the selection of alpine sweetvetch patches by grizzly bears in subalpine and alpine regions of west-central Alberta, Canada. See Table 2-2 for variable definitions.

Model	Hypothesis	Model Structure
Null	Null model	$1+(1 \vert BEAR)$
1a.I	Functional response – linear model	$AV+(1 \vert BEAR)$
1a.SI	Functional response – linear model	$AV+(AV \vert BEAR)$
1b.I	Functional Response – non-linear model (quadratic)	$AV+AV^2+(1 \vert BEAR)$
1b.SI	Functional Response – non-linear model (quadratic)	$AV+AV^2+(AV \vert BEAR)$
2a	Sex dependency differences – each class	$F_{COY}+F_{1YR}+F_{SOL}+(1 \vert BEAR)$
2b	Sex dependency differences – COY separate	$F_{COY}+F_{OTHER}+(1 \vert BEAR)$
3a	Functional response + sex dependency each class	$AV^2+AV+F_{COY}+F_{1Y}R+F_{SOL}+(1 \vert BEAR)$
3b	Functional response *sex dependency COY + yearlings and solitary	$AV^2+AV*F_{COY}+F_{1YR}+F_{SOL}+(1 \vert BEAR)$
3c	Functional response *sex dependency COY & yearlings + solitary	$AV^2+AV*F_{COY}+AV*F_{1YR}+F_{SOL}+(1 \vert BEAR)$
3d	Functional response *sex dependency COY, yearlings & solitary	$AV^2+AV*F_{COY}+AV*F_{1YR}+AV*F_{SOL}+(1 \vert BEAR)$
4a	Winter PDO	$PDO_{Winter}+(1 \vert BEAR)$
4b	Spring PDO	$PDO_{Spring}+(1 \vert BEAR)$
4c	Combined PDO	$PDO_{Spring}+PDO_{Winter}+(1 \vert BEAR)$
4d	Combined PDO interaction	$PDO_{Spring}*PDO_{Winter}+(1 \vert BEAR)$
5a	Functional response (quadratic) + PDO	$AV^2+AV+PDO_{Spring}+(1 \vert BEAR)$
5b	Functional response (quadratic) * PDO	$AV^2+AV*PDO_{Spring}+(1 \vert BEAR)$
6a	Functional response + sex dependency + PDO	$AV^2+AV*F_{COY}+F_{1YR}*AV+F_{SOL}*AV+PDO_{Spring}+(1 \vert BEAR)$
6b	Functional response + sex dependency +FCOY* PDO	$AV^2+AV*F_{COY}+F_{1YR}*AV+F_{SOL}*AV+PDO_{Spring}*FCOY+(1 \vert BEAR)$
7a	Week (linear)	$WEEK+(1 \vert BEAR)$
7b	Week (quadratic)	$WEEK+WEEK^2+(1 \vert BEAR)$
8a	Winter PDO * Week	$PDO_{Winter}*WEEK+(1 \vert BEAR)$
8b	Spring PDO * Week	$PDO_{Spring}*WEEK+(1 \vert BEAR)$
8c	Spring PDO + Week	$PDO_{Spring}+WEEK+(1 \vert BEAR)$
9	Functional response + sex dependency + spring PDO + week	$AV^2+AV*F_{COY}+F_{1YR}*AV+F_{SOL}*AV+PDO_{Spring}+WEEK+(1 \vert BEAR)$
9b	Functional response + sex dependency + spring PDO*week	$AV^2+AV*F_{COY}+F_{1YR}*AV+F_{SOL}*AV+PDO_{Spring}*WEEK+(1 \vert BEAR)$

Table 2-4. Model structure, Akaike Information Criterion with small sample size correction (AIC$_c$), change in AIC$_c$ relative to the top ranked model (Δ AIC$_c$), and Akaike weights (w_i) of candidate models used to predict the spring selection of alpine sweetvetch habitat in subalpine and alpine regions of west-central Alberta, Canada. The top model (model 3d) and models 3c and 6a (in bold) were selected as the confidence set of models and used for model averaging of parameters.

Model	Model Structure	AIC$_c$	Δ AIC$_c$	w_i
3d	**AV^2+AV*F$_{COY}$+AV*F$_{1YR}$+AV*F$_{SOL}$+(1|BEAR)**	**380.5**	**0.0**	**0.60**
3c	**AV^2+AV*F$_{COY}$+AV*F$_{1YR}$+F$_{SOL}$+(1|BEAR)**	**383.0**	**2.5**	**0.17**
6a	**AV^2+AV*F$_{COY}$ +F$_{1YR}$*AV+F$_{SOL}$*AV+PDO$_{Spring}$+(1|BEAR)**	**383.7**	**3.1**	**0.12**
6b	AV^2+AV*F$_{COY}$ +F$_{1YR}$*AV+F$_{SOL}$*AV+PDO$_{Spring}$*F$_{COY}$+(1|BEAR)	385.3	4.8	0.05
3b	AV^2+AV*F$_{COY}$ +F$_{1YR}$+F$_{SOL}$+(1|BEAR)	386.8	6.3	0.03
5b	AV^2+AV*PDO$_{Spring}$+(1|BEAR)	389.8	9.2	0.01
3a	AV^2+AV+F$_{COY}$ +F$_{1YR}$+F$_{SOL}$+(1|BEAR)	389.8	9.3	0.01
9b	AV^2+AV*F$_{COY}$ +F$_{1YR}$*AV+F$_{SOL}$*AV+PDO$_{Spring}$*WEEK+(1|BEAR)	390.2	9.7	0.00
5a	AV2+AV+PDO$_{Spring}$+(1|BEAR)	391.9	11.4	0.00
9	AV^2+AV*F$_{COY}$ +F$_{1YR}$*AV+F$_{SOL}$*AV+PDO$_{Spring}$+WEEK+(1|BEAR)	391.9	11.4	0.00
1b.I	AV+AV^2+(1|BEAR)	392.5	12.0	0.00
1b.SI	AV+AV^2+(AV|BEAR)	394.2	13.7	0.00
2a	F$_{COY}$+F$_{1YR}$+F$_{SOL}$+(1|BEAR)	399.7	19.2	0.00
1a.SI	AV+(AV|BEAR)	401.3	20.8	0.00
1a.I	AV+(1|BEAR)	402.1	21.6	0.00
4b	PDO$_{Spring}$+(1|BEAR)	402.1	21.6	0.00
2b	F$_{COY}$+F$_{OTHER}$+(1|BEAR)	403.5	23.0	0.00
Null	1+(1|BEAR)	403.7	23.2	0.00
4a	PDO$_{Winter}$+(1|BEAR)	405.6	25.1	0.00
4c	PDO$_{Spring}$+PDO$_{Winter}$+(1|BEAR)	407.1	26.6	0.00
8b	PDO$_{Spring}$*WEEK+(1|BEAR)	409.5	29.0	0.00
4d	PDO$_{Spring}$*PDO$_{Winter}$+(1|BEAR)	410.3	29.8	0.00
8c	PDO$_{Spring}$+WEEK+(1|BEAR)	410.4	29.9	0.00
7a	WEEK+(1|BEAR)	411.6	31.1	0.00
8a	PDO$_{Winter}$*WEEK+(1|BEAR)	414.6	34.1	0.00
7b	WEEK+WEEK^2+(1|BEAR)	420.8	40.3	0.00

Table 2-5. Model averaged parameter estimates, standard errors (SE), and 90% confidence intervals for the confidence set of candidate models used to model selection of alpine sweetvetch habitat by grizzly bears in west-central Alberta's sub-alpine and alpine habitats. See Table 2-2 for variable definitions.

			90% CI	
Parameter	Estimate	SE	Upper	Lower
Intercept	3.293	1.374	5.547	1.040
Proportion available (AV)	-15.941	10.498	1.275	-33.157
Proportion available^2	30.038	20.415	63.519	-3.443
F_{COY}	-0.683	1.163	1.225	-2.692
F_{1YR}	0.364	2.987	5.262	-4.535
F_{SOL}	0.877	0.777	2.151	-0.397
PDO_{Spring}	-0.022	0.026	0.021	-0.065
F_{COY} × AV	1.118	3.650	7.104	-4.867
F_{1YR} × AV	-2.857	8.750	11.486	-17.200
F_{SOL} × AV	-2.138	2.086	1.283	-5.559

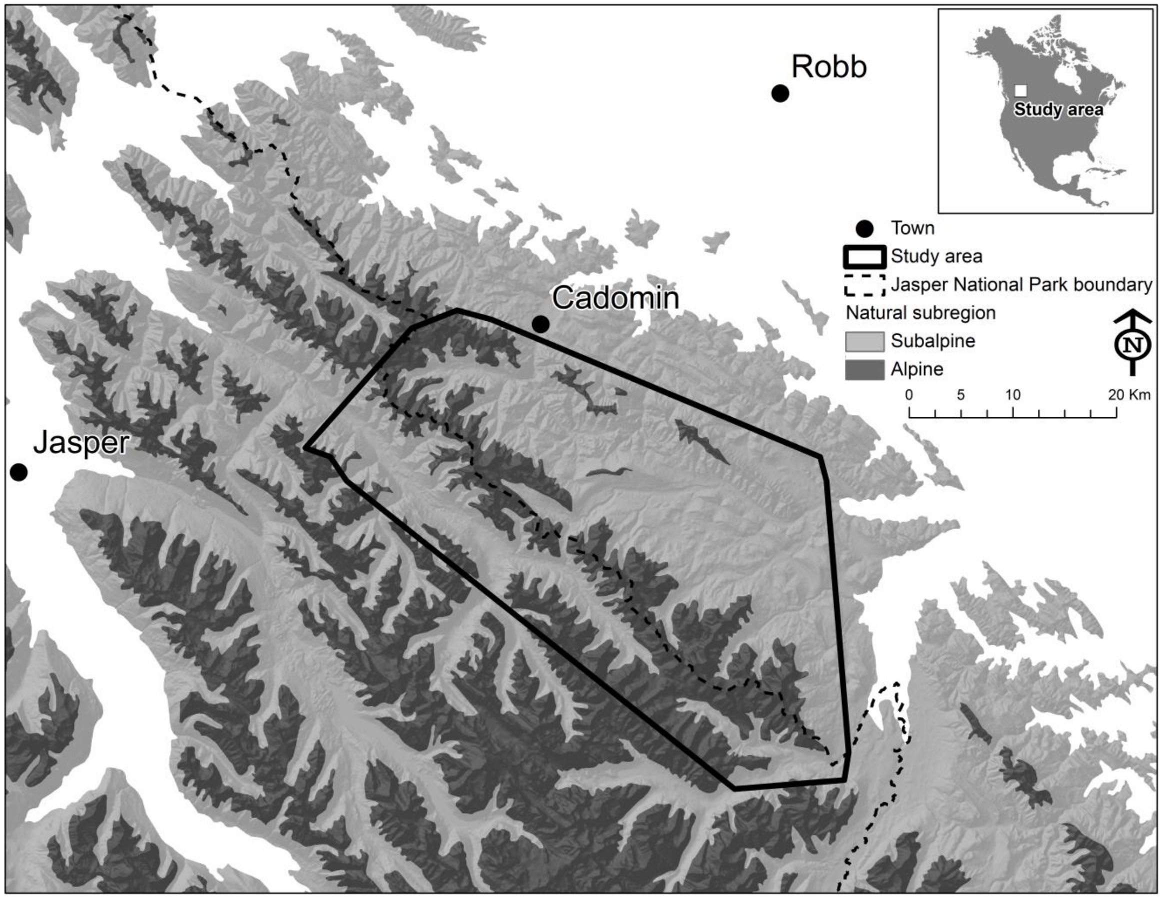

Figure 2-1. Study area with towns, Japer National Park eastern boundary, and Subalpine and Alpine natural subregions.

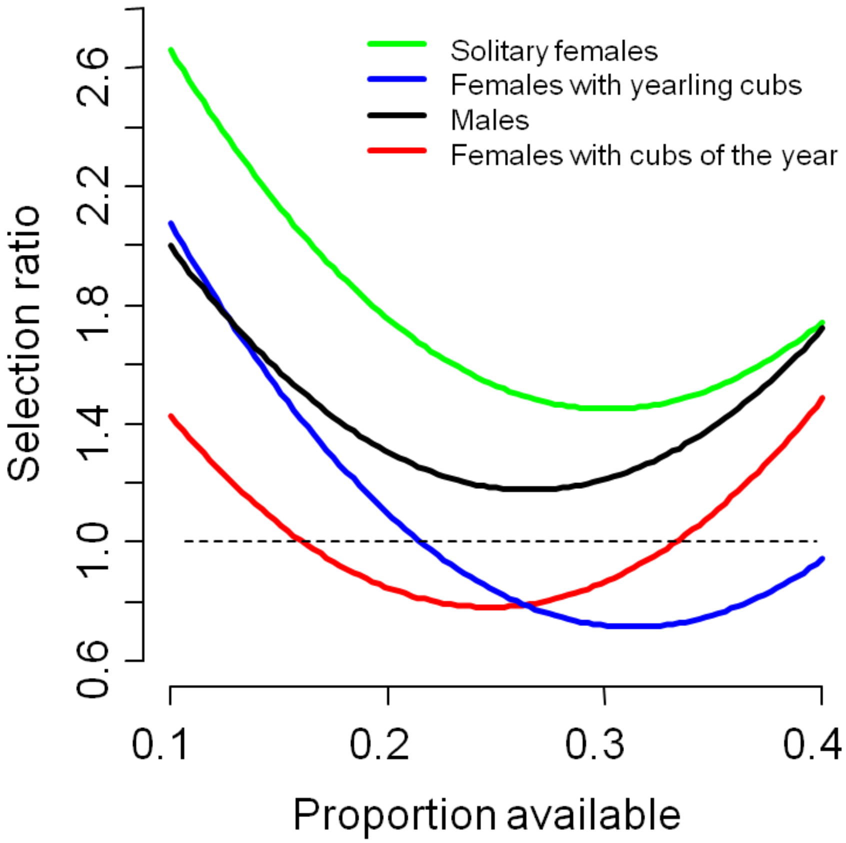

Figure 2-2. Predicted selection ratios ($w_{(x)}$) of alpine sweetvetch habitat as a function of proportion of habitat available by grizzly bears of different sex-dependency classes in the subalpine and alpine regions of west-central Alberta, Canada. Selection ratios above the dashed line ($w_{(x)} > 1$) indicate selection for habitat, while those below the dashed line ($w_{(x)} < 1$) indicate avoidance.

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CHAPTER 3

SPATIAL AND TEMPORAL HETEROGENEITY CREATE A ‘BROWN WAVE’ IN ROOT PHENOLOGY AND NUTRITION

1. INTRODUCTION

A central challenge in ecology lies in understanding the ways in which spatiotemporal variation in resources shape the biotic environment. While consumable above-ground net primary production limits the ability of a landscape to support herbivores (McNaughton et al. 1979; Cebrian and Lartigue 2004), this limitation may be altered by the timing and spatial patterns of plant growth. This is especially true for spatial heterogeneity that causes temporal variation in plant phenology (*e.g.*, budburst, flowering, and fruiting), because it provides nutritional benefits to herbivores by prolonging the period in which they can forage on highly nutritious immature plants (Pettorelli et al. 2007). Thus, variable landscapes increase the ability of animals to access highly nutritious plants by reducing spatial and temporal autocorrelation in plant growth (Searle et al. 2010). Without the influence of spatial heterogeneity on plant phenology, plant growth would be synchronized thereby reducing the time period during which animals can consume the most nutritious plants (Ims 1990). Access to landscape heterogeneity can therefore enhance population performance of herbivores, and may be a critically important feature of their habitat (Fryxell et al. 2005; Hobbs et al. 2008; Searle 2010).

Relationships between time, plant phenology and animal foraging are well established. For example, during springtime when green vegetation is immature, plants have higher protein and lower fibre content than during the summer when plants are maturing (Mattson 1980; Van Soest 1994). Migratory geese have been shown to follow this ‘green wave’ of nutritious spring growth as they travel from temperate areas to their Arctic breeding grounds (Drent et al 1978; van der Graaf 2006 et al.; Duriez et al. 2009). This ‘surfing’ of the green wave across space and time is also common to other migratory animals including, insectivorous passerine birds (Marra et al. 2005), and herbivores such as wildebeest (*Connochaetes taurinus*; Boone et al. 2006).

Local spatial heterogeneity in phenology can also be important to animal populations. This is because spatial variation in a wide range of abiotic factors (*e.g*., soil moisture and nutrients, sunlight, temperature, precipitation, topography, elevation, snow accumulation) can cause plants at different locations to initiate growth at different times. For instance, in the Serengeti plains of Africa, access to patches of grassland that varied in phenology as a result of spatial heterogeneity in topography, soils, and rainfall directly influenced the population viability of Thompson’s gazelle (*Eudorcus thomsonii*; Fryxell et al. 2005). Likewise, increased spatial heterogeneity in the normalized difference vegetation index is thought to result in higher ungulate carrying capacities within those habitats (Wang et al. 2006). Heterogeneity in elevation related to plant phenology has also been linked to population growth of ungulates in both North America and Europe (Wang et al. 2009). Many animals shift their distribution along altitudinal gradients in response to changes in plant phenology. For example, several deer species (Mysterud 1999; Mysterud et al. 2001; Sakuragi et al. 2003), and caribou (*Rangifer tarandus*; Skogland 1980) migrate along an elevation gradient to access newly emergent, high quality forage. Similar foraging behaviours have been observed for the omnivorous grizzly bear (*Ursus arctos*) which moves to higher elevations and north facing slopes as spring progresses to gain access to earlier phenology and thus higher nutritional quality plants (Hamer and Herrero 1987).

Studies of the spatial and temporal pattern of herbivory have necessitated that researchers focus on above ground plant growth. Roots are also a critical resource, especially for omnivorous species (Iguchi and Izawa 1990; Hill and Dunbar 2002; Herrero et al. 2005; Munro et al. 2006). Little is known, however, about root phenology and nutrition (Jackson et al. 2001) despite that root production accounts for 50 – 90% of the primary production in temperate vegetation (Ruess et al. 2003; Steinaker 2006). In the Central Canadian Rockies of western Canada, roots of alpine sweetvetch (*Hedysarum alpinum*) are an important source of seasonal food for grizzly bears. Nutritional quality of alpine sweetvetch roots are known to vary temporally based on plant phenology (Hamer and Herrero 1987). As spring progresses, roots of alpine sweetvetch decline in crude protein content and digestibility (Hamer and Herrero 1987), a pattern common for many short stature perennial plants where above ground spring growth is dependent on resources that have been translocated to roots the previous winter (Clark 1977). Following sexual reproduction in late summer (development of seeds), roots of alpine sweetvetch again increase protein and digestibility as resources are translocated to the root to support next year's growth (Hamer and Herrero 1987). This temporal pattern in nutritional quality has also been observed for the closely related yellow sweetvetch (*H. sulpherescens*; Hamer and Herrero 1987; McLellan and Hovey 1995).

Grizzly bears respond to sweetvetch phenology and nutrition by consuming roots during the spring and fall when they are most nutritious (McCrory and Herrero 1981; Holcroft and Herrero 1984; Hamer and Herrero 1987; McLellan and Hovey 1995; Munro et al. 2006). Considering the 'green wave' phenomenon observed in herbivores, omnivores like grizzly bears are therefore also riding their own 'brown wave' in root foraging that depends on plant phenology which is affected by among other things elevation and aspect (Hamer and Herrero 1987).

The objective of this paper is to test the hypothesis that spatial heterogeneity in local abiotic and biotic factors influence temporal variation in the nutritional quality of alpine sweetvetch roots, thereby potentially offering nutritional benefits to species that use the roots, such as grizzly bears. I first describe general temporal trends in crude protein content of alpine sweetvetch roots by phenological stage of plants in west-central Alberta, Canada and then evaluate the importance of spatial heterogeneity in crude protein content of roots. Specifically, I hypothesize that the following five factors influence spatial and temporal patterns in crude protein content in roots: (1) time (Julian day and year), (2) temperature (*i.e.*, growing degree days which is influenced by elevation), (3) soil moisture and nutrients, (4) solar radiation (slope/aspect), and (5) plant community. I predict that, as well as observing general temporal trends and an elevation lag in phenology related to growing season temperature (*i.e.*, interaction between time and growing degree days), crude protein content in alpine sweetvetch roots will be affected by local site factors including soils, solar radiation, and plant competition. Finally, I map spatial-temporal predictions of crude protein levels of alpine sweetvetch roots across a 2,376 m elevation gradient and an 11,436 km^2 spatial scale to examine brown wave patterns in alpine sweetvetch root protein content in west-central Alberta, Canada.

2. STUDY AREA

The study area (Figure 3-1) is located in the Canadian Rocky Mountains and Foothills of west-central Alberta, Canada (53^o15'N, 117^o30'W). Average summer temperatures range from 11.9 °C in montane regions to 9.4 °C in the subalpine, while average winter temperatures are -7.8 °C and -8.9 °C respectively (Beckingham et al. 1996). Annual average rainfall in the lower elevation montane area is 464 mm versus 568 mm at the higher elevation subalpine area (Beckingham et al. 1996). The foothills contain a diverse array of habitats, including black spruce (*Picea mariana*) and tamarack (*Larix laricina*) bogs; lodgepole pine (*Pinus contorta*) stands; open marshes; riparian areas; and mixed forests composed of lodgepole pine, aspen (*Populous tremuloides*), and white spruce (*Picea glauca*). Subalpine forests consist of spruce (*Picea englemannii* × *glauca*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine, with alpine meadows and rock outcrops occurring at higher elevations.

3. METHODS

3.1 Sample collections and nutritional laboratory analyses

To understand how spatial factors influence the timing of alpine sweetvetch nutritional quality, I determined the crude protein content of alpine sweetvetch roots (n=117) across three years (2008-2010) from 14 permanent sample sites located in the montane, lower foothills, upper foothills, and subalpine habitats (Figure 3-1). Nutritional analyses of crude protein content were performed in the Proximate Laboratories of the Department of Agriculture, Food, and Nutritional Sciences at the University of Alberta. All samples were frozen following collection and then later dried in the laboratory at 60°C for 48 hours. Crude protein (N × 6.25) was determined via combustion analysis using a LECO TruSpec N/C Analyzer (Leco Corporation, St. Joseph, Michigan, USA). Moisture was determined by oven drying at 110 °C (a small number of samples were determined by oven drying at 105 °C). All estimates were corrected to a 100% dry matter basis. For additional nutritional and digestibility estimates see Appendix A.

3.2 Phenological changes in nutrition (crude protein content)

To examine temporal (seasonal) patterns in crude protein content of alpine sweetvetch roots, root samples (n=112, as I could not identify the phenological stage of all 117 root samples) were grouped into six phenological stages (pre-leaf, leaf, bud, flower, seed, dormant). For each phenological stage, mean and standard error of crude protein was estimated and an ANOVA used to test for significant differences between groups (phenological stages). A histogram plot of residuals and a Shapiro-Wilk test was used to assess normality, while heterogeneity of variances was assessed by examining a residual plot and a Bartlett test. Pair-wise one-way t-tests with adjustments (Holm's) for multiple inferences were used to test for significant differences between phenological classes. I calculated digestible protein for bears for each phenological stage by using the following equation from Pritchard and Robbins (1990):

$$dp = -3.46 + 0.881 \times cp \tag{3-1}$$

where dp is digestible protein (g/100 g) and cp is percent crude protein content as measured by combustion analysis.

Because phenology of alpine sweetvetch varies by elevation, I describe the dates of each phenology stage according to two broad elevation classes representing alpine (≥1700 m) and foothill/montane (<1700 m) habitats based on Munro et al. (2006).

3.3 Spatial and temporal heterogeneity of crude protein content in alpine sweetvetch roots

To examine how spatial heterogeneity influences temporal variation in the crude protein content of alpine sweetvetch roots, I evaluated support for a series of *a priori* candidate models that describe both temporal and spatial heterogeneity of root crude protein content. Spatial factors hypothesized to influence crude protein content in roots included soil moisture and nutrients, temperature, solar radiation, and competition (Table 3-1).

Soil moisture and nutrients were represented by both geological formation (GEO; Hamilton et al. 2004) representing regional differences in parent material, and for local soil conditions by the steady state terrain wetness index called the compound topographic index (CTI) derived from a 30-m digital elevation model (DEM) and the CTI.AML ArcInfo script from Evans (2004). CTI is positively related to soil moisture, horizon depth, percent silt, organic matter, and phosphorous (Moore et al. 1993; Gessler et al. 1995) and was previously used for modelling the distribution of several grizzly bear plant foods in the study region, including alpine sweetvetch (Nielsen et al. 2004; Nielsen et al. 2010). Annual growing degree days (GDD) was used as a measure of temperature (heat accumulation), which in the study area was controlled primarily by elevation (short, cool growing seasons or low GDD for the alpine and longer, warmer growing seasons or a high GDD in the montane and lower foothills). I used annual GDD with base 5 °C (Anon. 2003), since that is considered the minimum threshold for general plant growth and forage in Alberta (Chetner et al. 2003). Global solar radiation (sum of shortwave and diffuse radiation) was again measured for each site using a 30-m DEM and the SHORTWAVC.AML and DIFFUSE.AML ArcInfo scripts from Zimmermann (2000). And finally, influence of plant community (*e.g.*, competition for soil and light resources, influence on soil chemistry, associated organisms) were based on a remote sensing classification of landcover and a landscape canopy closure model from McDermid et al. (2005).

Candidate models included univariate models, simple multivariate models without interactions, and multivariate models with interaction terms believed to be relevant to nutritional dynamics of roots. Candidate models were ranked for support using the Akaike Information Criterion with small sample size correction (AIC_c; Burnham and Anderson 1998). Because samples were collected over multiple years, year of collection was used to test for annual variation in nutritional quality. Models were fit using generalized linear models (GLMs) with site used as a random effect to account for multiple samples collected at a site. However, I found no difference between sites (all intercepts were statistically equivalent), which was supported by lower AIC_c ranks (AIC_c $w_i > 2.0$). Site level variation was likely explained instead by our spatial and temporal variables. I therefore only report here on models without random effects. The most supported model was checked for normality by examining a histogram of residuals followed by a Shapiro-Wilk test. All statistical analyses were conducted in the program R (R Core Development Team 2009).

To interpret spatio-temporal patterns in the nutritional quality of alpine sweetvetch roots I used our most supported model to predict spatially the bi-weekly patterns of crude protein content in roots from May to mid-October. Model predictions were combined with an existing presence/absence model of alpine sweetvetch from Nielsen et al. (2010) to limit predictions of root quality to areas where the species was predicted to occur.

4. RESULTS

4.1 Phenological changes in nutrition (crude protein content)

Phenological stage of alpine sweetvetch varied between mountain (elevation ≥1700 m) and foothills habitats (elevation <1700 m; Table 3-2).

Observed phenology in the mountains lagged behind the foothills by 29 days for the pre-leaf stage, 7 days for the leaf stage, 26 days for the bud stage, 14 days for the flower stage, and 6 days for the seed stage. No lag, however, was observed for the onset of the dormant stage. While there was a lag in the onset of phenological stages between foothills and mountain habitats, the last observations for a particular stage in the mountains and foothills were often close to one another in dates, with the exception of plants in the seed stage lasting up to 17 days later in foothills habitats (Table 3-2). This suggests that despite general lags in the phenological stages of alpine sweetvetch between the two ecosystems, there was local variation potentially due to site level effects.

Crude protein content of alpine sweetvetch roots ranged from 9.0 to 22.4% with seasonal crude protein contents ranging from 17.0 % for the pre-leaf stage (n= 15, SE = 0.51), 17.9% for the leaf stage (n = 6, SE = 1.50), 15.8% for the bud stage (n = 14, SE = 0.51), 14.6% for the flower stage (n = 19, SE = 0.54), 14.8% for the seed stage (n = 40, SE = 0.40), and 17.1% for the dormant stage (n = 18, SE = 18; Table 3-2; Figure 3-2). Seasonal differences were significant (ANOVA, $p < 0.001$) with the pre-leaf period having higher average crude protein content than both flowering ($p < 0.05$) and seed bearing ($p < 0.01$) stages. Roots of dormant plants were also significantly higher in crude protein content than flowering ($p < 0.05$) and seed bearing ($p < 0.05$) plants.

Average digestible protein content of alpine sweetvetch root was estimated at 11.5% for the pre-leaf stage, 12.3% for the leaf stage, 10.5% for the bud stage, 9.4% for the flower stage, 9.6% for the seed stage, and 11.6% for the dormant stage.

4.2 Spatial and temporal heterogeneity of crude protein content in alpine sweetvetch roots

Temporal patterns in the crude protein content of alpine sweetvetch roots were influenced by spatial heterogeneity in annual growing season temperatures and soils with the most supported *a priori* model including factors for Julian day (non-linear response), soil moisture and nutrients (CTI), annual growing degree days (GDD base 5 °C), and a three-way interaction between Julian day, CTI and GDD (Table 3-3; 3-4). This suggested that temporal patterns in crude protein content of roots were dependent not only on elevation lags (*i.e.*, temperature), but also local soil conditions. Specifically, during springtime roots were predicted to have higher protein content in areas with both low soil moisture and annual growing season temperatures, as well as areas with high soil moisture and growing season temperatures. Crude protein content in these sites during the spring (21 May) was predicted to be as high as approximately 21%. In contrast, roots growing in areas where annual growing season temperatures where high and soil moisture low were predicted to have lower protein values (~16%). Areas of high soil moisture and low growing season temperatures were predicted to have very low crude protein content at approximately 4%. As spring progressed, spatial patterns in crude protein content of alpine sweetvetch roots were attenuated and equalized across the region by approximately 21 July with increases in crude protein content during late summer and fall following the mirrored response of springtime trends. Thus, during the late summer and fall, areas having high soil moisture and low growing season temperatures, as well as low soil moisture and high growing season temperatures, were predicted to have higher crude protein content of roots. By 21 September crude protein content of roots was predicted to be as high as 21% for optimal sites and as low as 10% for areas of high moisture and growing season temperatures.

Figures 3-3 to 3-13 illustrate spatial-temporal predictions of crude protein content for each bi-weekly period from 7 May to 7 October. A lag in the decline of crude protein at high elevations during the first half of the season is apparent. In contrast, during late summer and fall an increase in crude protein content occurred first at lower elevations followed by increases at higher elevations. On 7 May, roots with high protein content (> 18% crude protein) were widely predicted for both high and low elevations (Figure 3-3). From 21 May to 7 June, protein levels decreased to moderate levels (16 – 18 %) for most low elevation sites, while many higher elevation mountain slopes and valleys retained high protein levels (Figures 3-4; 3-5). By 21 June the protein content of roots at low elevations decreased to low (14 – 16 % crude protein) levels, while at higher elevations crude protein was reduced to more moderate levels (Figure 3-6). This pattern continued until 21 July, at which time protein levels of alpine sweetvetch roots throughout the entire region (with the exception of a few low elevation pixels near Jasper) had been depleted and were at low or very low (< 14 %) levels (Figure 3-8). On 7 August protein levels began to rise in low elevation river valleys and continued to increase through 7 October (Figures 3-9; 3-10; 3-11; 3-12; 3-13).

During this time the crude protein content of roots at high elevations lagged behind those at low elevations and along the bottoms of river valleys. By 7 September low elevation valleys had moderate protein levels, while high elevation sites were still in a low protein state (Figure 3-11). By 21 September protein content of roots were predicted to be quite high at low elevations with increases to moderate protein content at high elevations (Figure 3-12). By 7 October protein levels of roots were predicted to be close to early spring (7 May) levels (Figures 3-3; 3-13).

5. DISCUSSION

Similar to Hamer and Herrero's (1987) study, crude protein content of alpine sweetvetch roots were highest early in the year, declined as phenology advanced to the flowering stage, and increased again to spring levels when dormant. The autumn rebound in crude protein content of roots suggests that a lag in phenology is the main driver of crude protein content in alpine sweetvetch roots. This pattern of root protein content is consistent with many perennial plants, as early in the season resources would be translocated from the taproot to support above ground growth, while in the fall resources would be translocated back to the root to support the next season's growth (Clark 1977). Despite the similarity between my results and Hamer and Herrero (1987), alpine sweetvetch roots in west-central Alberta had higher crude protein content, which may be due to differences in laboratory methods. A similar phenological pattern in crude protein content was found for yellow sweetvetch (*Hedysarum sulphurescens*) roots on the eastern slopes of Banff National Park and the Flathead River valley (Hamer and Herrero 1987; McLellan and Hovey 1994), although crude protein content of yellow sweetvetch roots were noticeably lower than that of alpine sweetvetch (Hamer and Herrero 1987). Hamer and Herrero (1987) also examined fibre (acid detergent fibre) content of alpine sweetvetch roots as it related to phenology with fibre inversely related to protein. While total dietary fibre is now generally accepted to be most appropriate measure of digestibility (Pritchard and Robbins 1989), I would expect that the relationship between fibre, protein, and phenology would remain the same.

I expected spatial heterogeneity in growing season temperature along an elevation gradient to influence the crude protein content of alpine sweetvetch roots. This is because high elevation sites experience later spring green-up and earlier fall frosts than low elevation sites, which results in regional differences in plant phenology and gradients of forage quality (Mårell et al. 2006). Unlike Hamer and Herrero (1987), a slope/aspect relationship based on my measures of solar radiation was not supported.

I not only found spatial-temporal lags due to elevation gradients, but also local effects on root quality due to variations in soil moisture and nutrients. The effect of soils moisture and nutrients may be due to its influence on the timing of phenology and/or the overall protein content of alpine sweetvetch roots. For instance, the lower protein content of roots in dry low-elevation areas may be due to advanced phenology within the pre-leaf stage, since spring growth in wet areas may be delayed from excessive water caused by snow melt and/or precipitation.

Soil moisture and nutrient composition is also an important factor for nitrogen fixation in legumes such as alpine sweetvetch, where soil moisture is often a limiting factor (Buttery 1987). This may be the case in wet alpine regions, where spring conditions leave those areas wet or saturated with water due to high snow packs. However, I expect that the extremely low protein value predicted for wet high-elevation roots may be an artefact of sampling, as fewer roots were collected in the alpine at this time (in fact, I would expect many alpine areas at this time to be snow covered). As well, it is possible that roots with higher spring protein content growing in both dry high-elevation areas and wetter low-elevation areas may experience a combination of temperature and soil moisture conditions that are suitable to nitrogen fixation. My measure (index) of soil moisture is also correlated with other soil nutrients including phosphorous (Moore et al. 1993; Gessler et al. 1995), which is often a limiting factor in nitrogen fixation (Lioi and Giovannetti 1987). Further examination of the effects of moisture and nutrients on alpine sweetvetch root quality is therefore needed.

Tracking the phenology and nutritional quality of abundant yet low quality resources over heterogeneous landscapes is an important mechanism by which herbivores increase diet quality, individual health, and population performance (Mysterud et al. 2001; Wang et al. 2006; Hebblewhite et al. 2008). This is because spatial and temporal variation in plant phenology increases the efficiency of use of resources (Searle et al. 2010) by increasing heterogeneity in plant growth. This prolongs the availability of high nutritional quality plants to herbivores (Ims 1990; Pettorelli et al. 2007). My analysis of crude protein content in roots supports this assertion, and suggests that the benefits of resource heterogeneity over space and time extend not only to large herbivores and thus aboveground vegetation, but also to omnivores such as grizzly bears and their below ground resources.

I found that alpine sweetvetch roots have moderately high protein values. This is not surprising, however, because it is a nitrogen fixing legume (Willey 1983; Kishinevsky 1996; Squartini et al. 2002). Alpine sweetvetch roots therefore likely serve as a significant seasonal protein source for animals, such as grizzly bears who most often consume the root when protein levels are highest and during periods of low resource availability (Hamer and Herrero 1987; Munro et al. 2006). Spatial heterogeneity and asynchrony in the protein content of alpine sweetvetch roots therefore benefits grizzly bears by prolonging the period they are able to forage on high quality resources. Grizzly bears are thereby able to 'surf' the 'brown wave' in root phenology and nutrition, just as herbivores 'surf' the 'green wave' in aboveground phenology and nutrition.

This work lends to the argument that grizzly bear habitat models should more explicitly consider spatial and temporal heterogeneity in food resources (Munro et al. 2006; Nielsen et al. 2010). In fact, modeling has successfully predicted movement patterns for other wildlife species when animals were assumed to track variations in plant phenology within heterogeneous landscapes (Wilmshurst et al. 1999; Boone et al. 2006). While I focused on crude protein as a measure of nutritional quality, this approach can also be extended to other nutritional (*e.g.*, starch, sugar, and fibre) and energetic (*e.g.*, digestible protein, digestible dry matter, and net digestible energy) estimates which would also require estimates of sweetvetch abundance and/or density (see Appendix A). Such an approach may be useful in understanding the effects of environmental change on wildlife when combined with factors that regulate populations from the top-down (Nielsen et al. 2010).

Table 3-1. Hypothesized factors, variable names, and abbreviations of variables used in candidate models.

Hypothesized factor	Variable names (predictor variables)	Abbreviation
Temporal	Julian day	JDAY
	Julian day squared (quadratic)	JDAY2
	Year	YEAR
Soils	Terrain wetness (Compound Topographic Index)	CTI
	Bedrock formation	GEO
Temperature	Growing degree day (5 °C)	GGD
Slope/Aspect & Sunlight	Global solar radiation (on Julian day 172)	GLBL172
	Crown cover	CROWN
Community	Landcover category	LANCOV

Table 3-2. Range of dates, average crude protein content (based on % dry weight), and digestible protein (DP) of alpine sweetvetch (*Hedysarum alpinum*) root by phenological stage for both mountain (elevation ≥1700 m) and foothills (elevation <1700 m) environments. Roots (n=112) were sampled in 14 areas between 2008 and 2010.

Elevation	Pre-Leaf	Leaf	Bud	Flower	Seed	Dormant
≥1700 m	26 May –17 Jun	04 Jun†	30 Jun – 06 Jul	08 Jul – 29 Jul	04 Aug – 12 Sep	17 Sep – 13 Oct
<1700 m	27 Apr – 17 Jun	28 May –08 Jun	04 Jun – 06 Jul	24 Jun –30 Jul	29 Jul –29 Sep	17 Sep – 17 Oct
Average Crude Protein	17.0 *a* §	17.9 *ab*	15.8 *ab*	14.6 *b*	14.8 *b*	17.1 *a*
n	15	6	14	19	40	18
S.E.	0.51	1.50	0.51	0.54	0.40	0.59
DP	11.5	12.3	10.5	9.4	9.6	11.6

†There was only one observation made of the Leaf phenological stage in mountain habitats.

§Unique lower case lettering indicates significant differences in crude protein content.

Table 3-3. Hypothesized candidate models, model structure, Akaike Information Criterion with small sample size correction (AIC_c), ΔAIC_c, and Akaike weight (w_i) of the top 10 candidate models used to predict crude protein content of alpine sweetvetch (*Hedysarum alpinum*) in west-central Alberta, Canada. The final model (in bold) was selected based on the highest Akaike weight (w_i).

Candidate models (hypotheses)	Model structure	AIC_c	ΔAIC_c	w_i
Temporal + Soil * Temperature * Temporal	**JDAY + JDAY2 + CTI * GDD * JDAY**	**529.17**	**0**	**0.71**
Temporal + Soil * Temperature * Temporal + Year	JDAY + JDAY2 + CTI * GDD * JDAY + YEAR	532.32	3.15	0.15
Temporal + Soil	JDAY+JDAY2+CTI	535.28	6.11	0.03
Temporal + Soil + Geology	JDAY+JDAY2+CTI+GEO	536.22	7.05	0.02
Temporal + Soil + Soil * Temporal	JDAY+JDAY2+CTI+CTI*JDAY	536.60	7.43	0.02
Temporal + Soil + Temperature	JDAY+JDAY2+CTI+GDD	536.95	7.78	0.01
Temporal + Soil * Geology * Temporal	JDAY+JDAY2+CTI*GEO*JDAY	537.75	8.58	0.01
Temporal + Soil + Temperature * Temporal	JDAY+JDAY2+CTI+GDD*JDAY	537.88	8.71	0.01
Temporal + Soil + Geology + Competition	JDAY+JDAY2+CTI+GEO+LANCOV	538.43	9.26	0.01
Temporal + Soil + Geology + Temperature	JDAY+JDAY2+CTI+GEO+GDD	538.43	9.26	0.01

Table 3-4. Estimated coefficients, standard error, t-value, and significance levels (*p*) of model variables used to predict crude protein content of alpine sweetvetch (*Hedysarum alpinum*) in west-central Alberta, Canada.

Variable	Coef.	Std. Err.	t-value	*p*
JDAY	-0.702	0.124	-5.64	<0.001
JDAY2	0.592†	0.105†	5.65	<0.001
CTI	-12.91	3.522	-3.64	<0.001
GDD	-0.100	0.027	-3.64	<0.001
CTI:GDD	0.014	0.004	3.56	<0.001
JDAY:CTI	0.063	0.017	3.74	<0.001
JDAY:GDD	0.503†	0.131†	3.85	<0.001
JDAY:CTI:GDD	-0.682‡	0.182‡	-3.75	<0.001
Intercept	133.4	24.96	5.34	<0.001

†estimated coefficients and standard errors are reported at 1,000 times their actual value

‡estimated coefficients and standard errors are reported at 10,000 times their actual value

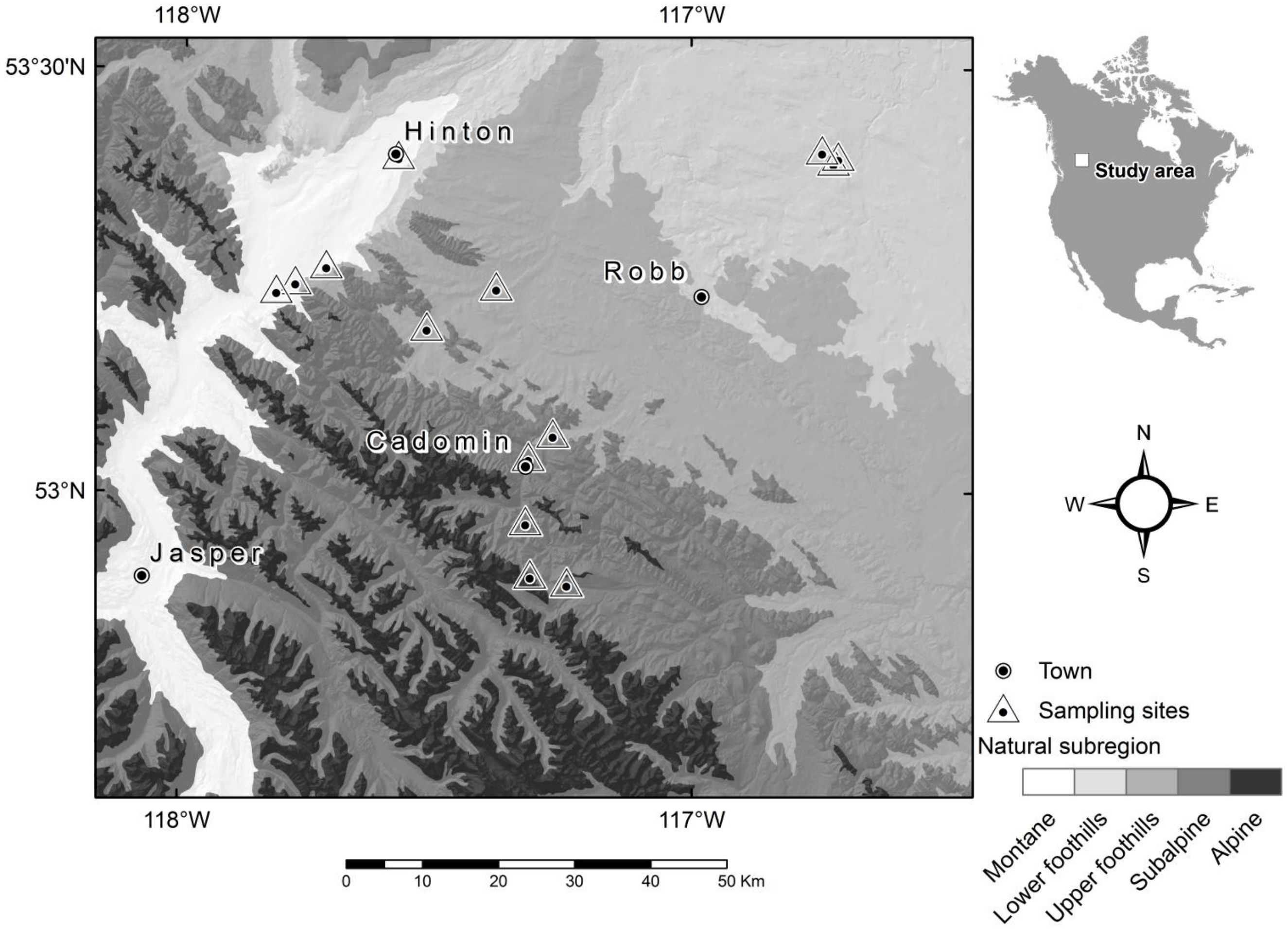

Figure 3-1. Study area depicting towns, alpine sweetvetch (Hedysarum alpinum) sampling sites, and Montane, Lower Foothills, Upper Foothills, Subalpine, and Alpine subregions.

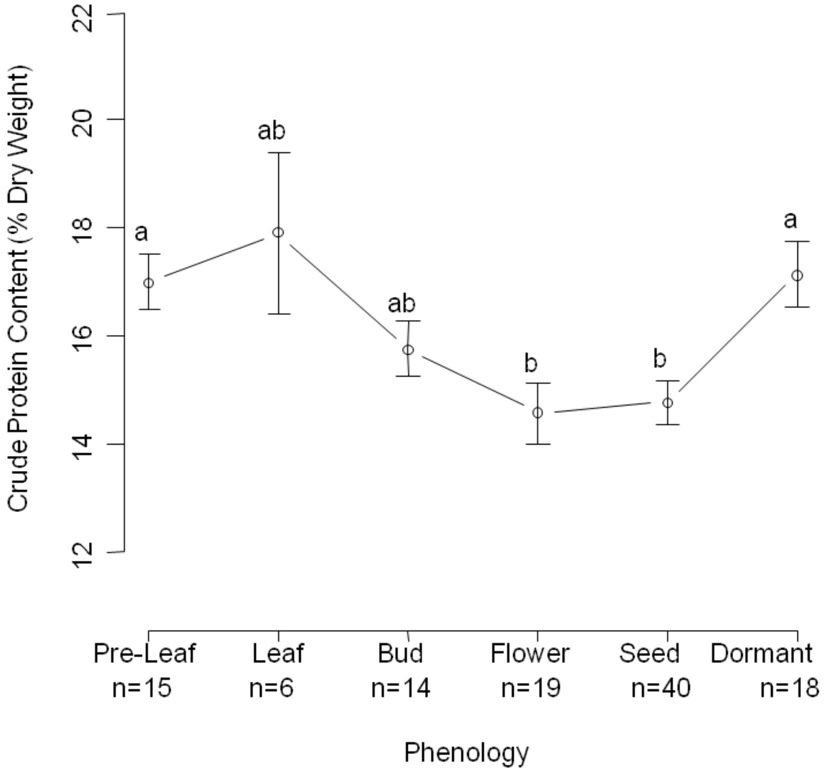

Figure 3-2. Average crude protein content (% dry matter basis) of *Hedysarum alpinum* roots sampled in west-central Alberta, Canada in different phenological stages. Error bars are 1 standard error above and below the mean. Lower case letters indicate phenological stages with significantly different levels of crude protein (*i.e.*, pre-leaf & flower, pre-leaf and seed, seed and dormant, flower and dormant).

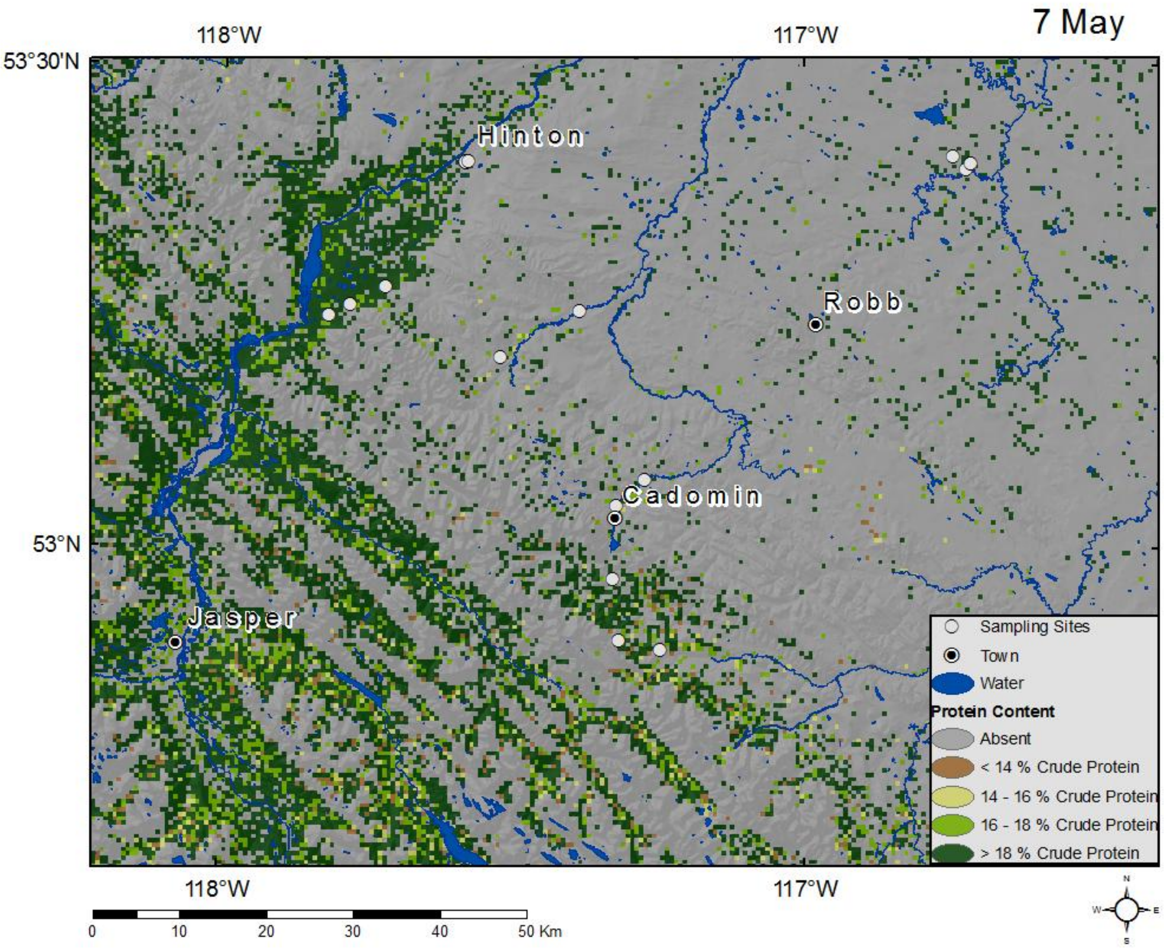

Figure 3-3. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 7 May.

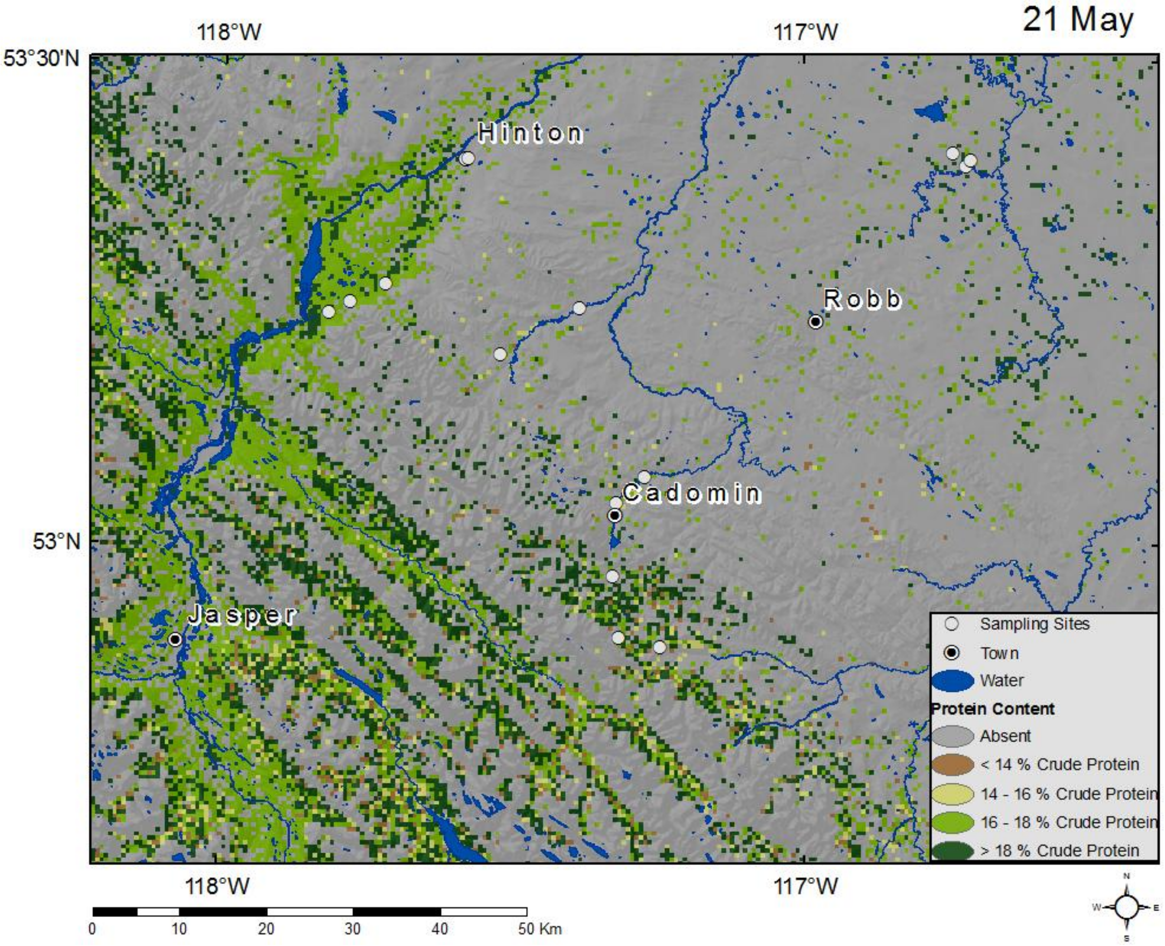

Figure 3-4. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 21 May.

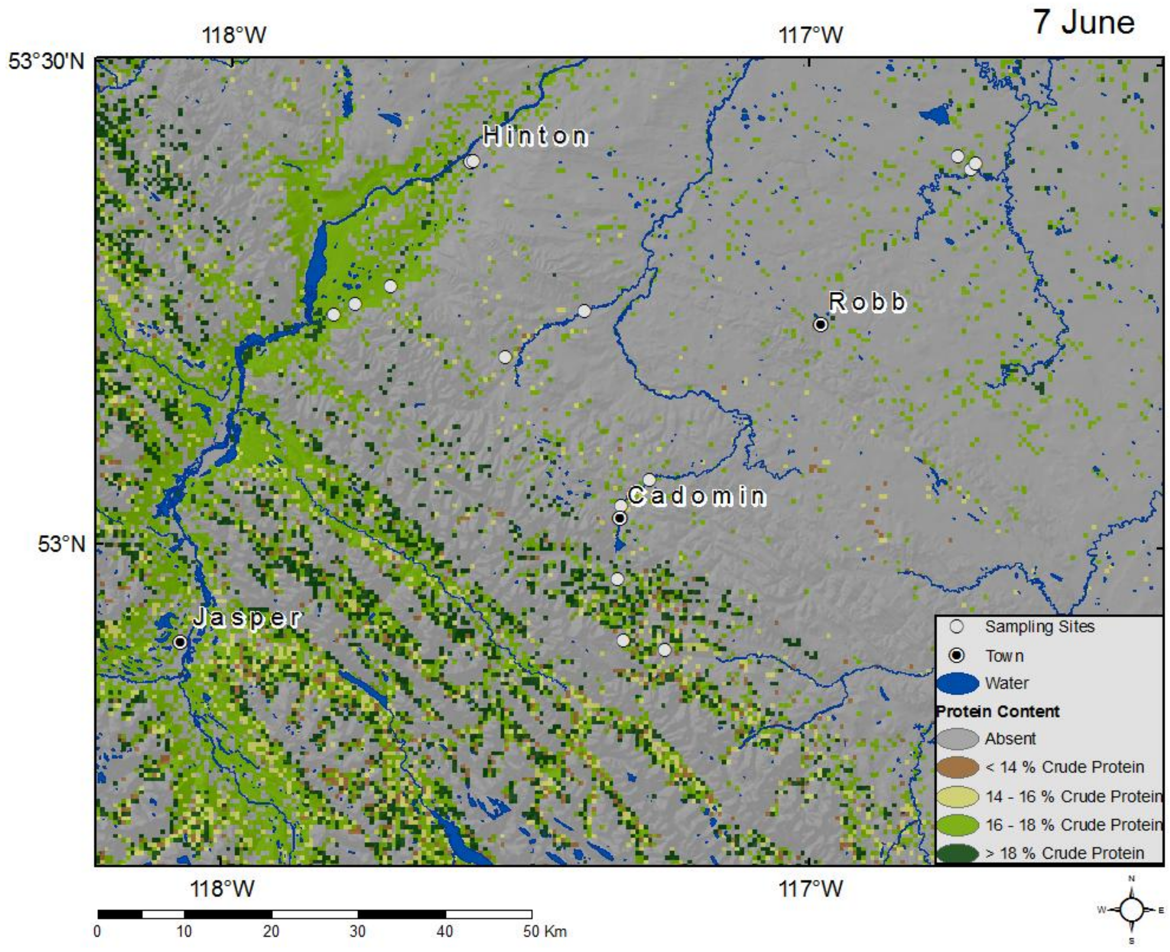

Figure 3-5. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 7 June.

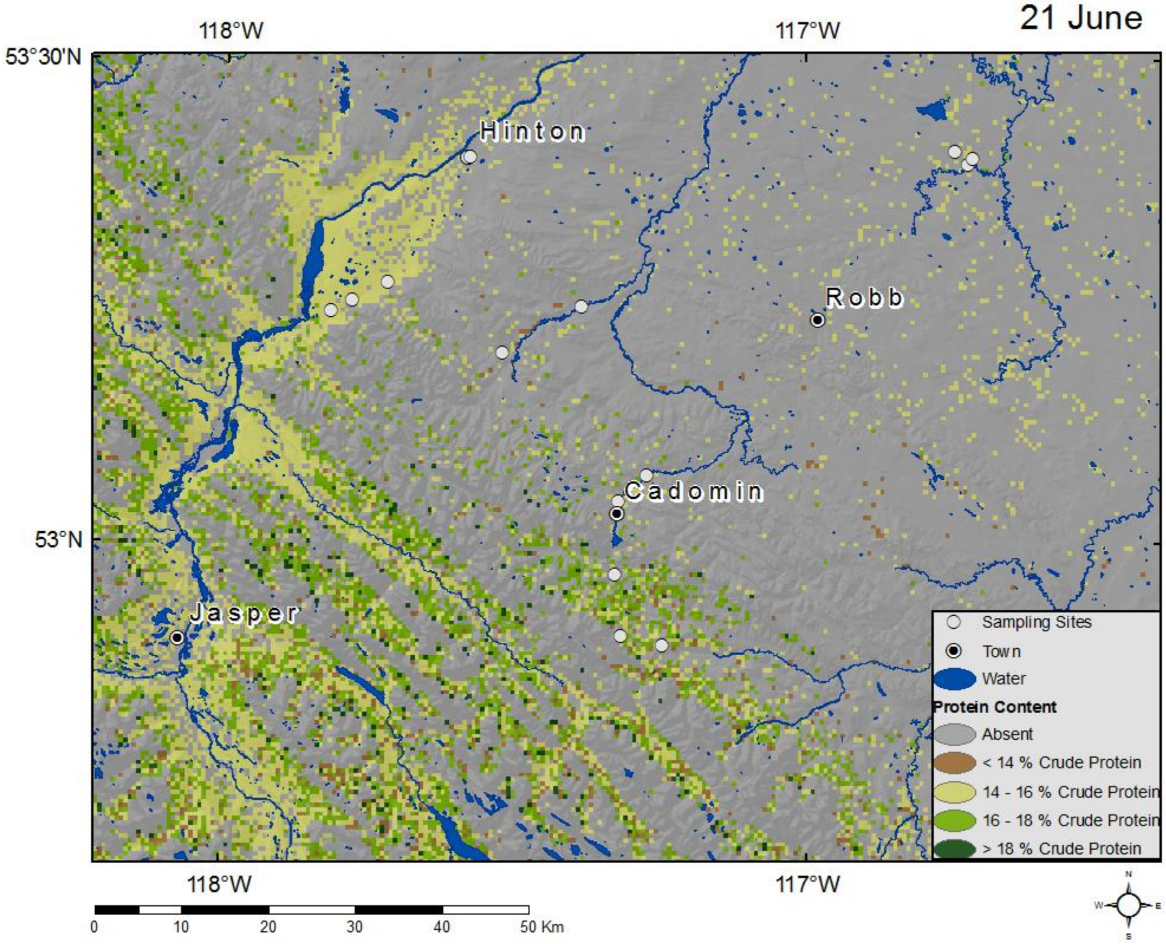

Figure 3-6. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 21 June.

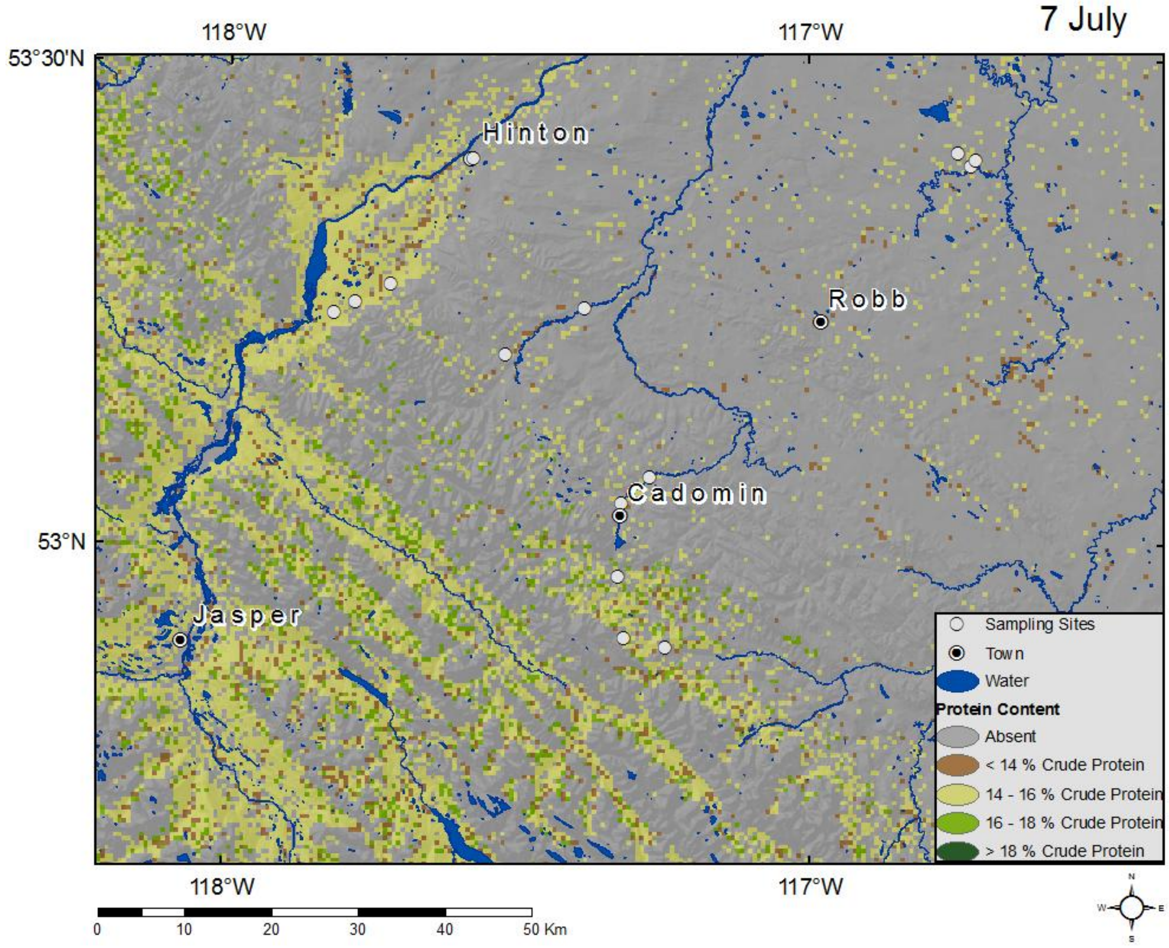

Figure 3-7. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 7 July.

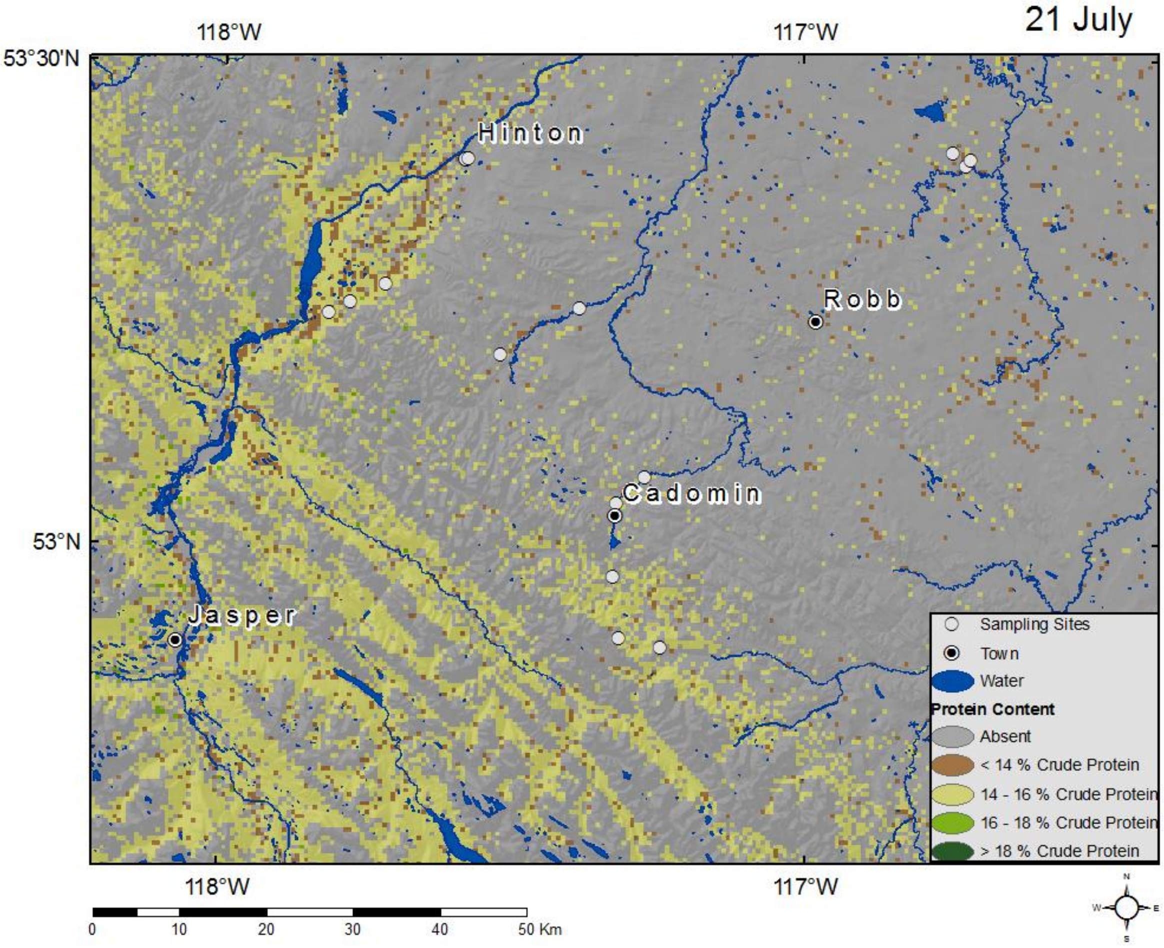

Figure 3-8. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 21 July.

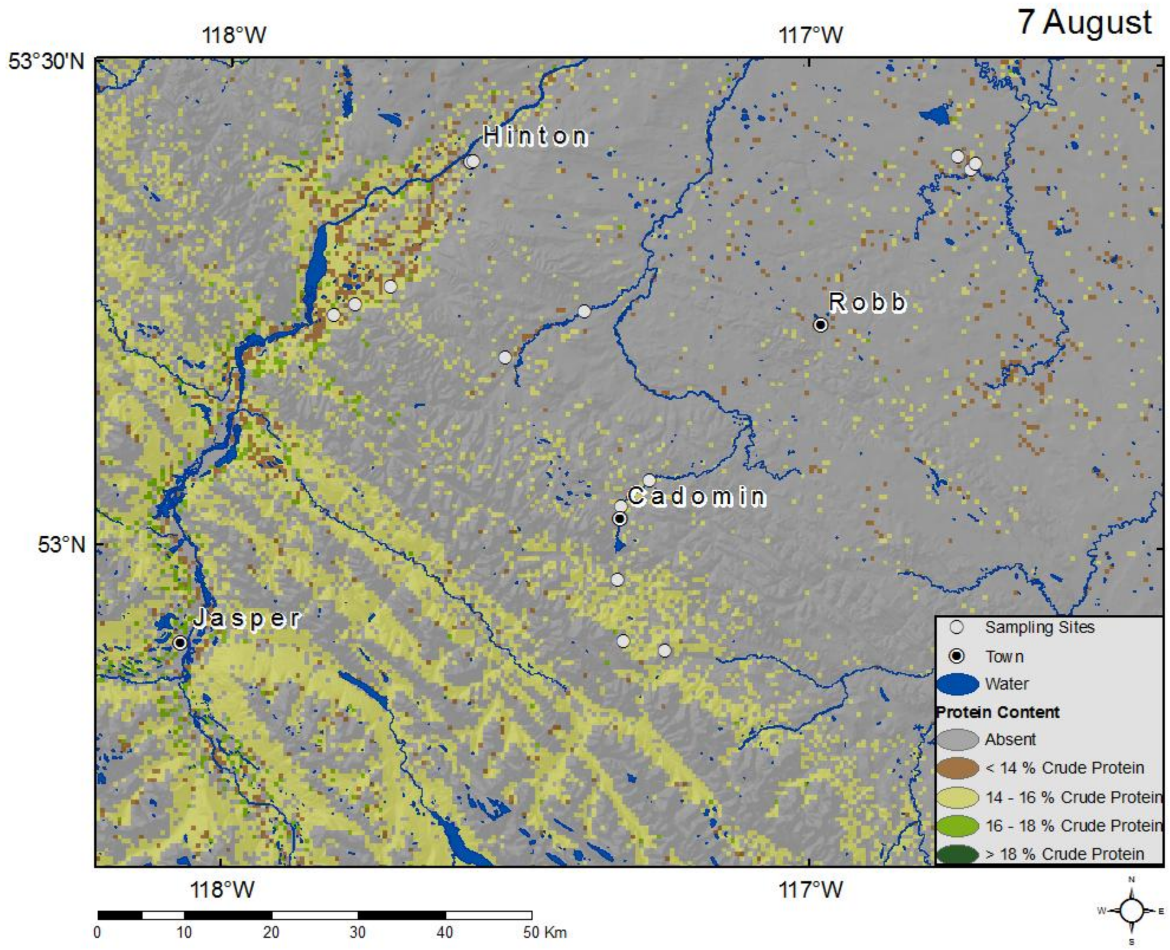

Figure 3-9. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 7 August.

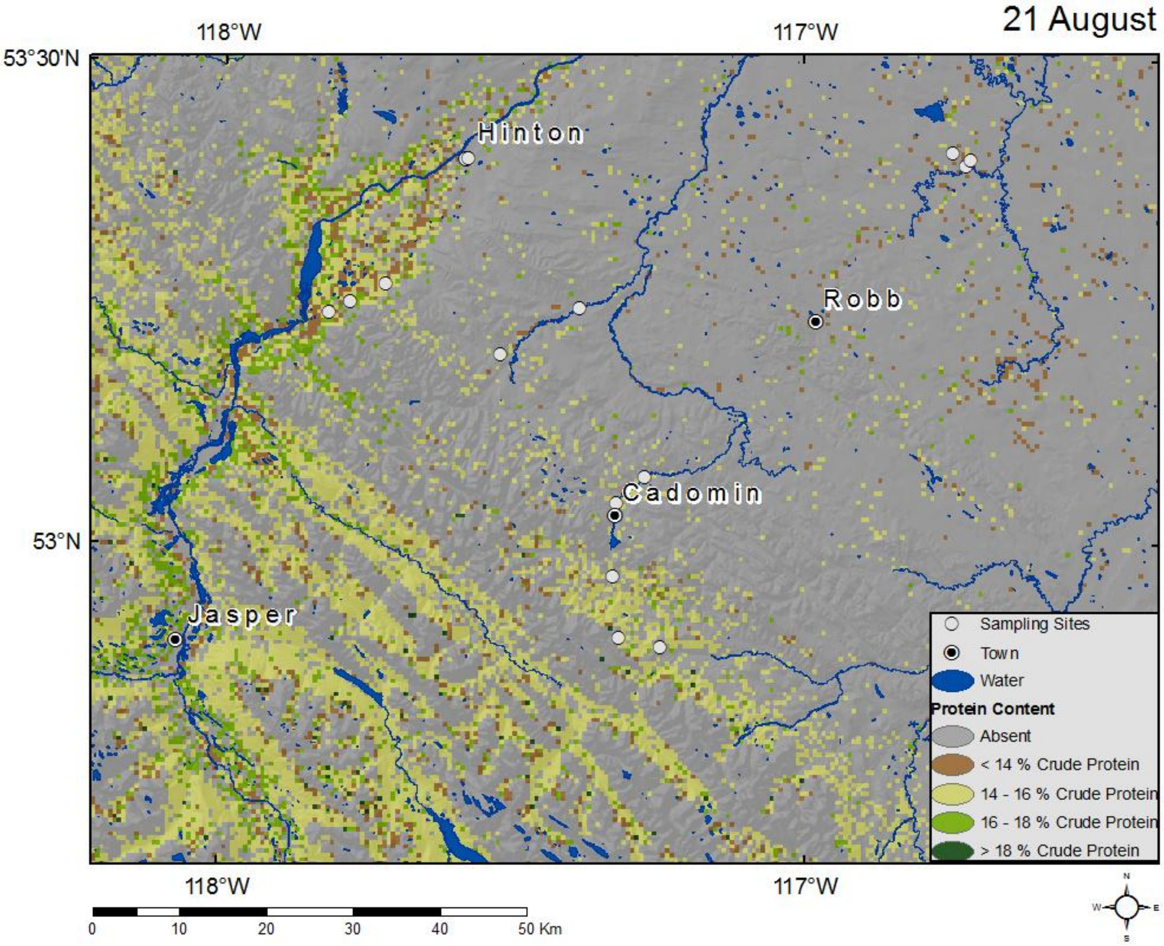

Figure 3-10. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 21 August.

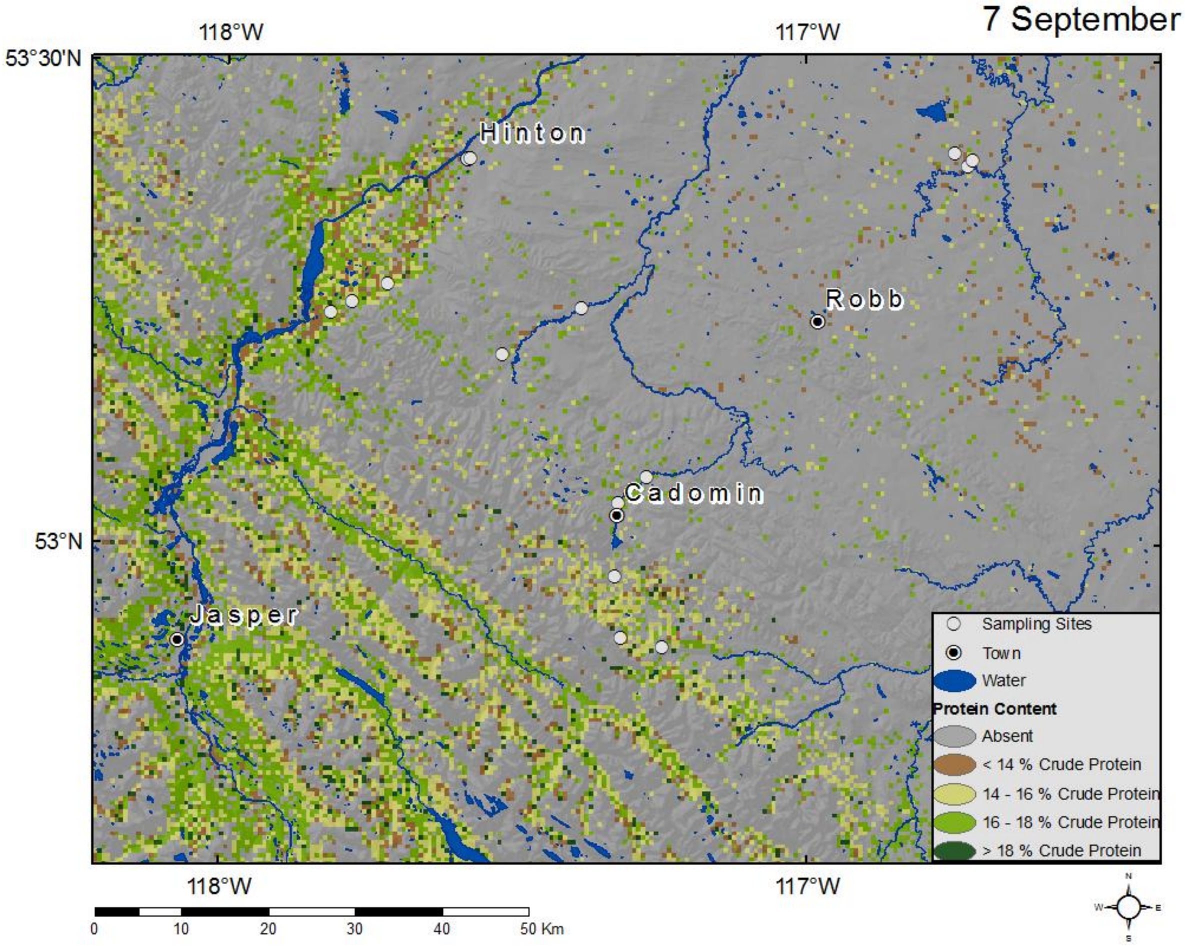

Figure 3-11. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 7 September.

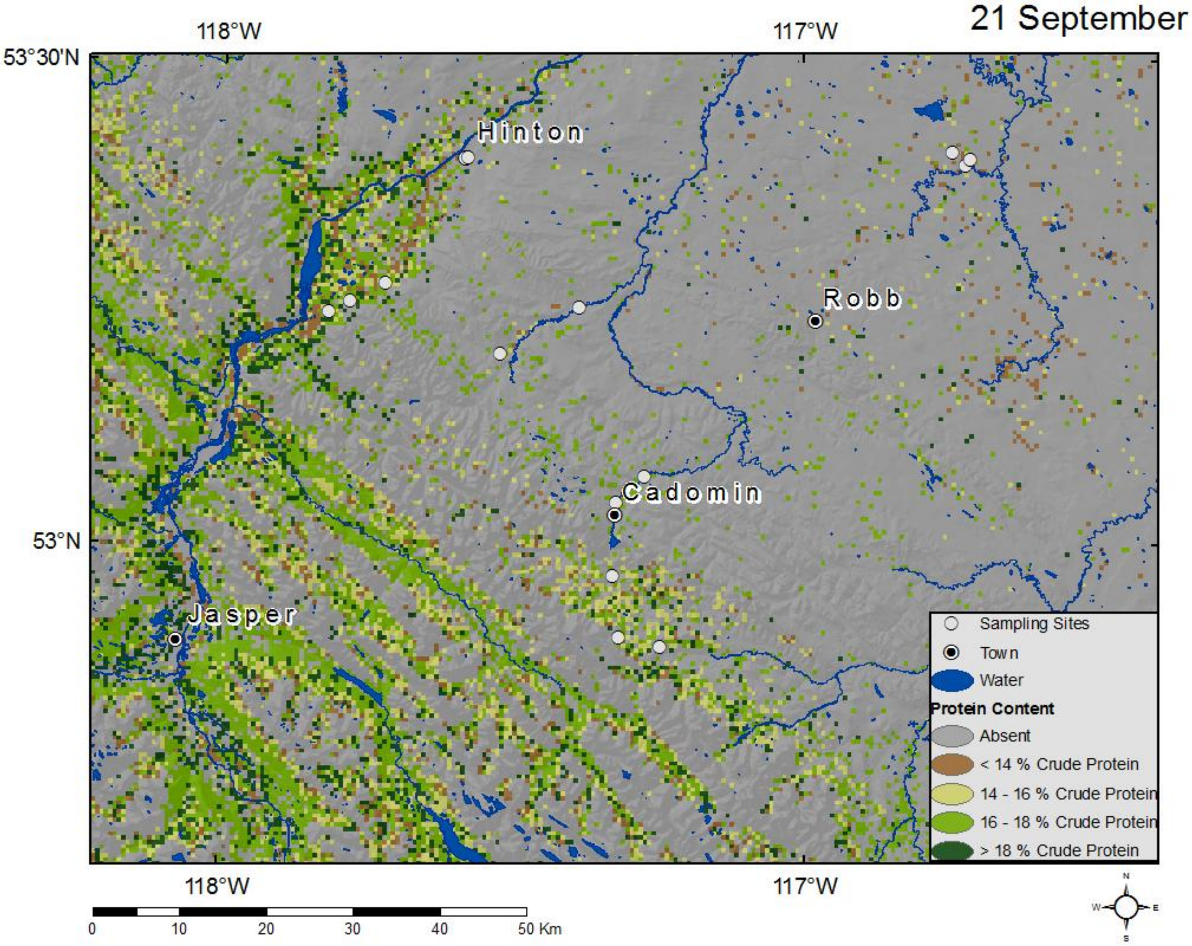

Figure 3-12. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 21 September.

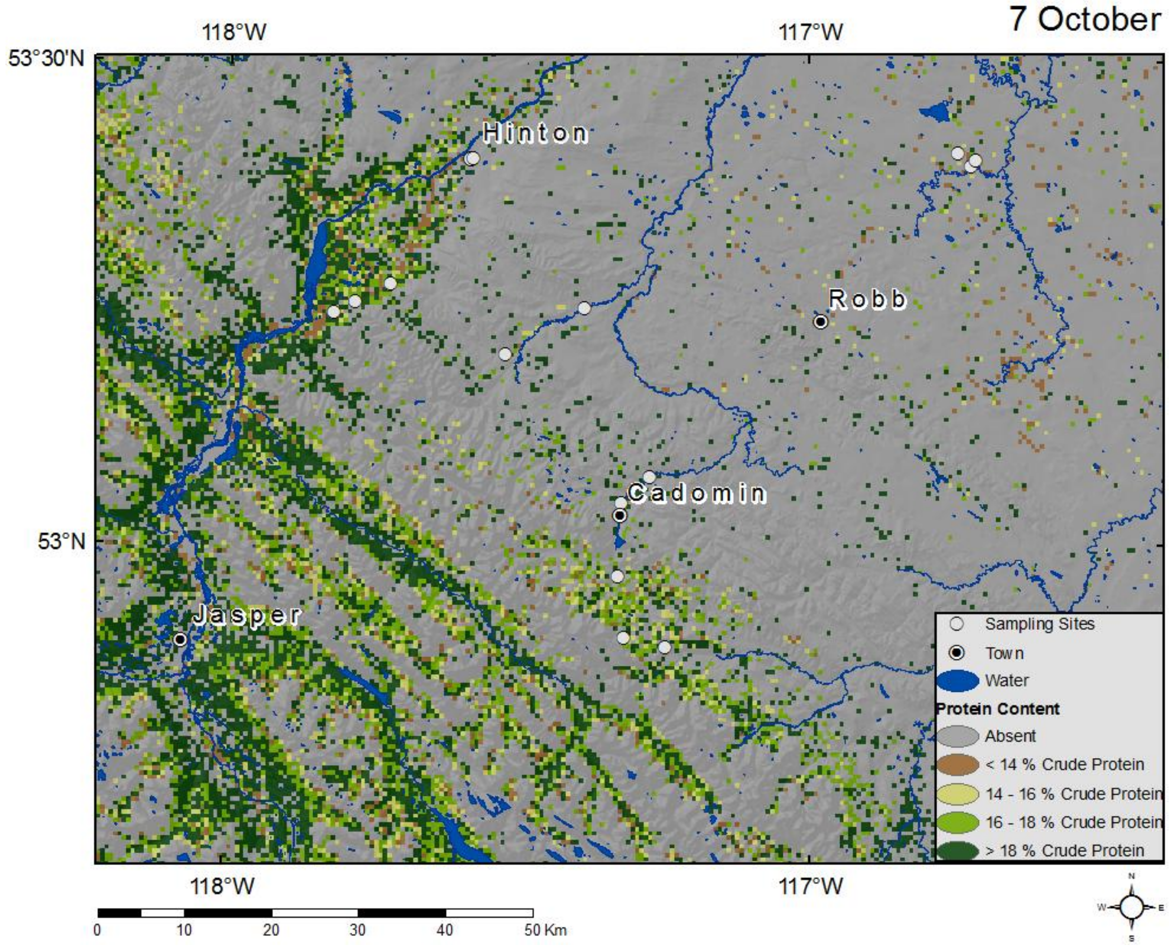

Figure 3-13. Nutritional landscape map predicting the percent crude protein content in alpine sweetvetch (*Hedysarum alpinum*) roots for 7 October.

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CHAPTER 4

GENERAL DISCUSSION AND CONCLUSION

In this thesis, I examined the relationship between grizzly bears and alpine sweetvetch in west-central Alberta, Canada. This work further demonstrates the importance of alpine sweetvetch roots to the regional grizzly bear population, especially in mountainous habitats (Chapter 2), and that this is in part due to spatial and temporal heterogeneity in environmental factors that prolong the availability of nutritious roots to bears (Chapter 3). Given this, the management of grizzly bears in west-central Alberta should incorporate strategies associated with alpine sweetvetch. One such example is the establishment of supplemental alpine sweetvetch food plots that provide grizzly bears with additional root resources. Alpine sweetvetch food plots may be especially beneficial to grizzly bears during periods of limited resource availability, such as cold (negative PDO) springs, and years of poor berry production. Of course, food plots would need to be established in suitable areas away from potential human conflict (*e.g.*, roads, etc.). Suitable areas for food plots may include sections of forest cut blocks away from roads, and the planting of alpine sweetvetch may be part of a forestry regeneration strategy. Alpine sweetvetch planting may also be used as part of land reclamation and restoration in the area, such as for decommissioned roads or mine areas suitable for grizzly bears. In fact, alpine sweetvetch is a recommended native plant for use in the reclamation of subalpine and alpine coal mines, as these legumes fix nitrogen to the soil, promote soil stability due to extensive taproots, and provide wildlife forage (Willey 1983).

The spatial and temporal model predicting the crude protein content of alpine sweetvetch improves measures of resource availability to wildlife (Nielsen et al. 2010), because, as demonstrated in Chapter 3, resource nutrition, and therefore habitat quality, is dynamic over time and space. Additionally, in combination with estimates of sweetvetch abundance and energetic expenditure by grizzly bears, this model can be used to quantify net nutritional gains to these animals (therefore, managers may wish to quantify the abundance and monitor the distribution of sweetvetch). The nutritional landscape maps created from the model can also be used for the identification and timing of critical habitats. That is, where and when grizzly bears are most likely to be digging. This may also be important in indentifying the location of possible attractive ecological sinks (Nielsen et al. 2006) or other areas of potential conflict, which may be especially important for grizzly bears given that human-caused mortality is the most important factor affecting survival rates (Benn and Herrero 2002; Nielsen et al. 2004; Alberta Sustainable Resource Development and Alberta Conservation Association 2010).

Also, consider that in west-central Alberta there is primarily only one root resource, while as we move further south along the Rockies, grizzly bears have access to multiple plants with edible roots. It may be that the limited number of root species (and therefore reduction in foraging options) available to bears in west-central Alberta during critical periods of resource limitation may have a bottom-up regulatory effect on the population. The fact that our population is dependent on a single root species may contribute to the relatively lower population density (4.79 bears per 1000 km^2; Alberta Grizzly Bear Inventory Team 2005) observed in the area.

That grizzly bears may have evolved to become physically adapted to digging underscores the importance of underground food resources for these animals. The importance of sweetvetch roots to bears in west-central Alberta, and digging in general, suggests that grizzly bears may have a larger ecological role in ecosystems through biopedturbation (*i.e.*, soil disturbance). Soil transport, plant community structure, and soil chemistry have all been shown to be affected as a result of grizzly bear digging (Butler 1992; Tardiff and Stanford 1998; Doak and Loso 2003; Hall and Lamont 2003; Nielsen, unpublished). It may be that the soil at alpine sweetvetch dig sites are especially rich in nitrogen, given that grizzly bear digging can increase soil nitrogen content (Tardiff and Stanford 1998) and alpine sweetvetch fixes nitrogen (Willey 1983). Therefore, additional research examining the ecological effects of grizzly bear digging for alpine sweetvetch roots in west-central Alberta is recommended.

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APPENDIX A

NUTRITIONAL ANALYSIS OF GRIZZLY BEAR FOODS IN WEST-CENTRAL ALBERTA, CANADA

1. PURPOSE

Grizzly bear (*Ursus arctos*) habitat studies often use resource patches defined by presence-absence to measure resource availability (Nielsen et al. 2010). However, researchers recognize the need to incorporate more explicit measures of habitat quality, such as estimates of food abundance, nutritional quality, and digestibility into grizzly bear habitat models (Nielsen et al. 2010). Such an approach was taken by Mattson et al. (2004), where net digestible energy was quantified across the Yellowstone ecosystem. Here I analyzed the nutritional quality of some common bear foods (vegetation and ants (Hymenoptera: Formicidae)) in west-central Alberta for use in regional ecological modelling and habitat studies for the grizzly bear. I further estimated digestibility of food items using relationships from Pritchard and Robbins (1990). Finally, I provide the dry weight of some common berries consumed by bears in the region.

2. METHODS

2.1 Nutritional analyses

Nutritional analyses were performed at both the University of Alberta and at an independent laboratory. Nutritional analyses performed at the University of Alberta (Table A-1; A-2) were performed in the Proximate Laboratories at the

Department of Agriculture, Food, and Nutritional Sciences. All samples were frozen following collection and then later dried in the laboratory at 60°C for 48 hours. Crude protein (N × 6.25) was determined via combustion analysis using a LECO Truspec N/C analyzer ((Leco Corporation, St. Joseph, Michegan USA). Crude fibre was estimate using AOCS procedure Ba 6a-05 (AOCS 2009a), and ash using AOAC method 942.05 (AOAC 2007a). Gross energy was analyzed with an IKA® C calorimeter (IKA® Works Inc., Wilmington, USA). Moisture was determined by oven drying at 110°C (a small number of samples were determined by oven drying at 105°C).

Nutritional analyses performed at the independent laboratory (Exova, Bay #5, 2712-37 Ave NE, Calgary, AB, Canada) followed Standards Council of Canada (SCC) accredited methods in the analyses of ash (AOAC 2007b), moisture (AOAC 2007c), crude fibre (method Am 01-04), carbohydrates (AOAC 2007d), protein (AOAC 2007e), fat (AOCS 2009b), and gross energy (AOAC 2007d). Nutritional estimates from both laboratories are reported on a 100% dry matter basis.

Total dietary fibre was estimated from crude fibre and ash using the following equation from Mattson et al. (2004):

$$tdf = 6.63 + (1.54 \times cf) + (3.84 \times \ln ash) \qquad \text{(A-1)}$$

where *tdf* is percent total dietary fibre, *cf* is percent crude fibre, and *ash* is percent ash content.

2.2 Digestability estimates

I calculated digestible protein, digestible dry matter, and digestible energy using equations from Pritchard and Robbins (1990). Digestible protein of plant material was calculated from crude protein estimates using the following equation:

$$dp = -3.46 + 0.881 \times cp \tag{A-2}$$

where dp is digestible protein (g/100 g), and cp is percent crude protein. Digestible protein of ant larvae was calculated from crude protein estimates using the following equation:

$$dp = -3.82 + 1.01 \times cp \tag{A-3}$$

where dp is digestible protein (g/100 g), and cp is percent crude protein. Digestible dry matter was estimated from total dietary fibre estimates using the following equation:

$$ddm = 101.3 - 1.39 \times tdf \tag{A-4}$$

where ddm is percent digestible dry matter, and tdf is percent total dietary fibre. Digestible energy of plant material was calculated from digestible dry matter using the following equation:

$$de = 8.05 + 0.83 \times ddm \tag{A-5}$$

where de is percent digestible energy, and ddm is percent digestible dry matter.

2.3 Berry Dry Weights

I calculated the dry weight (moisture content) of individual berries by oven drying at 110°C.

3. RESULTS AND DISCUSSION

Average nutritional estimates for food items are reported in Table A-1, while average digestibility estimates are reported in Table A-2. All berry estimates included both seed and pulp in analyses. Unexpectedly high protein values were reported for Buffaloberries (*Shepherdia canadensis*) from both laboratories, which (I hypothesize) may be due to their large seed and/or possibly the presence of nitrogen containing saponins. Crude protein of ants has not been adjusted for chitin content (see Wigglesworth 1972). Chitin content of ant larvae is assumed to be negligible (Noyce et al. 1997). The estimates of digestibility for alpine sweetvetch root should be interpreted with caution due to uncertainty in the digestibility of starch in natural roots and tubers for bears (Pritchard and Robbins 1990). The high fat and fibre content of nuts and seeds make whitebark pine seeds unsuitable for digestibility estimates using the equations from Pritchard and Robbins (1990). Dry weight per berry for Buffaloberries were lower than expected (see Welch et al. 1997), as such I recommend further analysis.

Table A-1. Average percent dry weight nutrient content (x̄), standard error (SE) and sample size (n) of foods consumed by grizzly bears in west-central Alberta, Canada. Instances where standard error could not be calculated due to n=1 are denoted by (-).

	Percent crude protein			**Percent crude fibre**			**Percent ash**			**Percent fat**			**Percent total dietary fibre**			**Percent available carbohydrate**		
Food	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**
Horsetails																		
(Equisetum arvense)	**20.4**	(2.2)	8	**19.3**	(1.6)	3	**19.4**	(1)	3				**50**	(2.4)	2			
(Equisetum sylvaticum)	**20**	(4.6)	2	**14.7**	(2.7)	2	**14.3**	(-)	1				**43.6**	(-)	1			
Cow parsnip																		
(*Heracleum lanatum*)																		
Leaves & stem	**13.9**	(2.2)	8	**30.5**	(1.8)	8	**18.7**	(1.3)	8				**64.8**	(2.7)	8			
Creamy peavine																		
(*Lathyrus ochroleucus*)	**19.9**	(3.8)	2	**30.4**	(1.8)	3	**6.5**	(0.1)	2				**63.2**	(1.6)	2			
Dandelion																		
(*Taraxacum officinale*)																		
Flowers	**17**	(0.3)	6	**15.4**	(0.5)	5	**8.2**	(0.2)	4				**39.2**	(1)	3			
Leaves & stem	**17**	(2)	11	**13.2**	(1.3)	6	**15.9**	(1.2)	6				**38.4**	(2.1)	6			
Clover																		
Leaves & stem	**19.4**	(1.3)	21	**25.7**	(2.1)	12	**9.6**	(0.3)	14				**58.5**	(2.6)	10			
Flowers	**27.1**	(-)	1	**18.9**	(-)	1	**10.9**	(-)	1				**44.9**	(-)	1			
Alfalfa																		
(*Medicago sattiva*)																		
Leaves and stem	**22.1**	(2.8)	2	**28.7**	(0.4)	2	**9.6**	(0.4)	2				**59.6**	(0.7)	2			
Whitebark pine seed	**14.8**	(-)	1	**51.6**	(-)	1	**2.9**	(-)	1									
Crowberry																		

(Empetrum nigrum)†	**3.5**	(0)	2	**25.1**	(1.5)	2	**1.6**	(0)	2	**5.3**	(0)	2	**47.2**	(2.5)	2	**42.4**	(2.6)	2
Vaccinium spp.																		
1. *(V. myrtilloides)*†	**4.7**	(0.1)	4	**11**	(0.7)	4	**1.8**	(0)	4	**2.9**	(0.3)	4	**25.7**	(1.3)	4	**64.9**	(1.3)	4
2. *(V. myrtilloides)*	**7.3**	(0.7)	2	**13.1**	(-)	1	**1.8**	(-)	1				**29.2**	(-)	1			
(V. scoparium)†	**4.9**	(-)	1	**9.3**	(-)	1	**1.9**	(-)	1	**4.4**	(-)	1	**23.4**	(-)	1	**65.4**	(-)	1
(V. vitis-idaea)†	**4.4**	(0.3)	5	**9.8**	(0.8)	5	**1.8**	(0)	5	**3.3**	(0.1)	5	**23.9**	(1.3)	5	**66.6**	(1.6)	5
Buffaloberry§																		
1. (Shepherdia canadensis)†	**14.4**	(3.6)	10	**8.8**	(0.5)	10	**2.7**	(0.2)	10	**8.3**	(0.3)	10	**23.9**	(0.8)	10	**50.7**	(2.1)	10
2. (Shepherdia canadensis)	**19.8**	(0.9)	8	**10.1**	(0.7)	8	**3**	(0.1)	8				**26.3**	(1)	8			
Alpine sweetvetch root																		
1. *(Hedysarum alpinum)*†	**12.6**	(1.8)	16	**18.3**	(0.8)	16	**9**	(0.8)	16	**1.5**	(0.1)	16	**43.1**	(1.3)	16	**33.8**	(1.9)	16
2. *(Hedysarum alpinum)*	**15.7**	(0.2)	117	**21.5**	(0.8)	60	**8.8**	(0.4)	74				**48.7**	(1.4)	51			
Ants‡																		
Formica aserva																		
Larvae	**55.9**	(8.5)	2															
Ants	**56.2**	(4.3)	2															
Formica ulkei																		
Larvae	**66.8**	(6.9)	2															
Ants	**74.6**	(-)	1															

All berry estimates included both seed and pulp in analyses.

§ High protein values for Buffaloberries may be due to their large seed and/or possibly as a result of chemical (saponin) content.

† Indicates samples that were analyzed at an independent external laboratory.

‡ Crude protein of ants has not been adjusted for chitin content. Chitin content of larvae is assumed to be negligible.

Table A-2. Average gross energy (kcal/100 g), digestible protein (g/100 g), percent digestible dry matter, and percent digestible energy of foods consumed by grizzly bears in west-central Alberta, Canada, with standard error (SE) and sample size (n). All results are reported on a dry matter basis. Instances where standard error could not be calculated due to n=1 are denoted by (-).

	Gross energy (kcal/100 g)			**Digestible protein (g/100 g)**			**Digestible dry matter (%)**			**Digestible energy (%)**		
Food	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**	**x̄**	**SE**	**n**
Horsetails												
(Equisetum arvense)				**14.5**	(2)	8	**31.8**	(3.3)	2	**34.5**	(2.7)	2
(Equisetum sylvaticum)				**14.1**	(4.4)	2	**40.7**	(-)	1	**41.8**	(-)	1
Cow parsnip												
(*Heracleum lanatum*)												
Leaves & stem	**364**	(5.7)	7	**8.7**	(1.9)	8	**11.3**	(3.8)	8	**17.4**	(3.1)	8
Creamy peavine												
(*Lathyrus ochroleucus*)	**482.7**	(-)	1	**14.1**	(3.3)	2	**13.5**	(2.2)	2	**19.2**	(1.8)	2
Dandelion												
(*Taraxacum officinale*)												
Flowers				**13.5**	(0.4)	6	**46.8**	(1.4)	3	**46.9**	(1.2)	3
Leaves & stem	**382.8**	(7.0)	3	**10.5**	(2.1)	11	**48**	(2.9)	6	**47.9**	(2.4)	6
Clover												
Leaves & stem	**438.2**	(2.7)	14	**13.6**	(1.2)	20	**20**	(3.6)	10	**24.7**	(3)	10
Flowers				**20.4**	(-)	1	**38.9**	(-)	1	**40.4**	(-)	1
Alfalfa												
(Medicago sattiva)												
Leaves & stem	**415.8**	(-)	1	**16**	(2.5)	2	**18.5**	(1)	2	**23.4**	(0.8)	2
Whitebark pine seed§	**611.1**	(-)	1	**9.6**	(-)	1						
Crowberry												

(Empetrum nigrum) †	**420**	(0.4)	2	**< 0**	(-)	2	**35.7**	(3.5)	2	**37.7**	(2.9)	2
Vaccinium spp.												
1. (V. myrtilloides) †	**407.7**	(1.6)	4	**0.6**	(0.1)	4	**65.5**	(1.6)	4	**62.4**	(1.3)	4
2. (V. myrtilloides)				**3.0**	(0.6)	2	**60.7**	(-)	1	**58.4**	(-)	1
(V. scoparium) †	**414**	(-)	1	**0.9**	(-)	1	**68.8**	(-)	1	**65.2**	(-)	1
(V. vitis-idaea) †	**410**	(0.7)	5	**0.4**	(0.3)	5	**68.1**	(1.8)	5	**64.5**	(1.5)	5
Buffaloberry												
1. (Shepherdia canadensis) †	**431**	(1.5)	10	**9.2**	(1)	10	**68**	(1.2)	10	**64.5**	(1)	10
2. (Shepherdia canadensis)	**542.7**	(-)	1	**14**	(0.8)	8	**64.7**	(1.3)	8	**61.8**	(1.1)	8
Alpine sweetvetch root‡												
1. (Hedysarum alpinum) †	**372**	(3.3)	16	**7.6**	(0.4)	16	**41.4**	(1.9)	16	**42.4**	(1.5)	16
2. (Hedysarum alpinum)	**420.4**	(4.3)	21	**10.3**	(0.2)	117	**33.7**	(1.9)	51	**36**	(1.6)	51
Ants												
Formica aserva Larvae	**52.6**	(8.6)	2									
Formica ulkei Larvae	**63.6**	(7.0)	2									

All berry estimates included both seed and pulp in analyses.

† Indicates samples that were analyzed at an independent external laboratory.

‡ The estimate of digestibility for alpine sweetvetch root should be interpreted with caution due to uncertainty with the digestibility of starch in natural roots and tubers for bears (Pritchard and Robbins 1990).

§ The high fat and fibre content of nuts and seeds make whitebark pine seeds unsuitable for digestibility estimates using the equations from Pritchard and Robbins (1990).

Table A-3. Average dry weight (g), standard error (SE), and sample size (n) of individual berries from four species eaten by bears in west-central Alberta, Canada.

	Dry weight (g)		
Species	**x̄**	**SE**	**n**
Vaccinium scoparium	**0.0149**	0.0011	24
Vaccinum vitis-idaea	**0.0320**	0.0030	24
Vaccinium myrtilloides	**0.0389**	0.0030	20
Shepherdia canadensis	**0.0172**	0.0004	24

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