"Nothing is more pleasantly exhilarating, or gives one a stronger sense of being really amid nature's untamed wilds, than, when encamped on the outskirts of a quiescent herd, to be awakened on a fresh June morning by their distant bellowing, and to see them, as daylight advances, quietly grazing over a vast expanse of green prairie."

JA Allen, 1887

University of Alberta

Scales of Forage Selection by Ungulates In Aspen Parkland

by

Maria Gayle Didkowsky ©

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

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Dr. Evelyn H. Merrill
Supervisor

Dr. David S. Hik
Supervisor

Dr. Robert J. Hudson
Committee member

Abstract:

Mixed herbivore grazing regimes are believed to be more sustainable for natural rangelands, though little research exists to show how species cope with mixed species guilds. I conducted a study on native ungulate foraging selection patterns in Aspen Parkland. I tested whether body size and physiology affects selection of bison (*Bison bison),* elk (*Cervus elaphus*), and mule deer (*Odoceilus hemionus*) at three scales: community, patches, and the bite in a mixed guild, and experimentally tested how a mixed feeder (elk) responds to the foraging effects of previous foraging by a grazer and selective feeder. Results showed that species did not respond to scales in proportion to body size, and that native ungulate guilds show evidence of facilitation in rotations led by large grazers. My results lend evidence of how native ungulates would have existed naturally in aspen parkland, and how they respond to vegetation through selection at multiple scales.

Acknowledgements

When I close my eyes, I see the rolling hills with long fescue blowing in the wind like waves on the sea. The smell of clean air, sweet grass and the sweat of a horse come back to me, and if only in spirit, for a brief moment, I'm back at the ranch, and I smile.

There are many people that have been influential in my recent personal development and that of my thesis. I want to extend my thanks to them all, as this has been an unforgettable experience. Above all, I feel I have gained so much from my committee. They are a group of brilliant scientists and good people. They genuinely care about their students, to push and encourage them to become good scientists and I will forever be thankful I changed projects, to join the Precision Ranching Initiative group. Bob, I look up to you with such respect. Your drive for this project has been so vital in its progress, and I would want no other on my committee. Evie, you are a phenomenal woman, with the energy of one hundred people. Thank you for taking me in and guiding me through this, especially with the help of your lab. Dave, you have always been there for input, no matter how busy you have been. You have kept my project focused, and I am thankful for the succinctness of your feedback. Vilis, though not on my committee, your encouragement gave me strength. Your enthusiasm for ecology and research inspired me to do my masters in ecology, and I have come to realize you are a rare gem in academia.

My family is at the root of my desire to travel, to experience new and sometimes wild adventures, to make friends and laughter and enjoy life. I hope I have made you

proud by taking these virtues west and giving them to so many others. I have missed my parents and siblings so much and wish they could have shared the highlights of this project. Thank you for your immeasurable support. I love you.

Iain, you have been my rock throughout this adventure. I appreciate your undying patience and support through all my troubles. You and your family have been called upon, time and time again for help, and have always been there for me. Thank you.

To those from the ranch: I wouldn't have made it through two summers in one piece without you all. It is rare to find a place where laughter is easy, and happens openly and freely every day. It ruptures uncontrollably until your whole body feels happy. Kinsella is this place, where I'm drawn to for renewal, for cleansing as it brings forth these feelings of happiness. It is a place where I am appreciated in my presence, because of who I am and how I relate to people and animals. My statistical abilities are not challenged, simple observations need not be disproved, and not knowing is ok. Instead, common sense, attitude, trust, appreciation of hard work, and the quiet understanding of animals are judged important. I would not give up the thousands of tears, the many nights not sleeping, the stress, and the years without my family, if it meant giving up Kinsella and the people who have made this thesis worthwhile.

Verne, your constant teasing, cursing and burly laughter were always a relief. My dear buffalo head and twin, I miss you. Dale you have given me the shirt off your back, which is now my favourite. Thanks for being my fellow R & C drinker. Dave, thank you for always listening, dancing, laughing with us, and being part of my temporary home. Barry, I always looked forward to spending moving days together. You are smart, practical, and your dry sense of humour brightens everyone's day. Tyler, thank you for sharing your horse, your home, your garden, your friends, and above all, your friendship with me. Jack, it is rare to find someone who appreciates the same things in life, and this truly made me feel at home. I have learned so much from you…about ranch life as well as about myself. Thank you all for an incredible experience and new memories.

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And lastly, I wish to thank NSERC, the University of Alberta, and the Province of Alberta for both monetary and educational support. I have had the freedom to focus on my research that many others never experience. I will be forever grateful that your support has allowed me to broaden my horizons as a scientist.

I close my eyes again, and remember blue sky, scattered with cumulous clouds and the great expanse of the rolling grassland spotted with clusters of aspen. I smell a thousand blooming roses that make each intake of breath a treat. To my right are three cowboys, teasing and smiling, left, a beautiful friend from home, and me, on muscular Quarter horse working cattle on the rangeland in Alberta. Surreal. That moment, I wish could have lasted forever.

Table of Contents **Page**

List of Tables

List of Figures

Chapter 1: General Introduction

Issues of Landscape Use in Canada

Less than 10% of Canada is currently protected from development (Deguise and Kerr 2006). Federally protected lands in Canada are scarce where species endangerment is highest; primarily in agricultural areas of southern Canada (Kerr & Cihlar 2004). Agriculture in the prairies and parklands reduces habitat availability through conversion to cropland and through indirect effects on diversity and species composition through vegetation modification by grazing livestock (Kerr & Cihlar 2004; Kerr & Deguise 2004). In 2002, in Canada, 323 species were listed as endangered: 16 of existing 193 mammals, 30 of 310 native bird species (World Conservation Monitoring Centre 2002). Rates of species endangerment and extinction in this area of Canada are comparable to that in other areas across the Americas, including tropical rainforests (Kerr & Deguise 2004). The prairie region is considered to be over 96 % modified by human use and primarily agriculture (Kerr & Deguise 2004). In some areas of the aspen parkland ecosystem, as little as 6% of native grasslands remain, of which 75% is considered to be in poor production areas (Hammermeister et al. 2002). With global warming, habitat loss, and sustainability of biodiversity as key environmental issues, prairie rangelands have been identified within Canada as having important global ecological functions (Kerr & Cihlar 2004; Kerr & Deguise 2004; Lynch et al. 2005). Not only are these rangelands the primary livestock producing areas of Canada, but they also serve the important role as carbon sinks and in reducing amounts of nitrogen leaching into groundwater (Bruce et al. 1999; Lynch et al. 2005).

Without a network of viable habitat for endangered species in highly impacted landscapes, there is little hope that maintenance of populations will occur in the tiny reserves that now exist as islands in a sea of agriculture. For example, only 0.3 % of mixed-wood plains is protected, and the average reserve is less than 4 km^2 (Kerr & Cihlar 2004). Without federal protection, Kerr and Deguise suggest that the key to creating a linking network of protected landscape, will be through the efforts of private landowners. By modifying agricultural practices to restore natural habitats, there is potential to alleviate substantial gaps, which now limits endangered species recovery (Kerr & Deguise 2004).

Eliminating agriculture in southern Canada is as impossible as it is undesirable. However, rangeland management may be improved through mimicking the processes of herbivory, which characterized pre-European ecosystems. This approach involves looking at which herbivores would normally exist in the ecosystem, then using their selection patterns to achieve the desired landscape changes, to recreate the preferred levels of vegetation heterogeneity and biodiversity.

Herbivores of various body size have differing morphological and physiological adaptations that lead to differential preference for vegetation quality (Wilson & Kerley 2003), which leads to resource partitioning (Bell 1971; Illius and Gordon 1987; Shipley et al. 1994). Considerable scientific debate has focused on the relative importance of size and morphophysiological adaptation. One issue is whether forages are properly categorized according to quality rather than considering the heterogeneity of plant tissues and the dynamics of breakdown. Grazers retain forages which digest slowly but rather completely whereas browsers propel differentiated forages rapidly through the digestive tract skimming readily available nutrients (Clauss et al. 2003). Also, low quality forages provided an unused niche. By switching digestive priorities (changes in gut volume, surface ratios, retention and fermentation time, and availability of vili for absorption) herbivores were able to becoming larger and capitalize on this niche (Bjorndal & Bolton 1992; Clauss & Hummel 2005). Either way, large grazers require high biomass quantities, but can retain digesta longer, thus they can consume large quantities of lower quality vegetation (Demment & Van Soest 1985; Illius & Gordon 1987). Conversely, small-bodied herbivores have morphological adaptations, such as mouth shape or size (Laca et al. 1992; Shipley et al. 1994), which allow them to select high quality plant parts and use vegetation which may be unavailable to larger herbivores (Murray & Illius 2000). Since herbivores have adapted to use the entire spectrum of available quality and quantity of vegetation, multi-species grazing regimes can have a positive effect on not only interspecies relationships (Coppock et al. 1983; Arsenault & Owen-Smith 2002; Gordon 1988; Hobbs et al. 1996), but also on landscape impacts and diversity (Wright & Connolly 1995; Bakker & Olff 2003; Rook & Tallowin 2003). The benefits of mixed grazing assemblages extend beyond the most important effects of landscape sustainability to include the agricultural, economic benefits of shifting from monoculture livestock production (Telfer & Scotter 1975; Kitessa & Nicol 2001; Abaye et al. 1994; Wright & Connolly 1995).

Telfer and Scotter (1975) proposed that mixed native ungulate production in the Aspen Parkland ecosystem has potential for becoming an important source of livestock production in Western Canada. They hypothesized that native ungulates, bison, elk, deer, and moose, that differ in their vegetation use, will use a larger variety of plant species, creating more even use of the landscape, and thus will be able to be stocked higher than a single species. Although their predictions are positive, there is little supporting data from detailed foraging studies on North American ungulates in mixed foraging regimes to back their hypothesis. This is primarily due to the absence of native species existing in free-ranging systems in Alberta today.

Bison (*Bison bison*) were extirpated from rangelands by mid 1800's (Allen 1877). At the same time, prong-horned antelope numbers declined, and elk were driven from the plains (Toweill and Thomas 2002). Even small mammal populations, such as ground squirrels and badgers suffered a decline. Grasses grew profusely and wild fires spread across the plains, changing the cyclic dynamics of growth and grazing which the migrating ungulate herds had previously controlled. By 1920, cattle and homesteaders dominated the landscape, having displaced many of the rangeland species (Johnston 1969). Because of these large-scale landscape changes through elimination of native species and conversion to intensive livestock production, the opportunities to study the foraging dynamics of native ungulates in natural systems are limited. The Multispecies Grazing Facility was developed at the University of Alberta Ranch at Kinsella to provide infrastructure for confined, mixed ungulate grazing regimes, and thus a rare opportunity to study and experiment with native ungulate grazing regimes and compare their impacts to cattle dominated landscape impacts.

Precision Ranching Initiative

The Precision Ranching Initiative (PRI), was launched with the support of an NSERC Strategic Grant and ASRIP infrastructure grant to address issues of mixed, native species, and cattle landscape use. The main goals are through research, to improve the productivity and sustainability of rangelands by "grazing the right animal at the right place at the right time" (Hudson et al. 2002). PRI aims to address the fundamental issues of how multiple species use the same landscape at multiple scales, to test for large-scale differences between native species and cattle foraging practices, and to experimentally test predictions of how species influence each other across multiple scales.

PRI focused on four main hypotheses which addressed questions related to integration of conventional and diversified livestock production, land stewardship, and grazing strategies to maximize seasonal production based on foraging patterns of domestic and wild ruminants: 1) The animal unit hypothesis determines stocking rates based on body size and metabolic weight (Scarnecchia 1985). The end product is a determination of the number of animals per unit area. PRI coupled this hypothesis with 2) the resource-partitioning hypothesis which posits that different animal species use different resources, and overlap in use of area may occur without associated overlaps in resource use (Voetin & Prins 1999). The third hypothesis was 3) the facilitation hypothesis. In a facilitative system, one species may improve grazing opportunities for another (McNaughton & Georgiadis 1986; Arsenault & Owen Smith 2002). Larger herbivores are believed to lead smaller herbivores, and overlap in vegetation use can occur. Although this hypothesis was designed based on a multiple species system in the east African Serengeti, historical North American ungulate abundance has been compared to that of the Serengeti and it may thus be applicable to Canadian rangeland systems. The facilitation hypothesis has been a subject of debate, however, because the opposite may also be true in some systems (Voeten & Prins 1999). The fourth and final hypothesis is known as 4) the high-grading hypothesis. Instead of larger ungulates leading smaller species, smaller ungulates may drive the forage utilization of larger ungulates by gleaning the highest quality forages, leaving lesser quality vegetation (Murray & Illius 2000).

Thesis objectives

Within the larger scope of the PRI, my research focuses on two fundamental objectives. The first objective is to determine how three different sized and physiologically distinct species, that are using the same landscape, respond differently to limiting factors, through selection across multiple foraging scales. I addressed this objective by looking at the community, patch, and bite selection of foraging bison, elk and mule deer in mixed, continuously grazed pastures across two seasons. More specifically, I tested predictions based on body size-related nutritional constraints. I predicted that forage quantity was most limiting for bison foraging, and thus they select most strongly where differences in quantity are greatest, which I predict will be at the community scale. In contrast, because of their energetic requirements and small mouth size I predicted mule deer would be limited by the quality of vegetation, and thus show selectivity for small-scale bite contents. Because elk are intermediate in size, and are known to forage on a wide range of vegetation types they will show selectivity to optimize the balance of quality and quantity of vegetation intake. I addressed issues of forage use, scales of selection, competition and the possibility for facilitative relationships among native ungulates.

My second objective was to use an experimental approach to test predictions made in Chapter Two. I tested whether elk, an intermediate forager, respond to landscape changes created by previous foraging of either a grazer (bison) or selective feeder (mule deer). I tested the prediction that because mule deer glean forages of the highest quality, elk would select fewer bites on these forage types than when bison were present, but not alter their overall selection of vegetation communities. In contrast, because I expected bison to select grasslands and grasses, elk would exhibit higher selection for grasslands and bites of grass if bison facilitated feeding for elk, but in comparison would avoid grasslands compared to after mule deer if bison and elk competed. I measured foraging behavior of bison and mule deer as well as elk at multiple scales to document whether elk off-take was consistent with our expectations of facilitation or competition for forage use.

Study Site Description

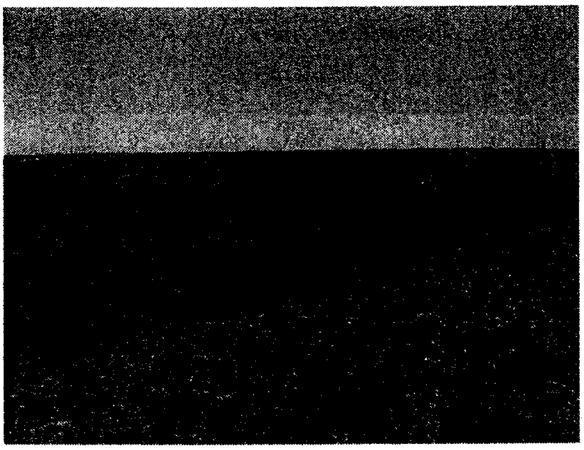

Figure 1-1: University of Alberta Kinsella Research Station rangeland

PRI is based at the University of Alberta's Kinsella Research Station (53°01'N, 111°34'W), located 150 km southeast of Edmonton in an aspen parkland ecosystem (Asamoah et al. 2003) at elevations ranging from 679-717 meters above sea level. Precipitation at the site ranged between 350 and 450 mm per year. The climate is continental, and more specifically, moderately cold, sub-humid cryoboreal (B. Irving unpublished). Aspen parkland ecosystems such as this are based on soil types such as Chernozerns and Solonetzs, which support a diverse array of vegetation types, and are distributed in a belt across central Alberta and Saskatchewan (Lynch, et al. 2005; Hammermeister et al. 2002).

The University of Alberta signed a 50-year lease on the Kinsella Ranch in 1961 to create a beef cattle breeding research station. The ranch mixes purebred Hereford, Charolais, Galloway and Angus breeds to create strong, easy calving, fast growing hybrid lines. The site was chosen for its native grasses, shelter in aspen stands, and topography, which made the land only marginal for other farmers, as tillage and crop production are more difficult on the terrain.

The PRI group was designated an area on the ranch where paddocks for treatments would be located. Four treatments were designed: 1) domestic cattle foraging, 2) mixed native ungulate grazing regime (comprised of bison, elk (*Cervus elaphus)*, and mule deer (*Odocoileus hemionus*), 3) rotational foraging of bison, elk and mule deer from largest to smallest, and 4) rotational foraging of mule deer, elk, and bison from smallest to largest. Treatments were replicated thrice, resulting in the use of twelve paddocks, distributed across the landscape to achieve equal relative abundance of vegetation community types and forage biomass in each treatment.

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Chapter 2: Multi-Scale Selection Patterns In Ungulate Assemblages

Introduction

When selectively foraging, ungulates make two primary decisions: (i) how to move through the community to encounter food items and (ii) which plants or plant parts to consume out of the array of vegetation they encounter. Because body size influences both of these processes (Mech & Zollner 2002), body size may influence the scales at which ungulates interact with their environment. Larger species should perceive coarser grains, or larger scales than smaller species (Ritchie & Olff 1999). For example, large ungulates may respond to environmental variation at larger scales either because they perceive their environment more coarsely (Kitie 2000); Mech and Zollner 2002) or because they move more widely to satisfy their requirements (Perry and Garland 2002; Holland et al. 2005). Because mouth morphology regulates bite size, small ungulates may achieve higher quality diets within the same feeding locations as larger ungulates due to their selective ability for plants or plant parts (Shipley et al. 1994; Illius & Gordon 1987).

Scale of response to the environment is important, because it should reflect limiting factors for the herbivore (Rettie & Messier 2000). In an ungulate guild where predation is not a factor, the most limiting factors are the distribution of quantity and quality of forage items (Cromsigt & Olff 2006). It is believed that because rumen and gut capacity are isometric with body size, and metabolic requirements scale to 0.75 of body mass (Bell 1971; Jarman 1974; Demment 1982; Demment and Van Soest 1985; Van Soest 1996), large ungulates are constrained more in areas of low forage biomass, but can tolerate low forage quality. Conversely, small ungulates can tolerate low food biomass but are constrained by forage quality because of high metabolic rate relative to body size (Demment & Van Soest 1985).

Another view is that herbivory itself, has led to differences in body sizes. Grass tends to form a fibrous matt in the rumen, which creates stratification of digesta. This leads to longer retention times and fermentation in order to retrieve nutrients. Small browsers cannot get enough energy from fermentation alone, and thus rely on more easily digested forages (Gordon and Illius 1994). Low quality forages provided an unused niche, and by switching digestive priorities (changes in gut volume: surface ratios, retention and fermentation time, and availability of vili for absorption) herbivores were able to become larger and capitalize on this niche (Clauss, et al. 2003; Clauss & Hummel 2005). Regardless of whether adaptation in physiology led to large herbivores that use lower quality forages, or digestive efficiency of larger herbivores allows for use of lower quality forages, differential preference for vegetation communities and forage types has been noted in many systems where herbivores range in body size (Bell 1970; Illius and Gordon 1987; Lamoot et al. 2005).

Rettie and Messier (2000) suggested that the strength of resource selection patterns across scales should reflect limiting factors. Studies with moose generally support this hypothesis (Rettie & Messier 2000; Dussault et al. 2006), but it is unclear if similar patterns exist in multi-ungulate systems. Our current understanding is that competition for resources is reduced through differences in body size, morphology, and physiological constraints that lead to resource partitioning (Jarman 1974; Illius and Gordon 1987; Shipley et al. 1994). Resource partitioning in assemblages of ungulates of different body sizes has typically been studied along forage and habitat gradients. For example, where rough distributions overlap, deer (*Odocoileus hemionus, O. virginianus*), elk (*Cervus elaphus*) and/or bison (*Bison bison)* have dietary differences where spatial overlap is high (Kirchoff and Larsen 1998; Sandoval et al. 2005; Beck and Peek 2005; Torstenson et al. 2006), but also segregate by habitat (Johnson et al. 2000) or use overlapping habitats but different areas within habitats (Lamoot et al. 2005). Indeed, because selection at different spatial scales may facilitate resource partitioning in heterogeneous environments, determining the important scales of selection to animals of different body sizes has implications for understanding species assemblages and their impact on the vegetation (Bakker & Olff 2003; Bowyer & Kie 2006).

I tested two general concepts: first, that large and small ungulates differ in their perception of scales, and second, that due to differences in limiting factors these ungulates select vegetation at different scales. In an aspen parkland ecosystem, I measured forage selection along the foraging paths of bison, elk and mule deer at three scales: the community, patches within communities, and bites within patches. I predicted bison, the largest ungulate, would be most limited by quantity, and would preferentially perceive the largest scales, and thus I would see strongest selection for resources at the community scale. I predicted mule deer would be limited by quality, and would perceive small high quality plant parts, and thus would show forage selection at the smallest, bite selection scale. Elk, being intermediate foragers would select at the intermediate scale, the patch.

Methods

Observations of foraging behavior were made in fall 2004 and spring 2005 on adult female bison, elk and mule deer within paddocks (6.69 ± 0.56 ha) located at the University of Alberta Research Station (53°01'N, 111°34'W) at Kinsella, approximately 150 km southeast of Edmonton, Alberta. Pastures consisted of rolling hills within the aspen parkland prairie ecosystem (Asamoah et al. 2003) at an elevation ranging from 679-717 meters above sea level.

A total of six animals, two of each species were grazed together in three paddocks in fall 2004, whereas three elk and bison and two deer were grazed together in spring 2005. Animals were conditioned to observers for up to 10 days prior to commencement of spring grazing trial. Stocking densities each year were designed to obtain 50% vegetation off-take over two 45-day trials in each paddock based on allometric relationships between intake, body size and preliminary estimates of available forage in 2003 for stocking rates in 2004, and refined estimates of available forage in 2004 for 2005 (P. DeWitt, in prep).

Foraging observations were taken on 1 to 3 animals per paddock from 1 June to 15 July (spring) and 1 September to 15 October (fall) in daylight hours under all weather conditions. Observations of animals within paddocks were conducted on approximately 4-day rotations. Observations of foraging bouts began when the focal individual rose from its bed site and commenced foraging, and it ended when the individual ceased cropping bites for a minimum of 3 minutes. One observer recorded the time when each bite and step (pace) occurred using Behaviour Tracker computer software, (v. 1.5; www.behaviortracker.com). Bites were classified based on majority of the bite content as one of 10 forage types: green graminoids, green forb, *Rosa* spp., *Ribes* spp., *Rubus ideaus, Salix* spp., *Symphoricarpus occidentalis*, *Populus tremuloides,* mushroom and "other". "Other" included infrequently used shrubs that comprised <0.1% of the bites. Immediately following the observations, 20 simulated bites were collected by hand plucking them along each foraging path. A second observer recorded the animal's location from the recorder's position every 30 seconds along the foraging path by measuring the distance to the animal to the nearest meter using a Bushnell Yardage Pro 1000 laser range finder and to the nearest 1° with a compass.. The observer was generally <50 meters from the animal. The observer' position was marked with a stake and later the location recorded using a Trimble Geoexplorer GeoXT GPS. These measures were used to recreate the foraging path.

Each animal location was classified according to one of 5 vegetation communities: grasslands, shrublands, aspen stands, riparian edge, and riparian meadows. Grasslands were dominated by graminoid species, including *Poa pratensis*, *Stipa curtiseta, Carex* spp., *Festuca hallii, Agropyron trachycaulum,* and *Bromus inermis* and forbs species, including *Achillea millefolium, Artemesia ludoviciana, Artemesia frigida, Thermopsis rhombifolia, Solidago missouriensis.* Shrublands were generally similar to grasslands except for high densities of *Symphorocarpus occidentalis and Rosa arkansana*. Aspen stands were dominated by *Populus tremuloides* saplings and an assortment of shrubs, primarily *Rosa aciculari, Rubus ideaus, Ribes* spp., forbs, such as *Fragaria virginiana, Thalictrum venulosum, Galium boreale,* and *Lathyrus ochroleucus,* and graminoids, such as *Poa pratensis, Bromus inermis, Carex* spp. *Dactylis glomerata, and Schizachne pupurescens*. Riparian edge contained primarily *Populus* and *Salix* spp.

as shrubs, riparian meadow graminoids, and a mixture of forbs including high densities of *Fragaria virginiana.* Riparian meadows were dominated by graminoid species, primarily *Carex* spp., *Poa pratensis,* and *Agropyron trachycaulum*, and had a lower diversity of forbs, containing small amounts of *Circium arvense, Taraxacum officinale, Potentilla ansenaria* and *Mentha arvense.*

Forage availability at each animal location was determined by visually estimating total biomass (g fresh mass/m^2) within a 0.25 m^2 quadrat adjacent to the foraging path, clipping the plot to 1cm, weighing the sample and recording wet weights to the nearest 1g in the field with a Pesola scale. Relationships between estimated and actual wet mass of total biomass were derived for spring 2005 and fall 2005 (Fig. 2-1). Although two observers collected the data, I used only one equation for each season because relationships between the 2 observers had similar slopes (F =1.67, df =74, *P*=0.367; F =1.45, df =184, *P*=1.86) and intercepts (F =2.13, df =75, *P*=0.688; F=1.03, df =185, *P*=0.311) in both 2004 and 2005.

Total wet mass (actual) was converted to dry mass (DM) using ratios of wet mass to dry mass (Table 2-1) calculated for each habitat (P. DeWitt unpublished data). Ratios were derived from 0.25m^2 plots clipped across the grazing trial periods where wet weights were recorded to the nearest 1 g in the field using a Pesola scale, biomass dried for 48 hrs at 50° C, and weighed to the nearest 0.01 g. I used wet to dry ratios for riparian edge taken in 2005 for conversions in 2004 because these data were not available in 2004. However, mean wet to dry ratios for the remaining classes overall did not differ between years (paired t-test, df=3, *P*=0.15). Dry matter biomass was converted from g/0.25m^2 to g/m^2 for presentation.

Biomass in each of 10 forage classes (green and cured graminoids, green and cured forbs, and current annual growth (CAG) of shrubs of *Rosa* spp., *Ribes* spp., *Rubus ideaus, Salix* spp., *Symphoricarpus occidentalis*, *Populus tremuloides*) was derived as the product of total dry mass and the visually estimated percent of total biomass in each of these ten forage classes. Biomass was considered "green" if the majority of the plant was green and/or not brittle. Cured herbaceous biomass included both current annual growth or previous years growth; shrub CAG included current year's production of woody and leaf growth either standing or on the ground, and graminoids and forbs were generally brittle and easily broken from standing vegetation.

Data Analysis

Plant community selection

I derived a mean plant community index of selection for each animal species following (Savage 1931) and tested whether it differed from zero using a one-sample mean comparison test using individual animals as the sample unit. The index was calculated as the ratio of the percent of animal locations within a given plant community type divided by the percent availability of plant communities within the paddock where the observations were taken. The percent use of plant communities of an individual while foraging was estimated by classifying each 30-second location into one of 5 plant communities (aspen, grassland, riparian, riparian edge and shrubland). Availability of the 5 plant communities in a pasture of the individual animal was based on the areal extent of the community from a vegetation map for the study pastures developed using LIDAR imagery (Su 2004), and boundaries adjusted through field validation (M. Coupe and P.

DeWitt, unpublished data). Selection indices were related to forage biomass and bite sizes of animals foraging in the community using a Pearson correlation (r).

Foraging Patch Characteristics

Foraging patches were defined as areas of foraging along the path of an animal, separated by non-foraging patches where the animal decided to stop eating and move to a new forage patch (Jiang & Hudson 1993). To distinguish foraging patches from non-patches (matrix), I used the general approach described by Sibly et al. (1990) to determine a "breakpoint" value in steps/bite at which an individual was considered to have stopped feeding in a patch. Because this approach assumed foraging patches to be mutually exclusive of non-foraging patch, I fit a constrained two-process model to the log-frequency of steps per bite (see Appendix I). The breakpoint value calculated from this approach was used to delineate the beginning and end point of foraging patches along the foraging path.

Mean vegetation characteristics of foraging patches were compared to matrix patches based on a two-tailed paired t-test using individual animals as the sample unit. *P* values <0.1 were accepted as significant.

Bite Sizes and Diet Selection

Differences in simulated bite sizes per kg body mass were compared among species within seasons using a one-way Analysis of Variance, with *post hoc* differences in mean bite sizes tested using multiple comparison tests with Bonferonni adjustments (Zar 1999). Body masses (kg) for all animals were taken on entry to paddocks and averaged for bison (364 ±45.5, n= 9; 414±81.4, n= 6), elk (252±22.7, n= 9; 308±18.8, n= 6) and deer (61±6.6, n = 6; 60±5.2, n= 6) in the spring and fall season. A forage selection index (Savage 1931) was calculated from bite counts for each of the major forage species and tested for differences from one using a one sample mean comparison test. The index was calculated as the ratio of use divided by availability. Use was measured as the percent of bites on each forage class (e.g. *Rosa*, graminoids etc) of all bites taken. Availability of that same forage class was measured as a percent of total available biomass in each patch where the bites were taken.

Results

Plant Community and Forage Availabilities

The areal extent (expressed as percentage) of vegetation communities across the 3 paddocks averaged 4.8±2.75 for riparian edge, 5.8±1.00 for riparian, 27.1±1.64 for shrubland, 7.9± 3.81 for aspen, and the remaining 54.4±5.45 was grasslands. A total of 1307 and 1507 quadrats were sampled at animal locations across plant communities in spring 2005 and fall 2004, which provided estimates of forage availabilities within these plant communities (Table 3-2).

Total biomass was highest in riparian community types, where live grass comprised over 75% of total biomass. Aspen communities contained the second highest available biomass, where CAG of an assortment of shrubs made up over 50% of total biomass. Shrub CAG was also abundant in riparian edges with *Salix* spp. CAG comprising 32% of the total shrub CAG, and forb biomass comprising 20% of total available biomass. Shrublands contained the highest percentage of shrub CAG of total biomass, dominated by *Symphoricarpus occidentalis.* Grassland habitats contained the least amount of total available forage biomass of all community types, but the second highest ratio of live graminoids to total biomass (Table 3-2). Riparian edges contained the highest biomass availability in the fall, closely followed by riparian edges, where live graminoids, dead graminoids and CAG *Salix* contributed 31, 28 and 14 % to total biomass, respectively. Graminoid relative abundance was highest in riparian meadows and grassland communities. Forb biomass was consistently less abundant in the fall across all communities, but was still relatively more abundant in riparian edges than the other communities. *Populus tremuloides* CAG did not change abundance in most community types, except for in aspen stands where abundance decreased and its presence increased in paths in riparian edges (Table 3-2).

Bite sizes and bite selection

Over 800 simulated bites per animal species were collected in spring 2005, and over 1400 simulated bites were collected in fall 2004. Average bite size of bison scaled to body mass were larger (P= 0.002, t=3.16, df=114) in the fall (0.001411±0.000596 g/kg, n=65) compared to spring (0.0010702±0.0005496 g/kg, n=51). Bite sizes of elk (0.0012848 ±0.0008315 g/kg, n=39) did not differ by season (P= 0.747, t=0.323, df=112), bite sizes of deer were larger (P< 0.001, t=5.42, df=175) in the fall (0.0018263 ±0.000666 g/kg, n= 93) compared to spring (0.001355 ±0.0004599 g, n=84).

Across species, allometric bite sizes of bison, elk and deer (Fig. 2) differed in both the spring (F= 3.79, df = 2, P= 0.024) and fall (F= 15.36, df=2, P<0.001). *Post hoc* comparisons indicated that bite sizes of deer were larger than bison in spring (P=0.012), and larger in fall than both bison (P=0.058) and elk (P=0.002).

Average bite size of bison did not differ between plant communities (F= 2.05, df=4, P= 0.109) or forage classes (F= 0.86, df=4, P= 0.358,) in spring. In fall, average bite size of bison differed among plant communities (F= 9.51, df=4, P< 0.0001) with larger bite sizes taken when foraging in riparian communities (0.0023304 ± 0.000832 g, n=6) compared to other communities. Average bite sizes by elk differed among plant communities (F=4.32, df=4 P= 0.011) with bite sizes being larger (P= 0.038) in the riparian community type (0.0019847 ± 0.0007382 g, n=3) than the other plant communities (see above). Deer bite size did not differ between plant communities in spring (F= 0.74, df=4, P= 0.57) or fall (F= 1.15, df=4, P= 0.344), nor did they differ among forage class (F=1.02, df=4, P= 0.41) in either spring or in fall (F= 1.58, df=4, P= 0.202).

Overall, bison showed strong and seasonally consistent selection for graminoids within patches (Fig. 3-3, Table 3-3) with >95% of bites primarily composed of graminoids in both seasons. In the spring, frequency of bites taken on forage classes by elk within patches did not differ from their relative availability, with percent of bites taken comprising over 38% forbs and 35% graminoids. In contrast, elk selected for grasses and forbs within patches in fall and increased their use of *Salix* (Fig. 3-3, Table 3-3). Deer did not show strong selection for forage classes within patches in either season, even though deer diets showed a decreased in forb consumption from spring (45%) to fall (22%), and a shift from consumption of *Salix* spp. (20%) to *Rosa* spp. (30%) (Fig. 3-3, Table 3-3).

Plant community and patch selection

At the pasture scale, bison avoided shrublands when foraging in the spring but used other plant communities in proportion to their availabilities (Fig. 3-5). The pattern of selection by bison for plant communities was strongly correlated with available live grass biomass (r=0.95 n= 5, *P*=0.013) and bite size (r^2=0.93, n=5, *P*=0.019). At the patch scale, there were no differences in biomass characteristics between patches at which bison foraged and the matrix in spring (Table 3-3). In the fall, bison selected grasslands, but showed no significant difference in biomass of any forage type between patch and matrix locations, or correlation between community selection and vegetation characteristics or bite size.

Elk avoided shrublands and selected riparian and aspen communities in the spring (Fig. 3-4), and selection was most closely correlated with the abundance of *Populus tremuloides* CAG (r=0.96, n=5, *P*= 0.009). No correlation (*P*> 0.1) was found with plant community selection and average elk bite sizes in the plant community in the fall. Further, elk foraged in patches with higher *Populus tremuloides* CAG than in the matrix (Table 3-3). In fall, elk increased their selection of riparian edge, although plant community selection was not correlated to bite sizes (*P*> 0.1). However, at the scale of the patch, elk foraged where forb and live graminoid biomass was higher, and *Artemesia* lower than in the matrix (Table 3-3).

Deer avoided grasslands and selected aspen communities in spring and their selection of plant communities was most highly correlated with DM forb together with *Populus* CAG (r= 0.92, n =5, *P*= 0.01), and *Rosa* (r= 0.9892, n=5, *P*= 0.001). In the fall, deer no longer avoided grasslands, but showed no selection for other plant communities, and selection was not correlated with the abundance of a particular forage class. No correlation was found with plant community selection and deer bite sizes in either season (*P*> 0.4). At the scale of the foraging patch, deer selected sites with the highest total biomass and shrub CAG during the fall season.

Discussion:

I made predictions about selection patterns by bison, elk and deer at multiple scales. Contrary to my predictions, bison selected graminoids at the bite rather than the community scale, and mule deer showed very little selection across scales and season. Elk, an intermediate forager, however, selected at both the community and patch scale in the spring, and at all scales in the fall. Although I did not find supporting evidence for larger species to respond to larger scales, and smaller species to be more selective at smaller scales, this may be a consequence of distribution and abundance of vegetation in my system in the following ways.

My predictions on limiting factors of quality and quantity assumed that certain forage types would be limited to specific vegetation community types. For example, grasses would be found in grassland community types, but not elsewhere. In the spring, graminoids occurred in all communities, ranging from 36 g/m^2 in shrublands to as high as 150 g/m^2 in riparian communities (Table 2-2). In the fall, graminoids ranged from 37 g/m^2 in aspen stands to as high as 130 g/m^2 in riparian communities (Table 2-2). This data shows that graminoids were not limited to only one community. Forbs, I assumed would be distributed in small amounts across all communities. Forbs were most plentiful along moist riparian edges in spring, with availability being 45 g/m^2 and lowest availability was in grasslands, at 23 g/m^2 (Table 2-2). In the fall, forb biomass along paths decreased to only 14 g/m^2 along riparian edges and as low as 5.2 g/m^2 in aspen stands (Table 2-2). Although this supports my prediction that forbs would be distributed across communities, some areas contained amounts of forbs well above what I predicted would be available.

Because availabilities were not as I predicted, I found that bison did not select graminoids at the community scale, even though their community selection pattern was highly correlated with graminoid abundance. Bison foraging behaviour showed that they were still focused on graminoid availability, just not at the community scale. Instead, because graminoids were available across communities in a mixture of other forage types, by being selective at the small scale, bison were able to obtain a diet containing over 95% graminoids. In the fall season, bison selected grassland communities even though these areas did not contain the highest abundance of graminoids. This could be due to quality changes in graminoid species. In a research project by Asamoah et al. (2004) cattle switched community selection from riparian areas in the spring to grasslands in the fall. This was attributed to a change in preferred graminoid species to those that are more nutritious in the fall season, and more abundant in grassland communities. A higher selection for grasslands in the fall could also be due to the fact that grasslands had one of the highest percentages of graminoids relative to other available vegetation in the fall(Table 2-2) and this made grass bites easy to chose.

Although deer did not show strong selection for forage types at the bite scale as I predicted, they still consumed forbs and browse 90% and 75% of the time in spring and fall, respectively. Perhaps this indicates that deer are indeed selective at the small bite scale, but instead of patches being the measure of available resource, deer perceive large scale community or landscape availability. In the spring, deer cued into communities that contained the highest percentages of forbs and browse (aspen stands). Aspen communities were made up of approximately 70% palatable browse and forb species. At the same time, deer avoided grasslands that contained the lowest availability of forbs and palatable browse *(Rosa, Ribes, Populus, and Salix)* 23g/m^2 (Table2-2). In the fall season, deer became less selective at the large scale, and instead of increasing within patch, bite selection, they altered diet, and more than doubled percent use of graminoids and *Rosa* (Table 2-3). Deer, through their path, rather than community, patch or bite selection, were able to encounter high abundances of preferred forages.

Elk had a variable diet (Table 2-3), and were able to be selective across community types by cueing into *Populus tremuloides* abundance in aspen stands (Fig. 2-3) in the spring. This was reflected in high abundance of *Populus* within patches compared to matrix locations along their paths in the spring. In the fall season, when forage quality changed, elk switched large-scale community selection away from riparian meadows and aspen stands to riparian edges. By chosing patches containing significantly higher abundance of green graminoids, elk were able to significantly increase graminoid intake small-scale intake selection (Fig 2-4), Elk were also able to maintain selection of forbs by using them along riparian edges where they were most abundant in the fall (Table 2-2).

Other research has shown multi-scalar landscale response by species (Wallis de Vries et al. 1999; Dussault et al. 2006; Rettie & Messier 2000; Johnson et al. 2002). However, in these studies, animals were exposed to a more natural environment: not confined or heterogeneity in forage abundance was patchier, and/or predation risk limited landscape use. My study lacked predation risk, animals were confined but at low stocking densities, and I did not have vegetation types which were limited to specific communities, or became unavailable with changing seasons. I may also have found strong selection patterns if forage availability was reduced to a level where forage types did not occur in all communities, or predators created vulnerability, and thus restricted foraging patterns. Although results of ungulate selection similar to mine were found in an African savannah where the largest species, the rhino, had the finest scale of selection, and the smaller species, the warthog and impala, had the coarsest scale of selection (Cromsigt & Olff 2006), they attributed the lack of support for the central body size/ scale of selection hypothesis (Ritchie & Olff 1999) on their project design, and their pre-determined size of patches. I did not create patches of a certain size, but instead based patches on the movement and intake of each ungulate type, and thus patch sizes could be different for each ungulate species. Even with this methodological difference, I found similar results, so perhaps their lack of selection patterns to predictions, were a results of forage abundance and distribution at a scale they did not measure.

In order to make predictions in relation to body size, I also assumed species would show allometry in bite size. I used a large grazer, an intermediate forager and a browser, all with different constraints on diet intake, due to both forage characteristics (Clauss et al. 2003) and digestive efficiency (Demment & Van Soest 1985). Although this difference in digestive capabilities can allow for more species within a given space (Ritchie & Olff 1999), it also means that these species focus on different plant characteristics, which are distributed differently on the landscape (Demment & Van Soest

1985). Thus the scales of selection that are characteristic of different species depend on other factors. The morphology and distribution of forages can influence bite size (Laca et al. 1992; Nakanishi et al. 1993), which in this study, may have caused lack of allometry between the three species. I found that deer, although 1/10th the size of bison, took larger bites per kilogram of body mass. While theory would predict smaller bite sizes, consistent with their predicted arcade width to body size relationship (Illius & Gordon 1987), their forage preference in this study resulted in significantly larger bites (Fig 2-2). This makes comparing three species, differing in foraging styles very difficult. For example, bison prefer graminoids, which tend to be uniformly distributed, with blades of grass in densities in all communities that allow for reasonable intake rates. Bite size, is regulated by size of mouth in this case. Bison will take the largest bites possible, with the width of their mouths limiting size. Forbs and browse, which deer and elk prefer, are distributed in clumps and are not found in all community types. The shape of clumps and the shape of individual plants make large bites easier. By biting lower on stems, and stripping branches, or by biting of entire groups of leaves, bite sizes is not limited by mouth width. Instead it is influenced by shape of plants and distribution of leaves. Although my measure of bite size has been considered subject to observer error, these methods have been used in other studies, and are comparable to other methods for collecting bite sizes (Hudson and Frank 1987; Hudson and Nietfeld 1985, Wallis deVries 1995). Also, my results fit the expected seasonal bite size ranges of both bison and elk. When bite size is expressed as grams per bite, the average bite size for bison was 0.39 g and 0.58 g, and elk bite size was 0.32 g and 0.41 g in the spring and fall respectively. Although we have no comparison of deer bite sizes in aspen parkland, results for bison and elk fell well within the ranges noted for bison by Hudson and Frank (1987) and Rutley and Hudson (2000) (0.42-1.2 g), and for elk by Jiang and Hudson (1994) and Hudson and Nietfeld (1985) (0.11- 0.51 g).

Generally, studies of animal selection focus on one or two species (Wilmshurst 1995; Wallis 1999), or in random locations where the animals are seen (Voetin & Prins 1999), though recent research has looked at diverse ungulate systems (Prins et al. 2006; Cromsigt & Olff 2006; Makhabu 2005). Because few studies have used a site-specific, experimental approach, this study offered insights into multiple scales of selection and resource partitioning of mixed ungulate guilds. Although my research is uncommon, in that I use three North America ungulates in a controlled but natural landscape setting, by limiting spatial use, predation and understocking the landscape in relation to abundance, we were unable to identify what drives different sized ungulates to select forages across scales. Instead, we were able to determine that in a non-limiting landscape, large grazers are able to be selective at the small scale for preferred forages and small browsers are able to focus on large-scale community availability, to cue into preferred forages. Perhaps in a more limiting ecosystem, either when forages are not re-growing, or when stocking densities are high, we would see selection patterns more similar to those predicted based on theory.

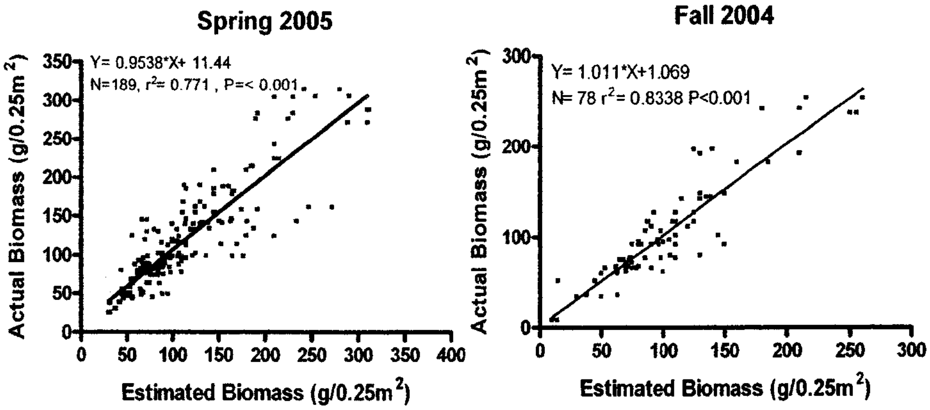

Figure 2-1: Calibration data of actual and visually estimated biomass within 0.25m^2 quadrats. Quadrats were visually estimated, then clipped for actual wet-weight in grams. Estimates were made in all community types in both spring 2005, and fall 2004.

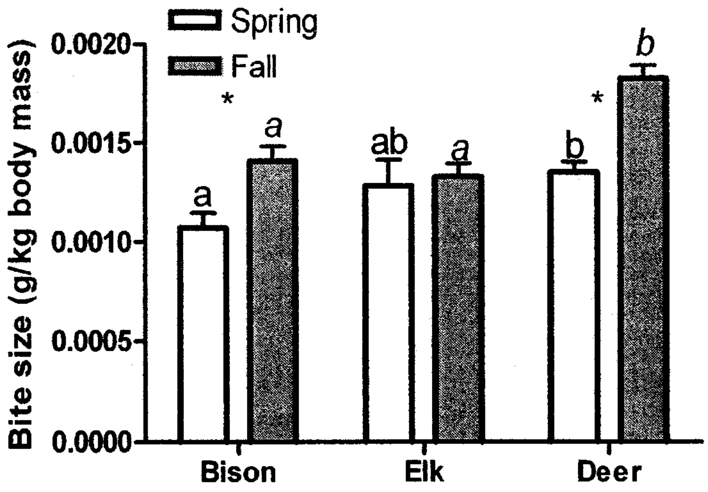

Figure 2-2: Bite size estimates of bison, elk and mule deer measured in spring 2005, and fall 2004. Bite sizes were measured using the hand plucking method, and divided by body size to show allometric comparisons. Intra-species significant differences between spring and fall bite sizes are depicted with an asterix, and inter-species differences within each season are depicted with lower case letters.

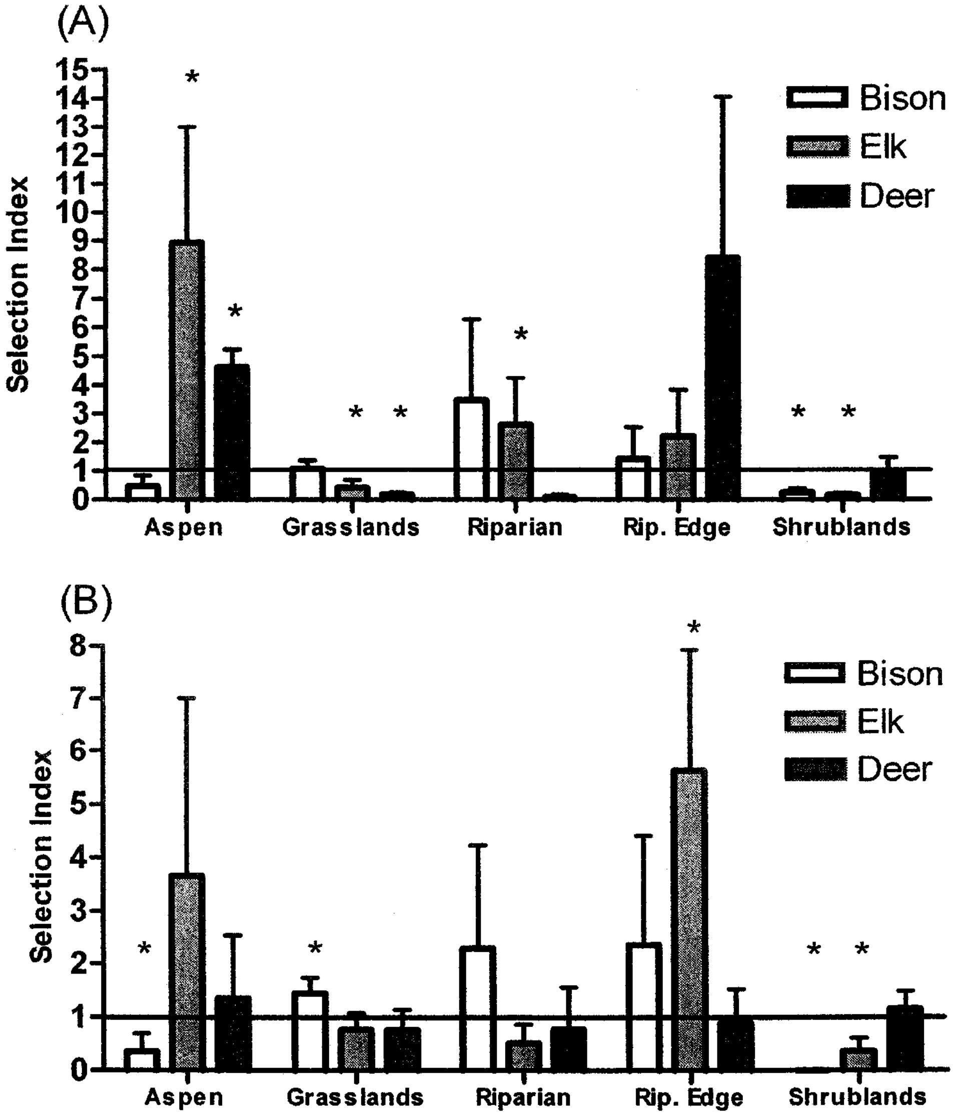

Figure 2-3: Community selection indices (%use/%available) for bison, elk and mule deer in spring (A) and fall (B) seasons. Animals were grazed simultaneously in mixed species paddocks from June 1 to July 15 and September 1 to October 15, and had the choice of being in aspen stands, grasslands, riparian meadows, riparian edges, or shrublands. Indices significantly different from 1.0 were tested using a one-sample mean comparison test and are indicated with an asterix.

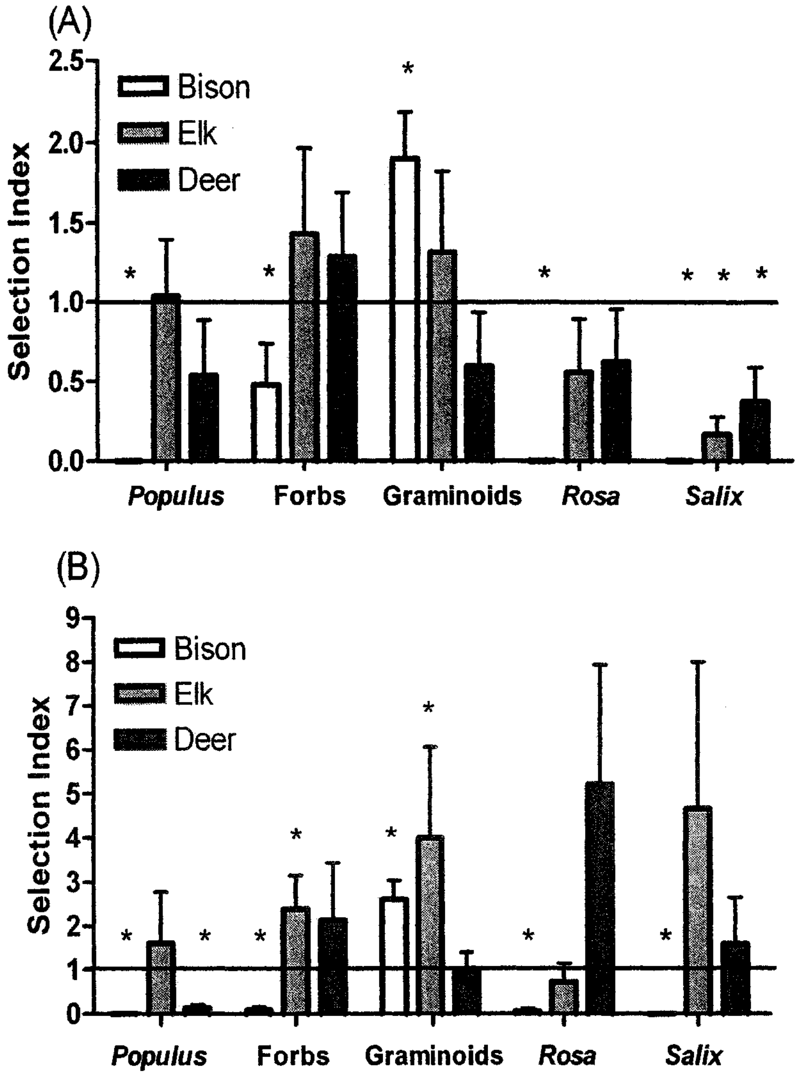

Figure 2-4: Bite selection (propotional use/available) of forage classes *Populus,* forbs, graminoids, *Rosa* and *Salix* for bison, elk and mule deer in spring (A) and fall (B) seasons. Animals were grazed together from June 1 to July 15 and September 1 to October 15. Indices significantly different from 1.0 were tested using a one-sample mean comparison test and are indicated with an asterix.

TABLE 2-1. Wet to dry mass conversions for total plant biomass within 5 plant communities in aspen parklands near Kinsella, Alberta during 1 June-15 July 2005 and 1 September-15 October 2004 (with unpublished data from P. Dewitt)

	Habitat	Ratio	S.D.	N
Spring	Aspen	0.309	0.068	50
	Grassland	0.421	0.063	72
	Riparian	0.219	0.053	28
	Riparian edge	0.348	0.066	33
	Shrubland	0.376	0.039	35
Fall	Aspen	0.448	0.104	20
	Grassland	0.566	0.086	25
	Riparian	0.473	0.147	18
	Riparian edge	0.442	0.146	13
	Shrubland	0.590	0.096	31

TABLE 2-2. Mean biomass (DM g/m^2) of herbaceous forage and shrub current annual growth (CAG) by season and plant community. Biomass was estimated along foraging paths from 1 June-15 July 2005 and 1 September-15 October in aspen parklands near Kinsella, Alberta.

	Aspen			Grassland			Riparian			Riparian Edge			Shrubland		
	Mean	S.D.	% of Total	Mean	S.D.	% of Total	Mean	S.D.	% of Total	Mean	S.D.	% of Total	Mean	S.D.	% of Total
Spring (n)	31			92			10			22			41		
Total	222.4	69.79		133.3	66.94		196.2	61.35		220.8	104.29		212.8	72.53	
Green graminoids	53.2	33.62	23.9	50.8	31.28	38.1	150.0	80.38	76.5	50.7	41.41	23.0	36.1	28.95	16.9
Cured graminoids	10.5	8.70	4.7	9.3	8.48	7.0	6.6	10.86	3.4	28.7	42.25	13.0	12.6	10.27	5.9
Forbs	37.9	24.97	17.0	23.8	21.83	17.9	29.9	48.69	15.3	44.5	27.75	20.2	38.6	32.32	18.1
Artemisia	0.2	0.87	0.1	8.0	16.36	6.0	2.1	6.67	1.1	0.0	0.21	0.0	3.6	9.34	1.7
Rosa CAG	29.8	31.98	13.4	2.8	4.92	2.1	0.8	2.50	0.4	5.6	15.19	2.6	9.9	18.08	4.7
Populus CAG	21.7	26.38	9.8	0.0	0.00	0.0	1.6	4.97	0.8	3.4	5.97	1.5	2.2	7.71	1.1
Salix CAG	0.3	1.84	0.1	0.1	1.33	0.1	0.0	0.00	0.0	71.4	88.96	32.3	0.0	0.00	0.0
Ribes CAG	6.7	14.06	3.0	0.4	2.63	0.3	0.0	0.00	0.0	8.5	23.45	3.8	7.5	38.83	3.5
Symph. CAG	57.4	48.70	25.8	33.0	34.03	24.8	3.9	11.40	2.0	6.4	11.09	2.9	92.1	53.60	43.3
Other[1]	4.6	9.40	2.1	4.9	16.04	3.7	1.3	4.17	0.7	1.6	3.13	0.7	10.1	24.80	4.8
Fall (n)	30			218			25			46			41		
Total	170.9	50.36		205.4	69.06		264.6	86.82		272.7	163.22		303.5	127.78	
Green graminoids	37.2	20.57	21.8	76.9	43.61	37.4	130.8	75.14	49.4	86.0	53.50	31.6	83.0	47.79	27.4
Cured graminoids	70.0	41.57	41.0	70.8	54.51	34.5	99.0	56.29	37.4	76.0	57.16	27.9	78.8	45.23	26.0
Forbs	5.2	9.18	3.0	6.7	13.95	3.3	8.9	11.59	3.3	14.2	21.49	5.2	10.8	16.89	3.6
Artemisia	9.2	13.82	5.4	16.2	21.15	7.9	11.1	21.89	4.2	9.8	16.11	3.6	14.0	19.86	4.6
Rosa CAG	10.5	13.68	6.1	3.8	9.48	1.9	4.4	12.03	1.6	4.6	11.00	1.7	26.7	38.05	8.8
Populus CAG	7.7	16.80	4.5	0.3	2.90	0.2	1.5	5.16	0.5	9.4	29.97	3.5	10.8	55.61	3.6
Salix CAG	0.1	0.65	0.1	0.1	1.74	0.1	0.3	1.50	0.1	40.1	101.25	14.7	12.6	64.14	4.1
Symph. CAG	14.3	14.63	8.4	16.9	18.78	8.2	4.2	12.77	1.6	7.2	16.41	2.6	42.5	37.97	14.0
Ribes CAG	5.6	13.04	3.3	0.3	2.46	0.1	0.3	1.52	0.1	8.3	24.78	3.0	12.3	56.28	4.0
Other[1]	7.5	17.49	4.4	8.8	13.21	4.3	3.8	12.62	1.4	6.4	14.59	2.4	6.9	15.22	2.3

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[1] Other includes: Other CAG shrubs, but does not include: cured and dead forb or *Artemisia* biomass, which comprised <1% of total.

TABLE 2-3. Percent of bites on a forage type of all bites on each forage class for bison, elk and mule deer (n= individual). 1 June-15 July 2005 and 1 September-15 October during foraging observations in aspen-parklands near Kinsella, Alberta. Forage classes comprising <1% of total bites were not included.

	Bison					**Elk**					**Deer**				
	n=5		n=6			n=6		n=5			n=3		n=3		
	Spring		Fall			Spring		Fall			Spring		Fall		
	%	S.D.	%	S.D.	P	%	S.D.	%	S.D.	P	%	S.D.	%	S.D.	P
Graminoid	95.4	2.31	99.1	1.40	<0.05	35.6	30.17	54.5	38.33	<0.1	9.4	6.26	24.7	16.52	N.S.
Forb	2.9	1.19	0.7	1.26	<0.05	38.3	36.90	4.8	3.79	N.S.	44.9	8.49	21.9	16.98	N.S.
Rosa	0.0	0.00	0.1	0.15	N.S.	14.0	26.84	7.0	9.07	N.S.	12.1	13.87	30.4	15.80	N.S.
Populus	1.4	3.16	0.0	0.10	N.S.	7.6	5.66	8.6	15.34	N.S.	11.0	10.69	0.8	0.93	N.S.
Salix	0.0	0.00	0.0	0.00	N.S.	3.9	8.00	22.9	34.37	N.S.	20.1	9.97	9.0	8.02	N.S.
Total	99.7		99.9			99.4		97.8			97.5		86.8[2]		

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[2] Fall: of three deer, one individual consumed > 18% *Ribes,* and 10 % *Symphoricarpus.*

TABLE 2-4. Estimates of herbaceous biomass and shrub CAG (DMg/m^2) within feeding and matrix patches of bison, elk, and deer during 1 June-15 July 15 2005 and 1 September 1 to 15 October 2004 in aspen parklands near Kinsella, Alberta.

	Spring Patch		Spring Matrix			Fall Patch		Fall Matrix		
	Mean	S.D.	Mean	S.D.	*P*	Mean	S.D.	Mean	S.D.	P
Bison	n=5		n=5			n=6		n=6		
Total	168.0	62.32	161.6	50.54	N.S.	203.0	38.13	195.6	71.35	N.S.
Green graminoids	108.7	83.40	50.7	14.60	N.S.	98.6	35.81	78.8	32.84	N.S.
Cured graminoids	8.7	7.38	11.8	11.50	N.S.	61.6	29.14	71.5	32.13	N.S.
Forbs	16.4	7.43	23.3	13.62	N.S.	7.4	5.84	6.5	6.63	N.S.
Artemisia	2.1	2.34	5.1	3.96	<0.1	13.0	8.88	9.7	5.36	N.S.
Rosa CAG	1.8	1.65	2.8	2.81	N.S.	1.7	1.43	5.2	5.81	N.S.
Populus CAG	0.7	1.66	0.6	1.20	N.S.	0.3	0.68	0.8	1.29	N.S.
Salix CAG	0.0	0.00	0.0	0.00	N.S.	0.2	0.51	0.0	0.00	N.S.
Symph. CAG	28.4	20.07	42.1	29.17	N.S.	14.7	10.20	14.9	10.57	N.S.
Ribes CAG	0.2	0.53	21.2	40.57	N.S.	0.0	0.04	0.0	0.00	N.S.
Other[1]	1.0	0.96	3.9	4.88	N.S.	4.1	2.86	5.6	5.70	N.S.
Elk	n=6		n=6			n=4		n=4		
Total	229.3	71.25	188.8	73.20	N.S.	304.3	142.44	226.2	30.67	N.S.
Green graminoids	59.0	27.46	65.4	33.48	N.S.	96.7	30.43	64.8	4.06	<0.1
Cured graminoids	9.4	2.63	8.4	2.81	N.S.	88.8	43.27	99.9	34.42	N.S.
Forbs	52.1	26.99	30.8	23.02	<0.05	8.8	4.45	4.2	3.49	<0.05
Artemisia	4.4	5.49	7.4	8.15	N.S.	13.0	12.31	20.0	11.65	<0.05
Rosa CAG	21.1	27.04	12.7	17.97	N.S.	8.3	11.09	4.3	2.39	N.S.
Populus CAG	7.7	8.31	4.2	7.50	<0.05	5.1	5.78	4.5	8.25	N.S.
Salix CAG	4.3	8.88	0.0	0.00	N.S.	52.5	106.17	0.0	0.00	N.S.
Symph. CAG	59.1	25.00	54.6	41.19	N.S.	13.3	8.16	10.8	4.32	N.S.
Ribes CAG	6.1	7.80	3.0	6.85	N.S.	5.3	4.68	3.3	6.66	N.S.
Other	6.2	8.20	2.3	2.83	N.S.	3.4	2.00	9.8	3.45	<0.05
Deer	n=3		n=3			n=4		n=4		
Total	215.4	12.67	176.1	28.34	N.S.	234.3	43.34	201.6	25.98	<0.05
Green graminoids	71.5	57.69	56.6	13.92	N.S.	63.5	17.29	61.1	35.53	N.S.
Cured graminoids	11.9	2.60	14.6	7.24	N.S.	75.8	20.13	75.8	17.08	N.S.
Forbs	43.8	6.88	42.6	35.47	N.S.	10.4	7.23	7.4	6.72	N.S.
Artemisia	0.8	0.77	4.5	4.87	N.S.	11.2	9.59	9.2	8.34	N.S.
Rosa CAG	11.2	10.04	2.7	2.80	N.S.	17.7	14.68	3.7	3.00	N.S.
Populus CAG	12.3	6.83	14.8	23.17	N.S.	6.1	9.94	1.9	3.39	N.S.
Salix CAG	18.7	18.06	0.0	0.00	N.S.	7.9	7.99	4.1	8.25	N.S.
Symph. CAG	34.1	30.47	35.5	30.72	N.S.	16.7	8.00	15.8	10.77	N.S.
Ribes CAG	3.0	3.39	0.8	1.42	N.S.	4.6	5.86	2.1	3.43	N.S.
Other	8.1	6.92	3.9	0.87	N.S.	10.6	5.95	18.1	21.22	N.S.

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[1] Other includes: Other CAG shrubs, but does not include: cured and dead forb or *Artemisia* biomass, which comprised <1% of total.

Table 2-5: Bite size of bison, elk and deer in communities. Each N represents the average bite size for a patch in a community type. Samples were collected in spring 2005, and fall 2004.

	Bison			**Elk**			**Deer**		
	N	**Mean**	**STD**	**N**	**Mean**	**STD**	**N**	**Mean**	**STD**
Spring									
Aspen	2	0.277	0.0057	7	0.292	0.1423	11	0.092	0.0260
Grassland	32	0.385	0.2051	11	0.280	0.0629	10	0.085	0.0195
Riparian	3	0.693	0.1903	2	0.752	0.5459	1	0.077	.
Riparian edge	1	0.563	*	2	0.279	0.0296	13	0.075	0.0289
Shrubland	1	0.290	*	4	0.301	0.0969	18	0.077	0.0302
Fall									
Aspen	2	0.834	0.0795	6	0.259	0.1088	6	0.078	0.0117
Grassland	34	0.525	0.1653	33	0.441	0.1529	33	0.111	0.0383
Riparian	6	0.965	0.3444	3	0.611	0.2273	2	0.088	0.0071
Riparian edge	1	0.651	*	12	0.384	0.1902	6	0.148	0.0470
Shrubland	*	*	*	4	0.458	0.2024	14	0.112	0.0319

Table 2-6 : Bite size of bison, elk and deer on any pure forage class samples (≥85% pure). N represents a sample of 20 bites from along the foraging path. Samples were collected in spring 2005, and fall 2004.

	Bison			**Elk**			**Deer**		
	N	**Mean**	**STD**	N	**Mean**	**STD**	N	**Mean**	**STD**
Spring									
Grass	48	0.393	0.2018	7	0.506	0.3582	2	0.073	0.0315
Populus	1	0.204	.	2	0.299	0.1104	4	0.070	0.0112
Forb	*	*	*	12	0.242	0.0713	32	0.084	0.0278
Rosa	*	*	*	2	0.167	0.0052	9	0.069	0.0302
Salix	*	*	*	1	0.300	*	13	0.071	0.0205
Fall									
Grass	63	0.588	0.2497	35	0.438	0.1502	10	0.131	0.0453
Populus	*	*	*	1	0.362	*	*	*	*
Forb	*	*	*	1	0.115	*	13	0.108	0.0371
Rosa	*	*	*	1	0.194	*	13	0.096	0.0376
Salix	*	*	*	8	0.489	0.2949	1	0.130	*

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Chapter 3: Evidence for Facilitation among Ungulates on Aspen Parklands

Introduction

Competition for resources among ungulates occurs when multiple species use the same resource, and one species reduces availability below that which is useable by other species (Illius and Gordon 1987; Murray and Illius 1996; Prins & Olff 1998). Large-scale resource projects, that are restricted beyond the use of small-scale intake data, often assume that overlap in community and forage use constitutes competition (Hobbs et al. 1996; Mysterud 2000; Campos-Arceiz et al. 2004). However, indirect effects of similar use in vegetation may lead to non-competitive relationships. Ungulates have adapted to reduce competition through specific morphophysiological adaptations, which result in differential preference for vegetation quality (Wilson & Kerley 2003). Large grazers require high biomass quantities, but can retain digesta longer so they can consume large quantities of lower quality vegetation (Demment & Van Soest 1985); (Illius & Gordon 1987). Conversely, small-bodied ungulates have morphological adaptations, such as mouth shape or size (Laca *et al.* 1992; Shipley et al. 1994), which allow them to select high quality plant parts, giving them the potential to out-compete larger herbivores by reducing overall sward quality (Murray & Illius 2000). Because ungulates have adapted to use the entire spectrum of available quality and quantity of vegetation, multi-species relationships can actually be facilitative (Arsenault & Owen-Smith 2002).

In some instances, foraging behaviour of one species facilitates the intake of another by changing the vegetation structure in a way that benefits another species. For example, (Gordon 1988) showed that cattle improved vegetation quality for red deer by enhancing green biomass availability in the spring. In the savannahs of Africa, the foraging of larger ungulates reduced the height of vegetation promoting compensatory re-growth that benefited smaller ungulates that followed in the grazing succession (Vesey-Fitzgerald 1960; Bell 1971). Vegetation regrowth promoted by large ungulate foraging, which is higher in cell solubles than mature vegetation of the previous season, is more palatable and can improve foraging for smaller ungulates (Kitessa and Nicol 2001). In systems where shrubs or trees limit access to quality vegetation, the removal of woody structure would allow for species that would not exist in a shrubland dominated system (Parker 1983). Although facilitation has been noted in a number of systems (Gordon 1988; Arsenault & Owen-Smith 2002; Randler 2004), there are few studies where detailed observations are possible to determine how facilitation actually changes animal behaviour in ungulates. As a result we lack a clear understanding of the associated mechanisms, and how these are affected by spatial heterogeneity and seasonal variances in vegetation resources (Arsenault & Owen-Smith 2002).

In this study, we use an intermediate forager, elk (*Cervus elaphus)* to determine how their foraging behaviour responds to previous feeding of a large, roughage-feeder, bison (*Bison bison),* and to a small, selective ungulate, the mule deer (*Odocoileus hemionus*). We selected elk because this species is an intermediate feeder that is likely to show high plasticity in their foraging behaviors given previous grazing. Because we expected mule deer to glean forages of the highest quality, e.g., forbs and shrub species from across all habitats (Chapter 1), we predicted elk would select fewer bites on these forage types than when bison were present, but not alter their overall selection of vegetation communities. In contrast, because we expected bison to select grasslands and grasses , we predicted elk would exhibit higher selection for grasslands and bites of grass if bison facilitated feeding for elk, but avoid grasslands compared to after mule deer if bison and elk competed. We measured foraging behavior of bison and mule deer as well as elk to document whether their off-take was consistent with our expectation of facilitation or competition for forage use.

Methods

Experimental pastures and grazing trials

The study was conducted at the University of Alberta Kinsella Research Station (53°01'N, 111°34'W), 150 km southeast of Edmonton, Alberta in Aspen Parkland ecosystem (Asamoah et al. 2003), Scheffler 1976) at an elevation ranging from 679-717 meters above sea level. Foraging trials were initiated on 1 June, 2005. Community availability in each treatment can be seen in Table 3-1. Grasslands were dominated by graminoid species, including *Poa pratensis*, *Stipa curtiseta, Carex* spp., *Festuca hallii, Agropyron trachycalum,* and *Bromus inermis* and forbs species, including *Achillea millefolium,Artemesia ludoviciana, Artemesia frigida, Thermopsis rhombifola,* and *Solidago missouriensis.* Shrublands generally had similar herbaceous species to grasslands but were distinguished from grasslands by their high densities of *Symphorocarpus occidentalis* and *Rosa arkansana.* Aspen stands were dominated by *Populus* saplings and a diversity of shrubs, primarily *Rosa aciculari, Rubus ideaus, Ribes* spp., forbs, such as *Fragaria virginiana, Thalictrum venulosum, Galium boreale,* and

Lathyrus ochroleucus, and graminoids, such as *Poa pratensis, Bromus inermis, Carex* spp. *Dactylis glomerata,* and *Schizachne pupurescens.* Aspen stands also included patches along the riparian edge that were contained primarily of *Populus* and *Salix* spp. Riparian meadows were dominated by graminoid species, primarily *Carex* spp., *Poa pratensis, and Agropyron trachycaulum*, and had a lower diversity of forbs, containing small amounts of *Circium arvense, Taraxacum officinale, Potentilla ansenaria,* and *Mentha arvense.*

Six bison or 3 mule deer were grazed for 15 days in 2005 in 3 paired replicate paddocks per treatment then removed and replaced with 4 elk for 15 days. Paddocks ranged in size from 3.5 to 5.5 hectares, and differences did not exist in 2005 between pastures in biomass of average live graminoids (Paired t-test, P=0.65), dead graminoid (P=0.93), live forb (n.s.), dead forb (P =0.83), live shrub (P=0.364), dead shrub *(P* =0.98), *Rosa (P*=0.34), *Ribes (P*=0.48), *Rubus, Salix (P*=0.852), *Symphorocarpus (P* =0.48), *Populus (P*=0.41) or other shrub biomass (Dewitt, unpublished data). Bison and mule deer numbers were chosen for each treatment to equate expected differences in offtake between available graminoids and forb use based on forage selection patterns of these species in aspen parkland (Chapter 1), intake to body-weight relationships and estimates of forage availabilities. Animals were habituated to close observation for up to 10 days prior to trials to ensure foraging patterns to minimize influence by human contact. Further, all animals had been used in foraging trials in years previous to this experiment (Chapter 1).

Animal observations

Observations were made on individually marked animals chosen prior to entering a pasture, and observations were taken on 2-4 individuals per treatment per day during daylight hours. Bison, elk and mule deer were followed by one observer along their foraging paths starting from when they rose from bedding and began to forage until they stopped cropping bites for at least 3 min, and started ruminating, traveling to a water source, or bedding. Location of the foraging animal was taken every 30 seconds by a second observer. Animal locations were derived from the distance and angle measured from the second observer to the animal. Distances were measured using a Bushnell Yardage Pro 1000 laser range finder, and the angle measured using a compass to the nearest 1° at distances < 100 m. Locations of the observer were marked with a metal stake during the trial, relocated at the end of the trial, and location recorded using a Trimble Geoexplorer GeoXT GPS.

Adjacent to each animal location along the path, biomass of 7 forage classes was visually estimated in a 0.25m^2 plot. Forage classes included live and dead graminoids (sedges and grasses), forbs (non-woody, non-grass, herbaceous plants), *Rosa* spp., *Symphoricarpus occidentalis*, *Salix* spp. *Populus tremuloides*, and a combined "other" for shrub species (*Rubus ideaus, Ribes* spp, *Elaeagnus angustifolia, Amelanchier alnifolia,* and *Prunus virginiana).* Only current annual growth (new twig and leaf growth) was considered as available biomass for shrub and *Populus* species. Calibration measurements were taken throughout the 30-day period to account for growth patterns by two observers. There was no significant difference in the slopes (P= 0.247) or the intercepts (P=0.311) of the two observers.

Along the foraging path, every bite and step that the focal animal took, and the time each event occurred was recorded by observer 1 using the computer program Behavior Tracker (v. 1.5; www.behaviortracker.com). A step was defined as the movement of an animal's foreleg to reorient that animal towards or away from forage. A bite was defined as the physical removal of vegetation by grasping forage in the mouth and tearing pieces from the plant, resulting in mastication. At the end of the feeding bout along a path, bites sizes were simulated by hand plucking 20 representative bites, estimated by visual observation and examining differences in grazed and ungrazed plants (blades or leaves taken by the animal) (Jiang & Hudson 1993a). Content of each sample by forage class was recorded. To minimize the variability among bite estimates, only one observer collected bites. Hand plucked bites were oven dried at 30° C for at least 24 hours and weighed to the nearest 0.001g.

Plant community selection

Availability of each of four major plant communities (grassland, shrubland, aspen-shrub, riparian) in a pasture was estimated as the areal extent of the community from a vegetation map for the study area developed using LIDAR imagery (Su 2004), and boundaries adjusted through field validation (M. Coupe and P. DeWitt, unpublished data). The use of plant communities while foraging was estimated by classifying each 30-second location along a foraging path to one of 4 plant communities. A selection index (SI_V)(Savage 1931)) was calculated for each individual as the percent of animal locations along the feeding path within a given plant community type divided by the percent availability for that community type in the paddock in which the observation was taken.

Forage selection and intake

Content of bites taken by foraging animals was determined primarily by direct observation and less frequently by examining the area where a foraging animal was observed cropping. Bites were classified based on majority of the bite content as to one of 8 forage types: live graminoids, live forb, *Rosa, Ribes, Rubus, Salix, Populus,* and "other". Other included infrequently used shrubs that comprised <0.1% of the bites. A forage selection index (Savage 1931) was calculated from bite counts for each of the major forage species and tested for differences from one using a one sample mean comparison test. The index was calculated as the ratio of use divided by availability. Use was measured as the percent of bites on each forage class (e.g. *Rosa*, graminoids etc) of all bites taken. Availability of that same forage class was measured as a percent of total available biomass in each patch where the bites were taken.

Foraging patches were defined as a sequence of biting with limited stepping and were distinguished from the non-foraging matrix, which occurred when the animal actually decided to stop eating and move to a new forage patch (Jiang & Hudson 1993b). To distinguish foraging patches from non-patches, I followed the general approach described by Sibly et al. (1990) to determine a "breakpoint" value of steps/bite at which an individual was consider to have stopped a feeding bout. For this analysis, I assumed foraging behavior reflecting foraging patch and non-patch were mutually exclusive and fit a constrained two-process model to the log-frequency of steps per bite (see Appendix

1). A breakpoint value was calculated for each species and used to delineate the beginning and end point of a foraging patch along the foraging path.

An average bite size (above), and bite rate (bites per minute) were found per patch, and by multiplying bite rate by bite size, the average intake rate (grams per minute) per patch was calculated. Mean bite size, bite rate, and intake rate within treatments were calculated by taking the mean values by treatment, from individuals, weighted by number of patches per individual in each treatment.

Data Analysis

Selection ratios for vegetation community (SI_V) and forage class (SI_F) different from 1 (random use) were tested for all 3 species by vegetation class using a one-sample mean comparison t-test in intercooled STATA (2003). SI_V and SI_F greater than one were considered selection for the vegetation community, and less than one was considered avoidance of that habitat or vegetation type. Differences in selection ratios of individual animals between treatments were calculated using a two-sample Mann-Whitney test, using an $\alpha < 0.10$ to determine a significant difference.

Results

There was no difference in areal extent of vegetation communities across the treatments (Table 3-1). Riparian areas comprised the smallest portion of the available plant communities, followed by aspen stands, shrubland and grasslands the largest, with no significant difference between the 2 treatments (Table 3-1).

Bison used all vegetation communities equal to their availabilities (Fig 3-1), but selected strongly for graminoids within foraging patches (Fig. 3-1), resulting in an average of 97 percent of the bites taken across all vegetation types (Fig. 3-2). In contrast, mule deer avoided grassland and riparian areas (Fig. 3-1), and used forbs and *Rosa* equal to availability and number of bites averaged highest on these species as well as *Populus* across vegetation types (Fig. 3-2).

Elk selection of vegetation communities did not differ between treatments (Fig. 3-4). Further, elk decreased the number of bites on forbs, and increased graminoid intake after bison compared to after deer (Fig. 3-4). Elk obtained similar bite sizes in each treatment (P=0.03, t=1.914, df=10) but at a faster rate after bison (P<0.001, t=9.019, df=10) This resulted in a higher intake rate after bison compared to after deer (P<0.001 t=10.267, df=10) (Fig. 3-5).

Discussion

Observed foraging behaviors of bison and deer were consistent with the expected effects of the grazing treatments by a roughage and specialist feeder Diets of bison were comprised of over 97% graminoids, whereas deer diets were 50% *Rosa* and 35% forbs. Because bison are grassland and graminoid specialists (Hudson & Frank 1987; Coppedge & Shaw 1998; Van Vuren 1984; Plumb & Dodd 1993), we expected grass consumption by bison to be greatest on grassland habitats. Instead, bison used grasslands in proportion to availability, which is likely due to the high availability of graminoids across all vegetation communities. In contrast deer, avoided grasslands and riparian area which were dominated by graminoids (38-76% of total biomass, Chapter 1).

Although, elk selection of vegetation communities remained relatively consistent between treatments, I found differences in forage use and intake by elk after deer and bison use that were more consistent with small-scale facilitation by the large roughage feeder than "high grading" by the concentrate feeder. When grazed together in aspen parklands, elk and deer showed higher overlap in forage use than bison and elk (Chapter 1), in particular for forbs. I expected shifts in elk diet to be greatest after deer use resulting in lower intake of forbs. However, elk selection for and percent use of forbs did not differ between treatments. In contrast, elk selection of graminoids increased and elk exhibited higher bite rates after bison relative to deer. Increased selection in graminoid selection was not due to reduced graminoid availability *per se* because percent of grass bites of total bites was higher after bison.

Two factors may explain the small-scale changes in foraging. First, previous defoliation has been shown to induce regrowth of graminoids by 900-1460 kg DM/ha in two weeks in single species grass swards, and up to 4710 kg DM/ha over 19 days on mixed forage pastures (Chilibroste et al. 2000; Ribeiro Filho et al. 2003). These rates of regrowth are well above the critical range of 542-1000 kg/ha needed by elk (Wickstrom et al. 1984; Hudson & Nietfeld 1985). In native grasslands, herbivores can improve regrowth of vegetation by upwards of 121% (Lardner 2002). By changing evenness of sward height, light can penetrate to previously shaded grasses, and increase leaf width and length, especially for *Bromus inermis* which occurs in abundance across our community types (Lardner 2002). By increasing leaf width and length, the overall shear strength of bites is decreased, as is chewing time, which decreases overall handling time of forages (MacAdam & Mayland 2003). Decreased handling and improved quality compared to old growth (upwards of 140% better) (Jaramillo and Detling 1988; Chilibroste et al. 2000), would attract elk to vegetation pre-grazed by bison.

Alternatively, even if regrowth were small during our study, bison may have altered vegetation structure sufficiently to increase visibility or access to graminoids to account for the altered selection for graminoids by elk. Removal of standing dead vegetation has been found in some studies to improve access to green vegetation for elk foraging (Gordon 1988).Bison could also affect visibility of bites, and hence search time, through simple bite impression on even sward height. Bison are known to remove bites in both the horizontal and vertical plane, similar to cattle (Hudson & Frank 1987). Ungar (2001) found cattle grazing created impressions in the sward height through bite removal, and produced variability across the entire sward structure. Swards that were uneven allowed for increased bite area and depth (without changing handling time or quality) compared to homogeneously tall or short swards (Ginnet et al. 1999). Variability in sward structure allowed for bite size and bite rate to increase simultaneously during the first stages of patch depletion, and allowed for higher intake rates during the entire patch depletion process (Ginnet et al. 1999), similarly to my results for elk foraging after bison.

Regardless of the whether bison grazing modified vegetation structure to improve access or resulted in regrowth, bite size was maintained as bite rate increased. Generally, elk bite size declines if bite rate increases (Hudson & Nietfeld 1985) unless handling/search time decreases. In a system where forage quality does not limit handling time (chewing), and improved access decreases search time, maintenance or even an increase in bite size and bite rate would result in higher intake rates. Although my measure of bite size has been considered subject to observer error (being able to see what the animals are eating and finding bite impressions on vegetation), these methods have been used in other studies, and are comparable to other methods for collecting bite sizes

(Hudson and Frank 1987; Hudson and Nietfeld 1985, Wallis deVries 1995). My results fit the expected seasonal bite size ranges of elk in aspen parkland (Hudson and Watkins 1985, Hudson and Neitfeld 1985, chapter 1), and ultimately, my observed increase in bite rate, not bite size created our high intake rates, which were 84% above other studies using the same methods in Aspen Parkland (Fig.3-6).

Although facilitative relationships have been noted among domestic and native species (Hobbs et al 1996; Gordon 1988), this is the first test for, and direct evidence of the occurrence of facilitation operating among only native ungulates in North American temperate rangelands. Behavioral changes that mediated facilitation occurred at the small-scale foraging rather than overall spatial use. Whether this is particular to the confinement and paddock sizes, or season, we don't know. However, it does provide mechanistic data, which is largely unobtainable on wild mixed species assemblages, and explains in particular how facilitation may occur during a growing season. In a forage-limited season, facilitation may no longer occur, and relationships among ungulates may become competitive.

Table 3-1: Mean areal extent (m^2) of 4 vegetation communities across 3 pastures by treatment calculated from LIDAR image (Su 2004, M. Coupe and P. DeWitt unpublished data). *P*-values indicate probability of a significant different in means using a Wilcoxon matched pairs test.

	Treatment Deer		**Treatment Bison**		
Community Classes	Mean	StDev	Mean	StDev	*P*-Value
Riparian	1.5	0.82	8.8	8.15	0.25
Shrub	30.4	3.10	32.6	9.99	--
Aspen	8.9	3.84	7.2	3.99	1.25
Grassland	59.2	6.95	51.4	2.90	0.50

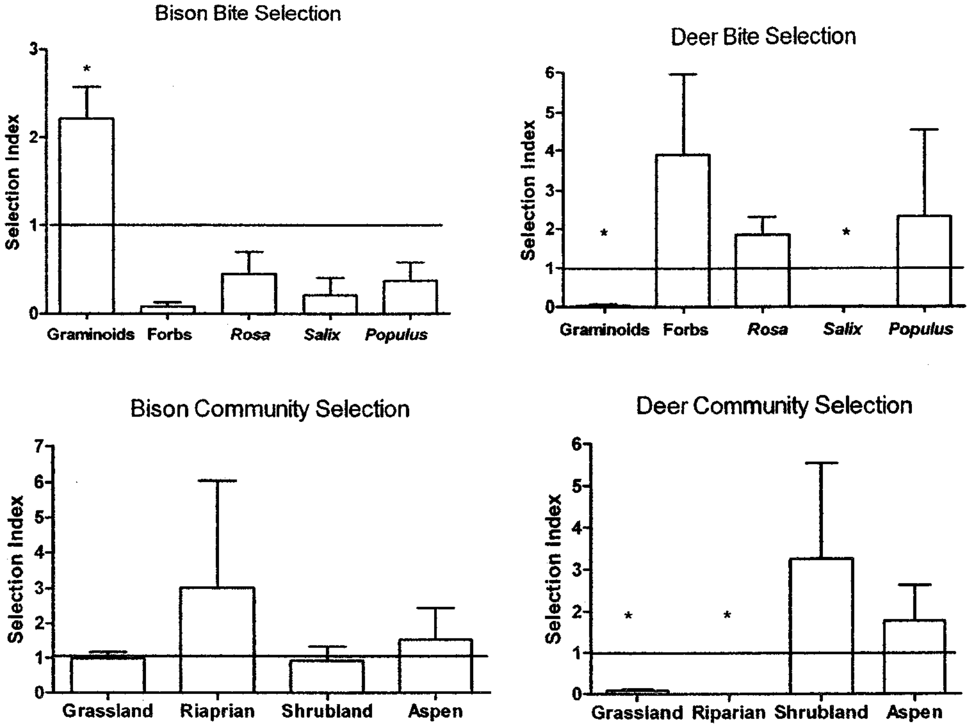

Figure 3-1: Bite selection (% bites of total bites used/ availability of biomass) and community selection (% of foraging locations within each community type/ availability in hectares) for bison and mule deer. Measurements were taken in spring 2005 at Kinsella Alberta. Asterisks represent indices significantly different from one.

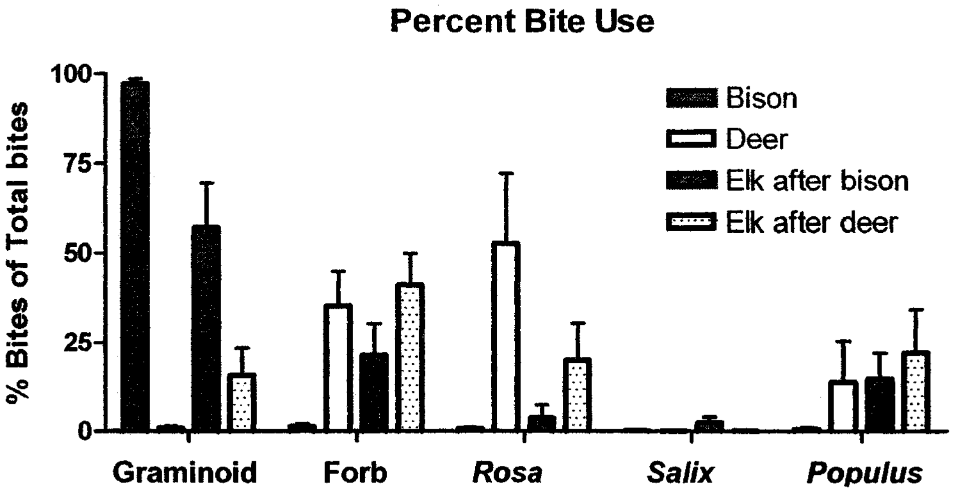

Figure 3-2: Percent bite use (bites of total bites) by bison, deer and elk after bison and deer. Bites were collected using the hand-plucking method from within foraging patches along the path of observed individuals.

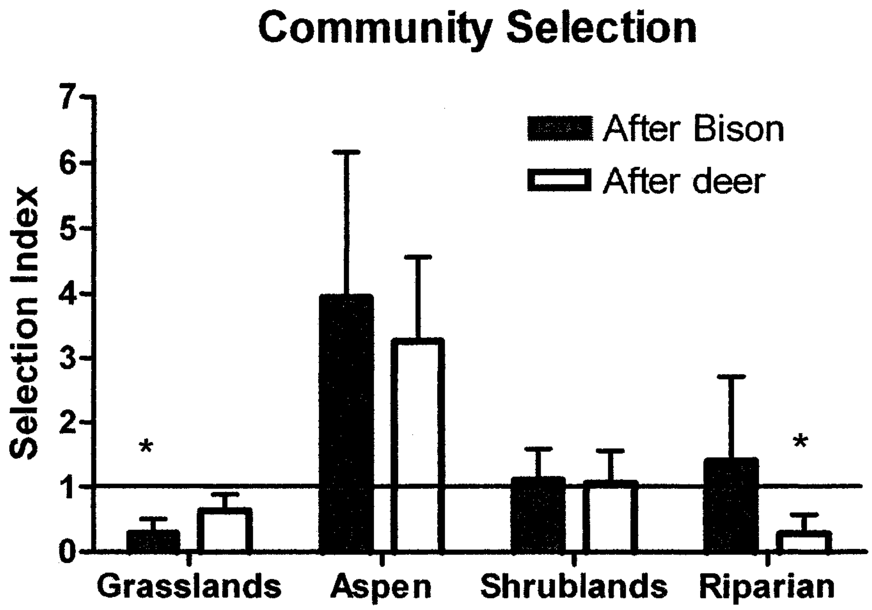

Figure 3-3: Community selection by elk (% foraging locations within community/ area) in paddocks previously grazed by bison or mule deer. Measurements were taken in spring 2005, and asterisks represent values significantly difference from one.

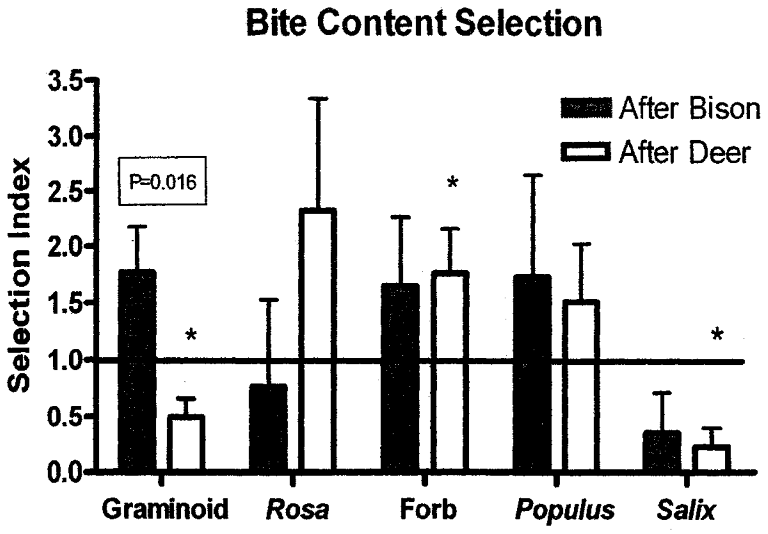

Figure 3-4: Elk bite selection (% bites of total bites/ biomass availability of each forage class) in paddocks previously grazed by bison or mule deer. Measurements were taken in spring 2005, and asterisks represent values significantly difference from one.

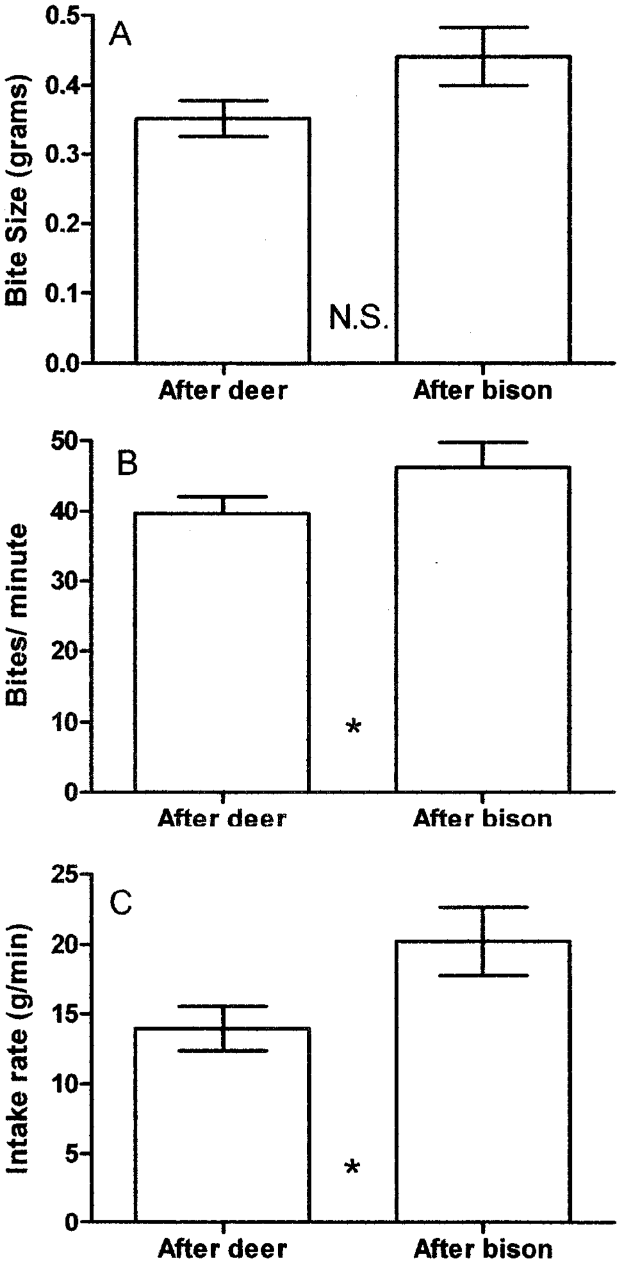

Figure 3-5: Bite characteristics of elk foraging in paddocks after bison or mule deer. Characteristics were measured from within foraging patches in spring 2005. Asterisks represent significant treatment differences, with p-values <0.1.

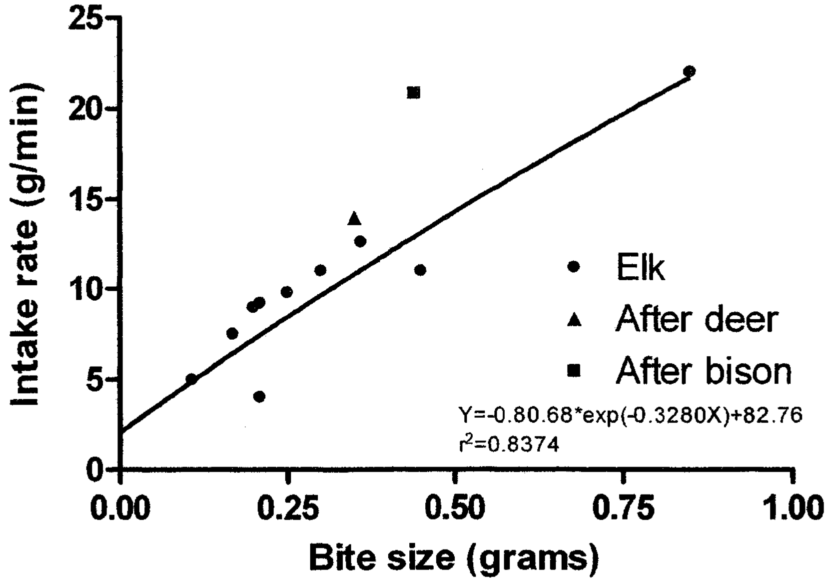

Figure 3-6: Intake rates and bite size of elk compiled from (Hudson & Nietfeld 1985) and (Hudson & Watkins 1985) (•) in an aspen parkland ecosystem, fit with an asymptotic curve. Results are compared to the intake parameters of elk from aspen parkland, spring 2005, foraging after either bison (▪) or mule deer (▲).

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Chapter 4: General Conclusions

Summary

In this thesis, I have provided some key findings that advance our understanding of native ungulate grazing systems in North America. Species assemblages are often assumed to be dominated by competitive interactions when multiple species share the same resources. Our current understanding is that competition for resources is reduced through differences in body size, morphology, and physiological constraints that lead to resource partitioning (Illius & Gordon 1987; Shipley et al. 1994). These factors may also influence the scales at which ungulates interact with their environment (Kitie 2000; Mech and Zollner 2002; Perry and Garland 2002; Holland et al. 2005). The strength of resource selection patterns across scales may also reflect limiting factors (Rettie & Messier 2000).

In my thesis, I addressed two main objectives. The first was to determine how three different sized and physiologically distinct species, that are using the same landscape, respond differently to limiting factors, through selection across multiple foraging scales. I found bison and deer had little overlap in selection of scales. Although I predicted bison would select communities, instead they selected at the smallest bite scale. I predicted graminoids, which are bison's preferred forage, would be limited to specific grassland community types. Instead, graminoids were distributed across all communities. Bison were able to preferentially use paths that gave them sufficient graminoid content to allow for a diet comprised of over 95% graminoids. Bison forage selection became closer to what I predicted for fall forage use, and they selected at the large grassland communities as well as graminoid bites.

Contrary to bison, mule deer selected strongest for communities in the spring season. I predicted their preferred forbs and browse would be distributed across communities, and thus mule deer would use all communities, but select strongly for high quality bites. Instead, they focused on communities that contained high densities of forbs and browse (aspen stands), and had a diet that was over 90% these two forage types in spring. In the fall season, deer selection of communities decreased, and although patch and bite selection did not compensate for this decline, they were able to maintain 70% forb and browse in their diets.

Elk forage selection across scales overlapped with both mule deer and bison. In the spring, elk had an evenly distributed diet over graminoids, forbs and browse. Elk selected at the largest community for riparian meadows where bite size was largest. Community selection in general was highly correlated to aspen and forb biomass, and thus elk selected for aspen communities in the spring as well, overlapping with deer community choice. At the patch scale, elk chose locations with higher forb and *Populus* biomass than matrix locations. At the bite scale, elk did not show selection until the fall. In the fall season, elk diet overlapped with both bison and deer, as they selected for forbs and graminoids. Elk avoided *Artemisia* similarly to bison in the fall, and selected for riparian edge communities.

Because elk forage selection overlaps with both bison and mule deer, my second objective was to use an experimental approach and test whether elk respond to landscape changes created by previous foraging of either a grazer (bison) or selective feeder (mule deer). I found that elk responded positively to the previous foraging of bison. Elk increased graminoid intake after bison compared to deer. Elk had similar bite sizes in the two treatments, but had a faster bite rate after bison, and thus a higher intake rate after bison than mule deer. Generally, elk bite size declines if bite rate increases (Hudson & Nietfeld 1985) unless handling or search time decreases. In order to maintain bite size and increase bite rate, elk must have decreased handling time in the treatment after bison. In order to decrease handling time, bison could have impacted two mechanisms: search time, or chewing time. Intake rates of elk after bison in this experiment were nearly 85% above intake rates of elk with similar bite sizes in aspen parkland tested using similar methods.

My results at the global scale:

Sustainable agriculture is becoming a more prominent topic for discussion and study worldwide, and focuses on farm productivity and profitability while minimizing environmental impacts (Faeth 1993). However, current agricultural accounting systems fail to assign a cost to landscape degradation (Faeth 1993). Technological advances in farm machinery, fertilizers, separation of livestock from crop production, and farm enlargement have allowed North American producers to maintain or increase productivity even with the threat of cumulative degredation on habitats, soil, and water (Stonehouse 1996).

There is little incentive for the average farmer to operate a sustainable business that focuses on conservation as well as production. This is because investment in conservation can be costly to farmers. Although there may be long-term benefits, shortterm losses cause farmers to sacrifice landscape stewardship for economic gains (Shiferaw & Holden 2001). Change may take place, however, through the increased effort to determine specific factors that allow farmers to increase conservation efforts (Shiferaw & Holden 2001), and by targeting specific government policies (Stonehouse 1996; 2004). In other countries, agriculture policy goes beyond livestock and crop production, to landscape stewardship. For instance, in Scotland, mixed species foraging regimes are used to maintain threatened heather shrublands. Perhaps policy in Canada can also be changed to protect threatened landscapes, including the fescue grasslands in this study, and others ecosystems in southern Alberta (Kerr & Deguise 2004; Deguise & Kerr 2006). With these changes, and an increase in market for organic, free-range products, perhaps Canadians through product choice, will improve incentives for farmers to produce more natural, sustainable products that reduce not only degradation of the landscape, but promote large scale landscape restoration.

In other mixed species assemblages, mostly domestic species, there has been an observed increase in production rates by one or more of the species involved (Abaye et al. 1994; Olson et al. 1999; Animut et al. 2005; Kitessa & Nicol 2001). My research has shown that bison, elk and deer cope well with mixed assemblages, and can be grazed either in rotation or continuously without adverse effects. These results are promising, as they support earlier predictions by Telfer and Scotter (1975), who suggested that multiple species could provide more sustainable use of Aspen Parkland rangelands (Telfer & Scotter 1975). A combination of these research results, an effort to improve market demand of these meat types, and increased output per hectare through multiple species use would make mixed assemblage production a viable landscape enterprise.

Future research

The results of this study contribute to our understanding of various factors influencing forage intake and selection patterns by native herbivore species. These results are useful for managers implementing grazing treatments, to know how mixed species will react to abundant vegetation, and give insight to how this could change with availability. My findings have also exposed the need to look more closely at assemblages over seasons, or over years, and to determine how competitive and facilitative relationships change with forage availability. Although the opportunity to compare results across seasons existed with this project, my results have lead to further questions regarding species-landscape interactions. In particular, I have suggested that under some conditions facilitation among herbivores is facilitated by reduction in handling time, through landscape changes. An interesting progression would be to determine how handling time is reduced through more specific experimental trials regarding sward structure and quality.

Other research emerging from the Precision Ranching Initiative focuses more on plant community and biomass heterogeneity across scales, mostly at a larger scale than I used in this project. Perhaps by combining my multi-scalar selection data with the multi-scalar vegetation data, combined with digestibility measures of available vegetation collected in other studies, one could make better inferences about what vegetation characteristics other than biomass influence forage use by mixed species assemblages.

Take home message:

Telfer and Scotter (1975) predicted that mixed native ungulate foraging regimes would use the landscape efficiently due to differential selection for vegetation across scales of heterogeneity. I found supporting evidence for this hypothesis, that bison and mule deer do not compete for similar scales of vegetation or intake, and thus show resource partitioning. I found elk forage selection overlaps with both bison and mule deer at multiple scales, and thus the potential for competitive relationships exist, if forage abundance is limited. I tested for competitive relationships between elk and bison and elk and deer, and found differences in forage use and intake by elk after deer and bison use that were more consistent with small-scale facilitation by the large roughage feeder than "high grading" by the concentrate feeder.

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Appendix 1: Using continual sequences of bites and steps to delineate foraging patches and non-foraging matrix along the foraging path.

Behavioural Data

Foraging behaviour data were collected on bison, elk, deer and cattle pastured at the University of Alberta Research Ranch in Kinsella, Alberta. The ranch is an aspen parkland system containing aspen stands, grasslands, various shrubs, and lowland riparian meadows (Asamoah et al. 2004). Foraging bouts began when a focal individual rose from its bedded site and commenced foraging and ended when the same individual returned to a bedded state, began to ruminate, or lost interest in foraging and no longer cropped bites. Bites and steps (paces) were recorded continuously (one second intervals) using a laptop computer running the program Behaviour Tracker (v. 1.5; www.behaviortracker.com). A step was defined as the movement of one foreleg in a reorientation process to reach new forage or move away. Lifting of a leg and placing it directly in the spot from which it was lifted was not considered a step (i.e. stomping to remove a fly). A bite was defined as the physical removal of vegetation by gripping forage in the mouth and tearing pieces from the plant, followed by mastication.

To delineate foraging patches from the non-foraging patches, we did not use time intervals between bites as in Sibly et al. (Sibly et al. 1990), because animals can be standing and chewing, without actually leaving the spatial extent of a patch, even though they have stopped cropping bites. The interaction between movement and the cropping of bites is a better definition of when the animal actually decides to stop eating and move to a new patch (Jiang & Hudson 1993). In this case, an animal must stop cropping bites and step away from their location in order to have left a foraging patch. Along the foraging path, animals exhibit two mutually exclusive behaviours: moving while cropping bites, and moving without cropping bites. Consequently, the log-frequency of paces (Hoffman 1989) per bite was used as the response variable for fitting both the tradition two-process "Sibly" and constrained two-process models. The resultant bout criterion was calculated as the number of paces per bite an animal must take to leave a patch, which delineated foraging from non-foraging matrix on the landscape. Sequences of biting and stepping could then be broken into either patch or matrix and matched to GPS locations taken while the animal was foraging. In this manner, behaviour could be linked to landscape metrics.

Statistical Methods

We fit the one-process or Sibly model to the log-frequency of steps per bite ($Ln(Y)$) as presented in the literature (Sibly et al. 1990) as:

$$\ln(Y) = \ln[N_a \lambda_a \exp^{-(\lambda_a x)} + N_b \lambda_b \exp^{-(\lambda_b x)}] \qquad \text{(Eq. 1)}$$

where N is number of events of behaviour a or b, respectively, λ is the probability of behaviour a or b occurring, respectively and x is the steps per bite. To delineate foraging from non-foraging patches within a bison foraging bout, we simplified the model to make the probability (λ_a) of being in a foraging patch non-independent (i.e. the probability of being in a non-foraging patch is one minus the probability of being in a foraging patch) as well as limiting the number of foraging patch observations (N_a) to the total number of observations made (N_T). We solve for model the log-frequency of steps per bite ($Ln(Y)$) as:

$$\ln(Y) = \ln[(N_T - N_a)(1 - \lambda_a)\exp^{-(\lambda_a - 1)x} + N_a\lambda_a \exp^{-(\lambda_a x)}] \qquad \text{(Eq. 2)}$$

where N_T is the total number of events observed (total number of data points), N_a is the number of observation in a foraging patches, λ is the probability of being in a foraging patch, and x is the number of steps per bite.

The Sibly patch criterion (PC_s) or number of steps taken per bite to differentiate a foraging from non-foraging patch follows from Eq. 1 (with the same notation) as:

$$PC_s = \frac{1}{\lambda_a - \lambda_b}\ln\left[\frac{N_a\lambda_a}{N_b\lambda_b}\right] \qquad \text{(Eq. 3)}$$

while the patch criterion (PC_c) of the constrained Sibly model developed above follow from Eq.2 (with the same notation) as:

$$PC_c = \frac{1}{1 - 2\lambda_a}\ln\left[\frac{(N_T - N_a)(1 - \lambda_a)}{N_a\lambda_a}\right] \qquad \text{(Eq. 4)}$$

The models were fit to observed bison, elk and mule deer data in Mathematica (v.5.0) and the parameters estimated using maximum likelihood estimation.

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Appendix 2: Cattle behavioural data, spring and fall 2004.

Selection indices were collected by paddock. Bite characteristics were summarized by species, by pooling all data. Patch and matrix vegetation was calculated from pooling all vegetation location data within patches and matrices and calculating mean and standard deviations. Selection and use data were summarized by individual and by paddock. All data was collected in a similar manner to that described in Chapter One. Three individuals were observed in spring (each collared, and one in each paddock), and five were observed in fall.

Table A2-1: Mean community type selection (% patch locations of total locations/ % hectares of community type of total hectares) and percent use of community types by cattle in spring and fall seasons measured June 1-July 15, and September 1- October 15, 2004 (no significant selection differences between seasons).

	Spring N = 3 Paddocks			Fall N = 3 Paddocks		
Community	Selection	StDev	% Use	Selection	StDev	% Use
Aspen	1.34	2.316	7.8	0.00	0.000	0.0
Grasslands	1.27	0.606	69.7	1.40	0.041	99.8
Riparian	12.76	22.103	15.0	0.00	0.00	0.2
Shrubland	0.32	0.286	7.5	0.01	0.014	0.2

Table A2-2: Mean bite selection (% bites of total bites/ % grams of total grams available) and percent use of forage types by cattle in spring and fall seasons measured June 1-July 15, and September 1- October 15, 2004. (no significant selection differences between seasons).

	Spring N = 3 Paddocks			Fall N = 3 Paddocks		
Forage Type	Selection	StDev	% Use	Selection	StDev	% Use
Graminoids	2.89	0.597	99.04	2.57	0.322	98.4
Forbs	0.01	0.022	0.20	0.02	0.019	0.25
Browse	0.05	0.077	0.77	0.65	1.121	1.34

Table A2-3: Bite characteristics of cattle in spring and fall seasons measured June 1-July 15, and September 1- October 15, 2004. * represent significantly greater values in fall (p-values <0.1)

	Spring N = 41 patches		Fall N = 49 patches	
Forage Metric	Mean	StDev	Mean	StDev
Bite Size (g)	0.53	0.18	*0.63	0.28
Bite rate (bites/min)	38.77	13.20	*59.43	35.43
Intake rate (g/min)	21.12	12.59	60.54	157.13
Movement rate (steps/min)	10.80	8.33	8.34	6.54
Time per patch (sec)	238.20	232.94	*367.17	443.00
Patch biomass	97.29	32.50	*87.83	23.74
% live of total	62.52	16.84	63.04	15.67

Table A2-4: Vegetation measurements recorded from within foraging patches and between patch matrix along the paths of cattle in spring and fall, 2004.

		Spring			Fall	
Biomass estimates ($g/0.25m^2$)	Patch N=186	Matrix N=60	P-value	Patch N=213	Matrix N=48	P-Value
Total	99.9 ± 3.46	97.3 ± 7.62	0.778	90.2 ± 1.90	99.0 ± 4.70	0.056
Live grass	31.6 ± 1.54	32.4 ± 3.85	0.861	39.1 ± 1.34	37.0 ± 2.45	0.491
Live CAG shrub	14.9 ± 1.52	15.6 ± 3.01	0.869	6.4 ± 0.64	12.6 ± 2.56	<0.001
Live forb	10.4 ± 0.74	12.2 ± 1.83	0.368	9.8 ± 0.90	9.6 ± 1.59	0.931
Live CAG aspen	-	-	-	0.2 ± 0.39	0.4 ± 0.32	0.606

Appendix 3: Interesting observations

Bison affect elk riparian meadow use:

For example, riparian use by elk was minimal when following deer, but elk tended to forage for graminoids in these wetlands when following bison, and when in the mixed treatment. After deer, there should be more biomass available, and quality should not be sufficiently different to make these graminoids indigestible after only 15 days of growth. Therefore, it seems, the simple changes in structure, or characteristics of the forages created by bison may positively influence elk use of these areas. It would be interesting to examine how bison influence elk use of riparian areas, as these wetlands provide large quantities of available vegetation concentrated in small areas which could be used by elk in a system having grazers, that could be left underutilized in another animal species guild.

Differences between deer and elk bite cropping methods:

Elk and deer seem use two very different methods of biting parts from plants. Elk sometimes overfill their mouths, either by stuffing them full of graminoids in riparian communities, or by stripping limbs of *Salix* or *Populus*. Is the behaviour adopted by elk, allowing them to spend more time vigilant in these communities where they are more vulnerable (aspen stands where they cannot see predators easily, and riparian meadows where it is difficult to move quickly), or is this so that they can spend more time inactive ruminanting, or performing other activitities? It would be interesting to test how elk foraging methods differ with or without the presence of predators, to determine if their bite method reflects vulnerability. Deer are very selective for specific plant parts when taking bigger bites is possible, and perhaps easier. In the case of *Rosa* they painstakingly avoid sepules while removing leaves. It is, in fact, easier to pull the leaves and sepules from the plant together. An interesting small research project could test if avoidance of sepules by deer is because of digestive constraints, or because they spend their "extra time", being more selective than they need to, by comparing selectivity in wild unconstrained individuals to those in captivity.

Mycophagy and Osteophagy

In 2004, 30 complete foraging bouts on elk and deer were observed, with an additional 100 hours of observations not during foraging bouts. In 2005, 61 foraging bouts were observed. No observations of osteophagy or mycophagy were noted in elk or mule deer in 2004. In 2005, 3% of mule deer observations contained osteophagy and 11% mycophagy. There were an additional 4 observations of osteophagy outside of normal foraging bout observations. Elk were observed to exhibit osteophagy in 15% of foraging bouts, and mycophagy in 3% of foraging bouts. These observations of osteophagy and mycophagy may be due to mineral deficiencies (Rozin 1967; Schryver *et al.* 1978; Houpt 1998).

Observations of mycophagy in 2005, and not 2004 could be because the availability of mushrooms was higher in 2005. Higher available biomass noted in 2005 could be directly related to higher water availability, which would lead to fungal growth. In this case, mycophagy may be realated to the availability of mushrooms on the landscape, and if they were available, elk and deer would eat mushrooms more frequently. Searching for mushrooms was evident, as walking became sporadic, and long, straight movements between mushroom "rings" were observed in elk. When deer and elk came across mushrooms, they often picked the caps from the mushrooms. Very little ingestion of the entire mushroom was noted and deer were noted to suck on the caps then spit them out before selecting another mushroom.

In 2004, riparian meadows had high grass and forb content compared to other habitats. In 2005, riparian meadows contained standing water as well as high grass and forb content. This is evidence of two very different years of rainfall. Rainfall variances also were evident in the availability of forages, which in Aspen Parkland is often limited by water availability. Average availability of total biomass along the foraging paths of elk and deer in 2004 and 2005, did increase significantly in 2005 compared to 2004. This increase in vegetation biomass in 2005 may be the direct cause of osteophagy and mycophagy in elk and mule deer in this study. High water availability may have increased biomass and the availability of preferred browse and forbs of elk and deer, while not affecting drier areas. Heterogeneity in availability of forages may cause lack of calcium in diet, as animals will preferentially select calcium low forages, even though other available forages contain adequate levels of calcium (Tomson and Lotshaw 1978). Another cause of dietary deficiency in calcium could be because young growth in shrub species, which are preferred by elk and deer, contain low amounts of calcium compared to old growth, or possibly the minimum requirements of plants are being met, but are inadequate for the amount required by ungulates (Van Soest 1982). Forages in these areas are known to be phosphorus deficient (Barry Irving, unpublished) and growth due to water availability may further dilute the concentration of phosphorus in preferred plants.

Deficiencies of phosphorus and calcium are normally controlled by offering bone meal, calcium phosphates, or oyster shells in feed (Van Soest 1982). These animals were given no dietary supplements, resulting in osteophagy and mycophagy.

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