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Impacts of cattle grazing on native ungulates in Sheep River Provincial Park, Alberta.

by

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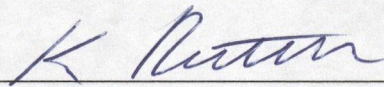
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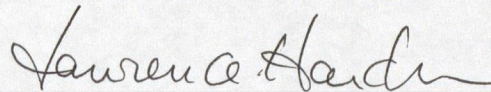
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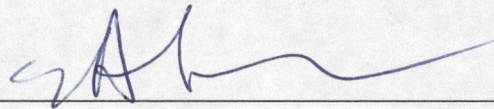


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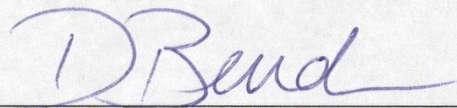
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Abstract

Livestock grazing can have negative and positive effects on native ungulates. This study investigated the impact of cattle on foraging and avoidance of bighorn sheep (*Ovis canadensis*), and evaluated the differences in vegetation quantity and quality, and ungulate use between cattle exclosures and grazed plots in Sheep River Provincial Park, Alberta. As predicted, bighorn sheep decreased bite rates and increased vigilance in the presence of cattle. However, sheep did not avoid cattle, as cattle and sheep used the same general areas. As expected, greater vegetation biomass of poorer quality was found inside the exclosures compared to areas that had been grazed by cattle. Sheep preferred grazed plots during summer. More forbs were found in this study than during the 1990's. The influence of cattle grazing on the vegetation varied with season, with the greatest negative impact found in winter. Some management implications are discussed.

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Chapter 1: Introduction

Overview of competition

Begon et al. (1996) defined competition as “an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned.” Two competition types are commonly described in the literature: exploitation and interference. The more obvious type, interference competition, occurs when one of the competitors monopolizes a common resource, such as a territory. All other individuals are then forced to use less profitable areas (Brown 1969). Interference competition is often displayed in species where harem-forming males physically combat for females, as in elk (*Cervus canadensis*), stellar sea lions (*Eumetopias jubatus*), or gorillas (*Gorilla gorilla*). Another type of competition, known as exploitation, leads to an “ideal free distribution” (Fretwell 1972), where every competitor is free to select a habitat with best per capita gains. Exploitation does not limit the potential number of competitors and territories are not established. Some individuals subject to exploitative competition may choose less profitable habitats with fewer competitors, because per capita gain is higher there than in rich habitats filled with many competitors. Large grazers are often characterized by exploitation competition (Illius and Gordon 1987), as they rarely display aggressive behaviour to protect resources. The vegetation is difficult to monopolize, so the benefits of territorial defence rarely outweigh the costs (Veiberg et al. 2004).

Indisputably, competition is one of the major influences on the evolution of many organisms and can often result in speciation, as famously illustrated by the variation in

beak shape of Darwin finches (*Geospizinae*) (Boag and Grant 1981). Extended periods of coexistence of two species that use a shared resource often result in decreased niche overlap. The competitive exclusion principle (Hardin 1960), also known as Gause's Law (Gause 1934), states that in a constant environment two species that use same resources can not coexist and one will eventually drive the other extinct. This principle, however, often appears to be violated. One of the best examples, known as "plankton paradox," questions the validity of this principle in the ocean surface systems, where many species of plankton coexist in an apparently well-homogenized environment under similar conditions (Hutchinson 1961). Recent studies suggest that the interactions of external and internal factors such as seasonal changes, predation, and competition destabilize the system and induce chaos, so that no single species is ever favoured (Scheffer et al. 2003).

Mutualistic and antagonistic interactions between species

The extent and outcome of interactions between species depend largely on environmental conditions, resource availability, and population densities. For example, the outcome of competitive exclusion between two species of chipmunks varied at different altitudes (Brown 1971), favouring one species at higher elevations and the other at lower elevation. Many other examples illustrate that the magnitude and effect of interactions between two species can change under different conditions. For instance, two species of iguana lizards competed for food only during dry periods, but not during the wet years when resources were abundant (Dunham 1980). Furthermore, the strength of mutualism between ants (*Formica altipetens*) and membracids (*Publilia modesta*) depended on the size of the membracid colony. Membracids supply ants with nutritious

excretions, whereas ants provide protection to membracid colonies. The positive impact of ant tending was stronger in large aggregations of membracids than in smaller ones, possibly because ants were more aggressive towards predatory spiders in the large colonies (Cushman and Whitham 1989).

Sometimes even interactions that were previously considered as negative can turn out to be positive after a closer look. For example mistletoe (*Phoradendron juniperinum*), which is often considered to be a parasite of juniper (*Juniperus monosperma*) may attract birds that disperse juniper seeds (van Ommeren and Whitman 2002).

Most interactions between large mammalian herbivores are viewed as antagonistic (Illius and Gordon 1987); however large grazers can also affect each other positively (Arsenault and Owen-Smith 2002) by creating grazing lawns with high food quality (McNaughton 1984). At low and moderate herbivore densities grazing can increase forage productivity and vegetation diversity (Frank and McNaughton 1993, Olff and Ritchie 1998). However, at high animal densities overgrazing can decrease vegetation biomass and diversity (Hobbs and Huenneke 1992, Biondini et al. 1998), ultimately decreasing populations of some grazers.

Cattle and their impact on other herbivores

Domestic cattle (*Bos taurus*), like other herbivores, can have both positive and negative effects on the vegetation and coexisting ungulates. For example, plant diversity was higher under light and moderate sticking rates than under no grazing or heavy grazing (Hart 2001). Livestock is often viewed to have antagonistic effects on native ungulates (Dunham et al. 2003, Jenks and Leslie Jr. 2003, Mishra et al. 2004), mainly by

reducing forage availability (Thill and Martin Jr. 1989, Rhodes and Sharrow 1990). High cattle density can also cause deterioration of range health and decrease vegetation productivity (DeMarchi 1973, Fleischner 1994, Westenskow-Wall et al. 1994, Clark et al. 2000, Yeo 2005). For example, white-tailed deer (*Odocoileus virginianus*) were found to have lower body mass and reproductive success on ranges with cattle grazing than on ungrazed ranges (Jenks and Leslie Jr. 2003). Presence of cattle was associated with a shift in habitat use in bighorn sheep (Bissonette and Steinkamp 1996), mule deer (*Odocoileus hemionus*; Loft et al. 1993, Stewart et al. 2002) and elk (*Cervus Canadensis*; Clegg 1994, Coe et al. 2004). However, under some conditions livestock can improve forage quality and productivity (Westenskow-Wall et al. 1994, Alpe et al. 1999, Clark et al. 2000, Holechek et al. 2006) and increase protein content and digestibility of vegetation (Ganskopp et al. 2006, Casasús et al. 2007). Managed livestock grazing improved range health and increased populations of native ungulates in Oregon, Utah, and Wyoming (Anderson & Scheninger 1975, Smith et al. 1979, Bastian et al. 1991, Vavra & Sheehy 1996).

Unlike wild herbivores, livestock populations are controlled by humans more than by competition with other species. During seasons when forage availability is limited, cattle meet their nutrient requirements through food provided by their owners. Native ungulates are usually not provided with this opportunity and their survivorship depends directly on the vegetation left on the range. The range managers can reduce range deterioration and negative impacts on native species by controlling the intensity of livestock grazing. Unfortunately, little has been done to investigate the magnitude of the effects of cattle grazing on wild ungulates and they therefore remain poorly understood.

Because the impacts of grazing can change under different conditions, more studies are needed to understand the effects of livestock on wildlife by doing controlled experiments.

This study focuses on the effects of cattle grazing on native ungulates, and in particular on bighorn sheep. The numbers of bighorn sheep have been decreasing in North America during the last few decades and more research is needed to understand the causes of this decline (Krausman 2000). Bighorn sheep are mainly grazers and have a larger diet overlap with cattle than browsing ungulates, such as deer, which makes them particularly suitable to look at impacts of cattle grazing. Most of the previous cattle grazing studies focused on elk and deer and we lack the sufficient knowledge to understand cattle impacts on a grazer, such as the bighorn sheep. The location of my study (Sheep River Provincial Park) allowed me to work with a well studied and tagged bighorn sheep population that has been coexisting with cattle since 1917. This population made it feasible to address the following objectives of my thesis.

Objectives

Most previous studies of interactions between native ungulates and cattle focused on either impacts on either vegetation or the behaviour of native ungulates. A more complete picture requires understanding of changes in vegetation quality and availability as well as the shift in ungulate range use and possible behavioural changes induced by livestock. Most vegetation research also investigated the impact of livestock on a year-to-year basis, without considering seasonal changes in forage availability.

Presence of cattle can be disturbing to the native ungulates due to the introduction of distracting visual and audible stimuli (Matiello et al. 2002). I hypothesized that the

presence of cattle will alter behaviour of bighorn sheep and influence their range selection. The primary goal of this study was to investigate the effect of cattle on vigilance and foraging behaviour of bighorn sheep. I expected that sheep would alter their behaviour in the proximity of cattle by decreasing bite rates used to obtain vegetation and becoming more vigilant, as previously shown in elk (Matiello et al. 2002). The second objective was to investigate the avoidance behaviour of bighorn sheep towards cattle. Based on previous research (Bissonette and Steinkamp 1996) I predicted that sheep would avoid cattle. I have defined avoidance as a greater distance between sheep and cattle locations than expected from random association.

Additionally, I hypothesized that cattle grazing should have both negative and positive effects on vegetation depending on the time of the year, as previously shown by Clark et al. (2000) and Ganskopp et al. (2006), and that this variability in vegetation biomass and quality would influence ungulate use of grazed and ungrazed plots accordingly. In order to investigate these changes, I looked at the seasonal vegetation differences between grazed and ungrazed plots. Based on previous research (Clark et al. 2000, Ganskopp et al. 2006), I expected that more vegetation would be found inside cattle exclosures, while higher live vegetation, protein concentration and digestibility would be found in grazed plots. However, because of the higher amount of forage inside the exclosures, I expected that the total protein and digestible energy would be higher in exclosures than grazed plots. I also predicted that native ungulates would show preference for exclosures over the grazed plots during the seasons when forage availability is limited, as previously shown by Coe et al. (2001, 2004). Since the stocking rates have decreased in Sheep River Provincial Park, I expected to see an increase in

biomass, decrease in proportion of green mass, and change in proportion of forbs over the decade.

This thesis comprises three major chapters. Chapter 2 reviews published literature concerning impacts of cattle grazing on native ungulates and vegetation (Chaikina & Ruckstuhl 2006). Chapter 3 addresses the first two objectives, describing possible changes in behaviour of bighorn sheep due to cattle presence and tests for the avoidance behaviour of bighorn sheep towards cattle. Chapter 4 addresses the last two objectives of this research, examining the differences in vegetation characteristics and ungulate use between the exclosures and grazed plots.

Overall, this research considers the effects of cattle grazing on forage availability, range use, and behaviour of native ungulates in the foothills of the Rocky Mountains, southwestern Alberta. This study investigates whether interactions between livestock and native ungulates are antagonistic or beneficial, and whether range management practices could promote favourable impacts.

Chapter 2: Literature review

Impacts of livestock grazing on vegetation and native ungulates have been an important concern for rangeland managers and livestock owners. Previous research demonstrates that cattle grazing decreases forage availability for wild ungulates such as mule deer (Austin et al. 1983; Bowyer and Bleich 1984), bighorn sheep (DeMarchi 1973), and elk (Skovlin et al. 1983). Several studies indicate direct forage competition between cattle and elk (Loomis et al. 1989), mule deer (Dasmann 1949), and bharal (*Pseudois nayaur*; Mishra et al. 2004). Intense cattle grazing has been associated with lower weights, fat content and reproductive rates in female white-tailed deer (Jenks and Leslie Jr. 2003), decreased translocation success of bighorn sheep (Singer et al. 2000), reduced survival of white-tailed deer (McMahan and Ramsey 1965), and decreased hiding cover for mule deer (Loft et al. 1987).

Although many previous studies have shown some negative impacts of cattle grazing on wild ungulates, the extent of these effects is not always clear. The objective of this review is to characterize how the presence of livestock affects wild ungulates. Furthermore, I will consider whether negative impacts could be reduced, and become neutral or even beneficial to native ungulates.

The impact sources

Diet overlap

For livestock and wildlife to compete, they must have a dietary and spatial overlap and share limited forage resources (Vavra et al. 1999). Many studies found a potential diet overlap between cattle and wild ungulates, but results varied depending on the

species, area of study, and time of the year. Campbell and Johnson (1983) considered the diets of cattle, mule deer, and mountain goats (*Oreamnos americanus*) on Chopaka Mountain, Washington and found the most overlap between mountain goats and mule deer (37%) and mountain goats and cattle (32%), with smaller overlap between the diets of mule deer and cattle (15%). Olsen and Hansen (1977) and Mackie (1978) found extensive diet overlap between cattle and elk. Similarly, Hansen and Reid (1975) reported up to 38% dietary overlap between deer and cattle and 51% between elk and cattle in Southern Colorado. Willms et al. (1980) reported significant range overlap between cattle and deer in British Columbia, because both used mainly open forests and clearings. Even though diet overlap between livestock and deer was not high, it increased as forage became less available. On the other hand, Kingery et al. (1996) reported some diet overlap between elk and cattle, but not between cattle and deer in northern Idaho: cattle and elk foraged mostly on graminoids, whereas white-tailed deer consumed mainly forbs and shrubs. Pordomingo and Rucci (2000) argued that, with proper management, cattle and deer could have minimal competition, as deer are more adapted to browsing and selecting better quality plants and cattle had a better ability to digest low quality grasses. Stewart et al. (2003) used stable isotopes from fecal samples of cattle, elk, and mule deer in western North America and found significant differences in their diets. Hansen et al. (1977) also reported limited diet overlap between cattle and deer in the Douglas Mountain area, Colorado.

Even though cattle and wild ungulates eat somewhat different kinds of vegetation, diet overlap increases when forage becomes less available, usually during winter and early spring. For example, Thill and Martin Jr. (1989) reported greatest diet overlap

between white-tailed deer and cattle on pastures in central Louisiana during winter (30.7%), and concluded that late fall and winter cattle grazing can be detrimental to forage availability for deer. Thill (1984) suggested that white-tailed deer and cattle diets on forested sites overlapped the most during winter and spring. Ortega et al. (1997) also found that the greatest overlap ($> 60\%$) in the diets of deer and cattle in Texas occurred during winter and spring.

Presence of cattle

The presence of cattle can negatively impact wild ungulates by causing behavioural changes that make ungulate foraging time less productive. Bissonette and Steinkamp (1996) reported that bighorn sheep in Big Cottonwood Canyon, Idaho, avoided cattle and decreased their use of areas where cattle were nearby. Female mule deer in Sierra Nevada, California, exhibited avoidance behaviour and temporal habitat partitioning when cattle were present (Loft et al. 1993). Stewart et al. (2002) reported that elk and mule deer avoided cattle by adjusting their use of the area and moving away from cattle, possibly to avoid forage competition. Mattiello et al. (2002) showed that elk spent less time resting and feeding when cattle were present. White-tailed deer in Louisiana altered their winter diets on sites that were continuously grazed by cattle by selecting more herbs and less browse (Thill and Martin 1986). Furthermore, Kie (1996) found that cattle grazing in California altered activity budgets of female mule deer, especially during late fall and winter when forage was limited.

Wild ungulates can also change their range use in response to the presence of cattle. Loft et al. (1991) found that in absence of cattle grazing in the Sierra Nevada, California,

mule deer preferred meadows and riparian habitat, whereas on moderately and heavily grazed ranges they used montane shrub more frequently. Yeo et al. (1993) also reported that elk and mule deer changed their habitat use as a result of cattle grazing in east-central Idaho.

In contrast, some studies indicate little behavioural change in response to the presence of cattle. For example, Halstead et al. (2002) showed that choice of grazing areas by elk in central Arizona depended more on tree growth patterns and terrain features than on the presence of cattle grazing in the area. Skovlin et al. (1968) showed that range use by elk and deer was minimally altered under light and moderate grazing.

Avoidance of areas grazed by cattle

In addition to behavioural changes, wild ungulates can avoid areas used by cattle by selecting ungrazed sites more often than grazed sites. Bowyer and Bleich (1984) observed fewer mule deer and pellet groups on the grazed areas. Clegg (1994) showed that elk preferred ungrazed areas during rest-rotation grazing in Utah. Similar conclusions have been drawn from the studies on elk and mule deer in Oregon (Coe et al. 2001, 2004), elk in Montana (Knowles and Campbell 1981, Frisina 1992), and mule deer in Arizona (Ragotzkie and Bailey 1991). Hart et al. (1991) found little overlap of elk used areas during winter with areas grazed by cattle during summer because cattle preferred to use level, lowland ranges, whereas elk concentrated mostly on higher elevations and steep areas. Whether elk actively avoided ranges grazed by cattle is unknown, because sites without cattle grazing were not considered.

Some studies indicate little or no avoidance of cattle grazed areas by native

ungulates, possibly as a result of habituation. Austin and Urness (1986) found only slight preference by mule deer for ungrazed sites at the beginning of the trial, which diminished with prolonged deer use of the area. Furthermore, mule deer did not avoid cattle in central Montana (Dusek 1975).

Positive impacts of cattle grazing

Some studies have demonstrated that controlled cattle grazing can improve forage quality for native animals. Vavra and Sheehy (1996) argued that grazing by cattle removed the previous year's growth, increasing the protein content of new vegetation. Range production was maximized by removing cattle during early summer, allowing plants to regrow. This regrowth occurred later during summer, so plants could not complete their growth cycle and transfer nutrients to the roots. Nutrients were instead trapped in the shoots, leaving them available to the grazing ungulates. A rest year was required between the grazing applications to allow vegetation recovery and ensure long-term range quality (Vavra and Sheehy 1996). A similar short-term increase in vegetation quality was achieved by clipping (Garrison 1953). On the other hand, the increase in vegetation nutrition was shown to diminish during winter, the most critical time for wild ungulates (Wambolt et al. 1997). Scotter (1980) suggested that range use by both livestock and big game helped to achieve and sustain the balance of browse and herbaceous forage within plant communities, thus increasing economic benefits of the land. Additionally, livestock grazing during early spring increased the protein content and digestibility of forage for mule deer during winter (Scotter 1980). Anderson and Scheninger (1975) argued that a specifically designed cattle-grazing system improved

winter vegetation on elk range in northeastern Oregon. In contrast to an average of 120 elk during the past 12 years, elk density increased to 1,190 elk, whereas cattle grazing increased 2.6 times during the same period (Anderson and Scheninger 1975). Another study of cattle and white-tailed deer in Mexico suggested that a grazed area had a more stable vegetation composition when used by two herbivore species with different foraging patterns than when used by a single herbivore species (Gallina 1993). Additionally, cattle grazing was reported to enhance forb production and increase deer abundance (Stuth and Winward 1977), to improve the nutritional status of white-tailed deer (Warren and Krysl 1983), to enhance forage conditions on deer winter range (Gibbens and Schultz 1962), and to increase deer spring preference for the pastures that were grazed by cattle during the previous fall (Willms et al. 1979). Gordon (1988) also showed that winter cattle grazing in Scotland increased the amount of new vegetation during the following spring. Elk preferred to use areas grazed by cattle during the previous winter and had more calves per hind on the grazed ranges (Gordon 1988). In some cases, complete removal of cattle can cause forage stagnation and make the vegetation less suitable for wild ungulates. Tueller and Tower (1979) defined stagnation as "the reduction in productivity of range plants resulting from a lack of grazing." Brown and Martinsen (1967) determined that exclusive deer and elk use of the areas in eastern Washington for more than 20 years improved ranges for cattle grazing, but reduced their suitability for wild ungulate use. Hudson et al. (1976) also found that grazing in southeastern British Columbia by white-tailed deer, mule deer, elk, and bighorn sheep alone caused a vegetation shift towards more herbs and less browse, making it less suitable for browsing ungulates.

Grazing can result in both positive and negative changes. Westenskow-Wall et al. (1994) studied the effects of clipping on bluebunch wheatgrass (*Agropyron spicatum*) that is used as forage by elk in the Blue Mountains of northeastern Oregon. Defoliation in fall helped to increase the digestibility and phosphorus concentration of the wheatgrass, but decreased the amount of available forage. Additionally, Wambolt et al. (1997) found that although grazing slightly increased nitrogen and phosphorus contents of bluebunch wheatgrass, this effect was not noticeable during the following winter. Sometimes, even an increase in the numbers of wild ungulates due to grazing might not be sustainable. For example, intense cattle grazing coupled with low fire frequency during the early 1960s in the United States increased antelope bitterbrush, which in turn, caused an increase in the numbers of mule deer (Clements and Young 1997). However, overgrazing during summer caused a nutrient deficiency for mule deer during the following early spring, and large numbers of mule deer contributed to overgrazing by deteriorating soil and vegetation (Julander 1962).

Impact mitigation

Given the contradictory results from previous grazing studies, can cattle and wild ungulates coexist as a part of a healthy ecosystem? To answer this question, we must consider how the effects of livestock vary under different applications and timing of grazing. Proper implemented short-duration grazing (cattle are present on range for a short time period followed by a short rest period) is thought to increase range productivity and livestock carrying capacity (Savory 1983). However, Cohen et al. (1989) reported that in southern Texas short-duration grazing had more impact on white-tailed

deer than continuous grazing, as deer avoided cattle and traveled more. Martinez et al. (1997) found greater similarities between white-tailed deer and cattle diets on rotationally grazed ranges (23%) than on continuously grazed ranges (15%). Ortega et al. (1997) found that diet overlap between cattle and white-tailed deer increased under short-term grazing, whereas deer consumed more forbs on the continuously grazed ranges. The study recommended continuous grazing under moderate stocking to achieve better white-tailed deer management (Ortega et al. 1997).

Timing of grazing applications is also important. Smith and Doell (1968) studied summer cattle grazing on mixed browse herbaceous ranges in Utah and reported that cattle should be removed by July 1st to avoid bitterbrush use by livestock and allow enough forage for wild ungulates. Similar studies in northeastern Oregon also showed that early summer cattle grazing minimally affected mule deer and elk foraging efficiency (Damiran et al. 2003).

Economic issues

One of the goals of cattle management is to achieve the best economic gain from an area used by both cattle and wild ungulates. For example, Bastian et al. (1991) found that economic returns from the Wyoming Red Desert were maximized when cattle and pronghorn antelope (*Antilocapra americana*) were allowed to graze together. Smith et al. (1979) also suggested that dual use of range by mule deer and domestic sheep (*Ovis aries*) would increase economic yield of the land. Economic models of mule deer foraging on Sierra Nevada summer range indicated that under a 3-year rest-rotation grazing management, increase in the number of rest years (from 1 to 2 years) would

increase mule deer populations, thereby increasing hunting and economic benefits that would cover the losses from reduced livestock (Loomis et al. 1991).

Conclusion and suggestions for future research

In summary, this review reported 13 studies that showed a positive impact of cattle grazing, 31 studies that indicated a negative impact, and 23 studies that had inconclusive results (Table I). Note that most studies focused on the impact of grazing on deer, even though deer and cattle have limited diet overlap. Grazers, such as elk, bighorn sheep, or bison have a greater diet overlap with cattle. Future research should concentrate more on investigating the effects of cattle on ungulates that consume graminoids as part of their diets, as the impact of grazing should be greater for this group.

The reviewed studies differed in methodology, which complicated comparisons. A systematic set of methodologies used to assess the impact of cattle on ungulate range is desirable. For example, direct examination of grazing competition between cattle and wild ungulates should include exclusion of cattle from parts of the range. The establishment of cattle exclosures and corresponding areas with cattle grazing would help to determine impacts of grazing on range selection by wild ungulates.

Overall, it was concluded that grazing by cattle at high stocking rates during late summer, fall and winter would most likely cause range deterioration, decrease forage availability, and negatively affect native herbivores. On the other hand, controlled cattle grazing with light to moderate stocking levels that stop early during summer would likely increase vegetation quality and balance vegetation composition in favour of forbs and browse, which would be beneficial for wild ungulates.

Table I. Summary of prior research of cattle grazing impacts on native ungulates.

Authors	Study area	Topic of study	Impacts of grazing
Coe et al. (2004)	Oregon	Effect of cattle on elk and mule deer	Cattle displaced elk and elk displaced mule deer
Mishra et al. (2004)	Indian Trans-Himalaya	Competition between cattle and wild bharal	Reduced forage availability, lower density of bharal and lower young: female ratio on heavily grazed rangelands
Damiran et al. (2003)	North-eastern Oregon	Effects of cattle and elk grazing on cattle, mule deer and elk	Early summer cattle grazing has minimal effect on deer and elk foraging efficiency
Jenks and Leslie Jr. (2003)	Oklahoma, Howard and Pike	Effect of cattle on white-tailed deer	Lower weights, fat content and reproductive rates in female white-tailed deer on ranges with winter cattle grazing
Stewart et al (2003)	North America	Diet overlap between cattle, elk and mule deer	Little diet overlap
Halstead et al. (2002)	Central Arizona	Effect of cattle on elk habitat selection	Presence of cattle grazing had little effect on elk choice of grazing areas
Mattiello et al. (2002)	Italian Alps	Effect of cattle on behavioural patterns of red deer	Elk spend less time resting and feeding with cattle nearby and more time foraging on the areas previously grazed by cattle.
Stewart et al. (2002)	Oregon	Effect of cattle presence on mule deer and elk	Elk and mule deer moved away from the cattle, likely to avoid forage competition.
Coe et al. (2001)	Oregon	Effect of cattle grazing on elk and deer in the summer	Potential competition between elk and cattle in late summer
Clark et al. (2000)	Oregon	Livestock effects on forage quality of elk winter range	Increased protein and digestibility of grasses. Decreased standing stock of forage.
Pordomingo and Rucci (2000)	La Pampa, Argentina	Elk and cattle diet composition	Minimal diet overlap
Singer et al. (2000)	Western States	Effect of livestock on translocation success of bighorn sheep	Negative impacts of grazing on translocation success of the bighorn sheep
Alpe et al. (1999)	Northern Idaho	Effects of summer sheep grazing on browse nutrition during fall and winter	Moderate grazing during early summer increased browse quality for following fall and winter. Heavy grazing during late summer decreased vegetation quality.
Clements and Young (1997)	Nevada and California	Effect of cattle on mule deer	Increase antelope bitterbrush production that caused increase in mule deer populations
Martinez et al (1997)	Mexico	Diet overlap between white-tailed deer and cattle	Greater diet similarities on rotationally grazed (23%) than on continuously grazed ranges (15%).
Ortega et al. (1997)	Texas	Diet overlap between deer and cattle	Greatest overlap (> 60%) found in the winter and spring under short-duration heavy stocking treatment
Bissonette and Steinkamp (1996)	Cottonwood Canyon, Idaho	Effect of cattle on bighorn sheep	Bighorn sheep avoided cattle and decrease the use of the grazed areas

Kie (1996)	California	Effects of cattle grazing on mule deer	Grazing altered activity budgets of the female mule deer
Kingery et al. (1996)	Northern Idaho	Dietary overlap between cattle, white-tailed deer and elk	Cattle and elk foraged mainly on graminoids, whereas deer consumed mainly forbs and shrubs. Some potential for competition between elk and cattle, but not cattle and deer
Vavra and Sheehy (1996)	United States	Effect of cattle on elk habitat	Grazing improved range conditions and quality of winter forage
Clegg (1994)	Utah	Effect of cattle grazing on elk and deer	Elk preferred rested areas during rest-rotation grazing
Westenskow-Wall et al. (1994)	North-eastern Oregon	Effect of fall defoliation on bluebunch wheatgrass	Increased digestibility and phosphorus concentration of wheatgrass. Decreased the amount of forage.
Gallina (1993)	Durango, Mexico	Effect of cattle on white-tailed deer	No evident forage competition
Loft et al. (1993)	Sierra Nevada, California	Effect of cattle presence on mule deer	Female deer avoided cattle
Yeo et al. (1993)	East-central Idaho	Influence of rest-rotation cattle grazing on mule deer and elk habitat use	Elk and mule deer changed habitat use due to rest-rotation cattle grazing; population size of both species did not change
Frisina (1992)	Montana	Effect of cattle grazing on elk area use	Elk preferred rest ranges in rest-rotation systems
Bastian et al. (1991)	Wyoming Red Desert	Antelope and cattle use of rangelands	Economic benefits of the area were maximized when cattle and antelope were allowed to graze together
Hart et al. (1991)	South-eastern Wyoming	Habitat overlap between cattle and elk	Little habitat overlap was detected, as cattle preferred level lowland areas, while elk concentrated mostly on high steep areas
Loft et al. (1991)	Sierra Nevada, California	Effect of cattle grazing on mule deer habitat use	Under no cattle grazing pressure deer preferred meadow-riparian habitat and on moderately and heavily grazed ranges deer used more of montane shrub habitat
Loomis et al. (1991)	Sierra Nevada	Effect of cattle grazing on mule deer population size	Increase in rest years (from 1 to 2) would increase the mule deer population size, increasing economic benefit
Ragotzkie and Bailey (1991)	Arizona	Effect of cattle grazing on mule deer habitat use	Deer preferred ungrazed over grazed areas
Rhodes and Sharrow (1990)	Oregon Coast Range	Effect of sheep grazing on vegetation	Grazing increased digestibility and protein content of grasses and forbs (by preventing plant maturation during growing season) and reduced biomass of forbs and browse plants by 55% and 45%
Cohen et al (1989)	South Texas	Effect of cattle grazing on white-tailed deer	Deer avoided cattle and traveled more under short duration grazing than under continuous grazing
Loomis et al. (1989)	Challis, Idaho	Effect of cattle on elk and deer	Direct competition for forage between livestock, elk and deer
Thill and Martin Jr. (1989)	Central Louisiana	Diet overlap between white-tailed deer and cattle	Diet overlap was greatest in the winter (30.7%)

Gordon (1988)	Scotland	Effect of cattle on elk	Increase in the green grass in spring. Elk preferred grazed areas and had more calves per hind on grazed areas.
Loft et al. (1987)	Central Sierra Nevada, California	Effect of cattle grazing on deer hiding cover	Decreased hiding cover of aspen and corn lily on moderately and heavily grazed ranges
Austin and Urness (1986)	Western Utah	Effect of cattle grazing on mule deer diet and habitat selection	Slight preference by deer for ungrazed areas in the beginning of the study
Thill and Martin (1986)	Louisiana	Effect of cattle grazing on diet of white-tailed deer	Deer altered winter diets continuously grazed sites by selecting more herbs and less browse
Bowyer and Bleich (1984)	San Diego County, California	Effects of cattle grazing on mule deer habitat selection	Fewer mule deer and pellet groups in grazed areas. Significant diet overlap between mule deer and cattle and greater plant cover in the ungrazed areas
Thill (1984)	Louisiana	Diet overlap between white-tailed deer and cattle	White-tailed deer and cattle diets on the forest sites had the greatest overlap during winter and spring seasons. Diet overlap on the clear-cut areas were minimal during the entire year
Austin et al. (1983)	Western Utah	Effect of cattle grazing on wheatgrass	Regrowth of wheatgrass and its winter use by deer were greater on the ungrazed areas
Campbell and Johnson (1983)	Chopaka Mountain, Washington	Dietary overlap between cattle, mule deer and mountain goats	Greatest overlap found between mountain goats and mule deer diets (37%) and mountain goats and cattle diets (32%), and least overlap between diets of mule deer and cattle (15%).
Skovlin et al. (1983)	South-eastern Washington	Effect of cattle grazing on the elk winter range use	Spring cattle grazing decreased elk winter use of the area in 1 of 3 years
Warren and Krysl (1983)	Central Texas	Effect of cattle on white-tailed deer	Positive effects on the nutritional status of white-tailed deer
Knowles and Campbell (1981)	Montana	Effect of cattle on elk	Elk preferred rest ranges in rest-rotation systems
Scotter (1980)	Western United States and Canada	Management of wild ungulate habitat	Grazing increased protein and digestibility of forage for mule deer and helped to achieve balanced between browse and grasses.
Willms et al. (1980)	British Columbia	Deer and cattle diets	Cattle and deer had significant range overlap. Diet overlap increased as forage became less available.
Smith et al. (1979)	Utah	Effect of sheep grazing on mule deer	Dual use of area increased economic yield. Change in winter diet composition of mule deer. Nutritional intake by mule deer was not significantly reduced
Willms et al. (1979)	British Columbia	Effect of cattle on mule deer	In spring deer preferred pastures that were grazed by cattle in fall
Hansen et al. (1977)	Douglas Mountain, Colorado	Diet overlap between wild horses, deer, and cattle	The overlap between wild horses and deer diets was 1%, cattle and deer was 4%, and wild horses and cattle was 77%.

Olsen and Hansen (1977)	Red Desert, Wyoming	Diet overlap between wild horses, cattle, and elk	Large diet overlap between wild horses, cattle, and elk
Stuth and Winward (1977)	Central Oregon	Effect of cattle on deer	Grazing increased forb production. Little diet overlap between domestic livestock and deer.
Hudson et al. (1976)	South-eastern British Columbia	Effect of cattle grazing on white-tailed deer, mule deer, elk, and bighorn sheep	Moderated cattle grazing only slightly altered range use by wild ungulates
Anderson and Scheninger (1975)	North-eastern Oregon	Effect of specifically designed cattle-grazing system on elk	Elk numbers increased 3.7 fold
Dusek (1975)	Central Montana	Competition between mule deer and cattle	No significant forage competition between mule deer and cattle
Hansen, and Reid (1975)	Southern Colorado	Diet overlap between deer, elk, and cattle	Some diet overlap, up to 48% between deer and elk, 38% between deer and cattle and 51% between elk and cattle.
DeMarchi (1973)	Chilcotin, British Columbia	Effect of cattle grazing on bighorn sheep habitat	Cattle grazing increased protein content of bluebunch wheatgrass, decreased total amount of protein per area, and reduced proportion of bluebunch wheatgrass
Skovlin et al. (1968)	North-eastern Oregon	Effect of cattle on deer and elk	Use of the ranges by elk and deer were minimally altered
Smith and Doell (1968)	Utah	Effects on summer cattle grazing on big game forage availability	Cattle grazing stopped by July to avoid bitterbrush use by livestock and allow enough forage for wild ungulates.
Brown and Martinsen (1967)	Eastern Washington	Effect of cattle removal on deer and elk range conditions	Exclusive grazing by deer and elk caused a decline in forb and browse species and made ranges more suitable for cattle grazing and less optimized for wild ungulate use.
McMahan and Ramsey (1965)	Central Texas	Effect of cattle grazing on deer	Continuous grazing by livestock adversely effects deer production through competition for food
Gibbens and Schultz (1962)	California	Improvement of shrub and browse production on big game range	Cattle grazing could be manipulated to improve forage conditions on a deer winter range
Julander (1962)	Utah	Effect of cattle overgrazing on mule deer	Overgrazing in the summer caused a nutrient deficiency for mule deer during early spring
Garrison (1953)	Oregon and Washington	Effects of clipping on shrubs	Increase in bitterbrush production
Dasmann (1949)	California	Competition between cattle and mule deer	Direct competition between deer and livestock for bitterbrush and bluegrass

Chapter 3: Changes in behaviour and spatial distribution of bighorn sheep due to cattle presence

Introduction

Of all human activities, farming has the most widespread effects on terrestrial ecosystems in North America (Fleischner 1994). Even though livestock agriculture played an invaluable role in the growth and development of our civilization, we still do not fully understand the extent of its impacts on the environment. The competition between cattle and native ungulates is a common concern (Pickford & Reid 1943) and the effect of grazing remains highly controversial despite many studies (Chaikina and Ruckstuhl 2006). Whereas some authors have suggested that cattle grazing benefits native ungulates (Anderson & Scheninger 1975, Bastian et al. 1991, Vavra & Sheehy 1996), others have claimed that livestock grazing may reduce forage availability and lead to the decline of some ungulate populations (Dunham et al. 2003, Mishra et al. 2004).

The introduction of livestock into a new area can cause a variety of problems, such as introduction of foreign pathogens and parasites (Bengis et al. 2002), increased disease transmission (Woodroffe 1999), decreased forage availability, and range deterioration (DeMarchi 1973, Westenskow-Wall et al. 1994, Clark et al. 2000). Grazing by high density of cattle can alter grassland ecosystems (Fleischner 1994) and negatively affect native ungulates (Jenks and Leslie Jr. 2003, Mishra et al. 2004).

Livestock ranching is an important component of agriculture and, if well managed, can increase winter forage quality and range productivity, allowing for a higher economical yield of the area (Westenskow-Wall et al. 1994, Alpe et al. 1999, Clark et al. 2000, Ganskopp et al. 2006). For example, introduction of a new management plan to a

range in north-eastern Oregon increased population size of both elk and livestock due to an improvement in range conditions (Anderson & Scheninger 1975).

Most previous studies of cattle grazing have focused on the vegetation availability (DeMarchi 1973, Alpe et al. 1999, Clark et al. 2000) and diet overlap between cattle and wildlife (Gallina 1993, Pordomingo and Rucci 2000, Stewart et al. 2003). However, some research also investigated changes in the behaviour of native ungulates resulting from livestock presence, such as avoidance of the areas grazed by cattle (Kie 1996, Coe et al. 2001, 2004). Livestock grazing has been shown to affect habitat use and cause preference for ungrazed sites over grazed sites by mule deer and elk (Knowles and Campbell 1981, Skovlin et al. 1983, Bowyer and Bleich 1984, Loft et al. 1991, Ragotzkie and Bailey 1991, Frisina 1992, Clegg 1994, Stewart et al. 2002). Livestock grazing can also cause native ungulates to change feeding behaviour or increase vigilance when cattle are in the vicinity, as previously observed in elk (Mattiello et al. 2002). On the other hand, Halstead et al. (2002) showed that cattle grazing had relatively little effect on elk choice of foraging areas. Elk and cattle had a large niche overlap, using similar areas and consuming similar foods (Torstenson et al. 2006). The findings of these studies indicate the need for additional research on behavioural changes of native ungulates in the presence of cattle.

The abundance of bighorn sheep in North America has decreased significantly during recent decades as a result of human influence and in part, due to cattle grazing (Krausman 2000). The presence of livestock reduces relocation success of bighorn sheep (Singer et al. 2000). Bissonette and Steinkamp (1996) argued that bighorn sheep avoided cattle and moved towards escape terrain when cattle approached. However, very few

studies of cattle grazing selected bighorn sheep as a study subject and more research is needed to conserve these animals.

In 2005, I began studying the influences of domestic cattle on behaviour of bighorn sheep, which are easily observed and well studied in the Sheep River Provincial Park, Alberta, Canada. Cattle grazing during summer was originally introduced to this area in 1917 (Alberta Community Development 2006). The impacts of this grazing on native ungulates, such as bighorn sheep are still unknown. The sheep numbers in the park have been declining over the years, and the population is facing threats from cougar predation (Ross et al. 1997), pneumonia outbreaks (Festa-Bianchet 1988), and hunting pressures. Forage availability may be a concern and the summer cattle grazing may also induce a response in bighorn sheep and cause changes in their behaviour. The physical presence of cattle can impact native ungulates by creating disturbance and introducing alarming visual and audible stimuli (Matiello et al. 2002). I hypothesized that bighorn sheep will change their behaviour when cattle are present nearby. I predicted that sheep would become more vigilant and graze less near livestock vs. further away. I also expected that bighorn sheep would avoid cattle and I have defined avoidance behaviour as a greater distance between sheep and cattle locations than expected from random association.

Methods

Study site

The study took place in the Sheep River Provincial Park at the foothills of the Rocky Mountains, southwestern Alberta (50°N and 114°W; Figure 1). Altitudes range from 1420m to 1740m (Ruckstuhl and Festa-Bianchet 2001) and the area is represented

mainly by grass and shrubland communities, with some deciduous and coniferous forests. Vegetation varies from native communities dominated by rough fescue (*Festuca scabrella*) to heavily grazed areas dominated by invasive species, such as Kentucky bluegrass (*Poa pratensis*) and timothy (*Phleum pratense*) (Willoughby and Alexander 2006). Glacial terraces, canyons, and foothills characterize the terrain of the study site. Hill slopes stay free of snow for much of the year and provide winter forage for native ungulates (Figure 2). Sheep River Provincial Park is home to bighorn sheep, white-tailed deer, mule deer, elk and moose (*Alces alces*). The park is accessible to public driving from May 15th to December 1st.

The park is leased to cattle farmers who use a grazing-rotation system. Grazing allotments were introduced in the area in 1917 (Alberta Community Development 2006). Currently, between the North and South Sheep allotments, approximately 3400 cow-calf pairs use the park (18522 hectares) from mid-June until mid-October (Alberta Community Development 2006). The park is divided into grazing allotments by fences and cattle gates. Cattle owners often rotate livestock through the park by moving them from one grazing allotment to another. Cattle are introduced into different areas of the park at different times during the grazing period to distribute grazing intensity.

The population of bighorn sheep within the park has been studied extensively since 1987 (Ruckstuhl 1998, Ruckstuhl & Festa-Bianchet 1998, Ruckstuhl and Festa-Bianchet 2001) and reproductive success, age, and survival of the individuals are monitored continuously. According to the field records, the number of sheep declined from 153 in 1985 to about 60 animals in 2006. Bighorn sheep segregate sexually into male and female groups, but both sexes forage in the same areas of the park (Ruckstuhl 1998). Female

groups include females, lambs and young animals. Male and female groups merge during the fall to rut (early November to late December). Females leave their winter range during May to give birth in the mountains and return during late August or September (Ruckstuhl & Festa-Bianchet 1998). Some males and females leave the park during the rut to find mating opportunities elsewhere. All sheep are marked with ear tags, and some are equipped with GPS collars to monitor locations and habitat use. The animals are habituated to people and easily observable.

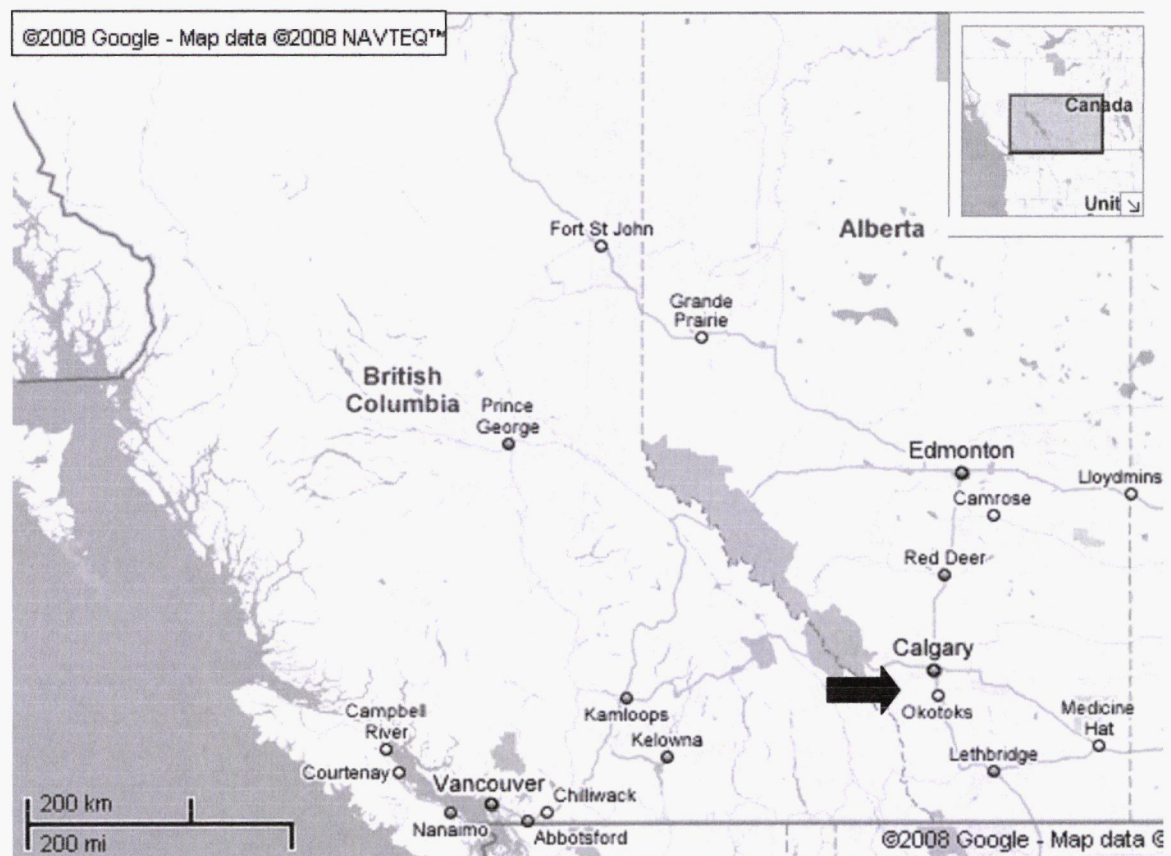


Figure 1. Location of the study site. Sheep River Provincial Park (marked by an arrow) is found east of the Rocky Mountains and southwest of Calgary, Alberta. Map was created using Google Map data @2008 NAVTEQ™.



Figure 2. Female bighorn sheep and lambs foraging on the snow-free hill slopes during the winter. Note the erosion caused by the movement of cattle during the previous summer. Photo courtesy of D. Brown.

Behavioural changes

I investigated changes in vigilance and bite rates of bighorn sheep to evaluate the effect of cattle presence. Observations were collected when cattle were either present or absent. Presence of cattle was defined as a group of at least 10 cattle within a 500-meter radius in a visible and audible (to humans) range of the sheep. The 500-meter distance allowed me to observe both sheep and cattle at the same time without being restricted by topographical features. Absence of cattle was defined when no cattle were present in the visible and audible (to humans) range of the bighorn sheep.

Observations were made from 08:00 until 21:00 from May to September 2006. Male and female sheep of all ages present in the park were observed using binoculars (Leica 10x40) and a spotting scope (Bushnell Spacemaster 60x10-45). Because the same researchers were present during observations of sheep with cattle present or absent, the impact of researchers' presence was assumed not to influence the results. Date, time of the day, animal ID, temperature and location of the sheep were recorded. I followed the methods from Ruckstuhl et al. (2003) for the vigilance and bite rates counts. Ten 1-min focal observations were made on vigilance and bite rates for each individual sheep throughout the day when the sheep were grazing. Vigilant posture occurred when a sheep stopped grazing and raised its head above its shoulders. A bite was defined as the vegetation intake with the mouth followed by a quick upward motion of the jaw. Vigilance and bite rates were recorded only when an animal was grazing. If an individual stopped grazing for longer than 30 s during the 1-min interval the observation was discarded. The observations continued once the animal resumed grazing for longer than 1 min. Bite rates and vigilance were recorded for each animal only once for each treatment.

Spatial avoidance

The avoidance behaviour of cattle by bighorn sheep can be tested in two ways: with and without accounting for the time component. The first method combines all of the animal locations during an entire time and assesses whether animals were found together less often than they were apart (Millspaugh et al. 1998). This method has been used to measure avoidance of human development by caribou (Dyer et al. 2001) and avoidance of roads by grizzly bears (Waller and Servheen 2005). Instead, I used a temporal test that measures the independence of animal locations through time (Minta 1992, DeCesare and Pletscher 2005). This test has been used to evaluate elk avoidance towards wolves (Fortin et al. 2005) and avoidance among cattle, elk and mule deer (Stewart et al. 2002). In our case spatial avoidance of bighorn sheep towards cattle was measured using the modified nearest-neighbour test (DeCesare and Pletscher 2005). This test assesses whether distances between simultaneous locations of a pair of animals are greater than the distances expected if animal locations were independent of each other (random).

To test avoidance, 9 GPS collars were used on selected cows from each of the 5 cattle groups and 5 GPS collars were fitted to female bighorn sheep in the park during the grazing season of 2006. GPS collars were programmed to emit a signal every hour and were equipped with an activity sensor that allowed monitoring of the animal's activity.

Most female bighorn sheep left the park prior to arrival of the cattle (early June) and moved into the mountains for lambing. After lambing, ewes moved from the mountains to the park and back several times during the summer (late June, late July, August-October). Only locations of sheep and cows inside the park (from 50.6243 to 50.6727 and from -114.5117 to -114.6790) were considered for analysis.

Information from 45 cow-sheep pairs (5 ewes \times 9 cows) was used to calculate a distribution of distances between simultaneous locations (further referred to as simultaneous distances) using Hawth's Spatial Analysis Tools (Beyer 2004) in ArcView 9.2 (ESRI 2004). Because GPS collars signalled every hour at approximately the same time, I defined simultaneous locations as locations of ewes and cows acquired within a 10-min interval. This interval allowed us to include locations from the GPS collars that were received a few minutes earlier or a few minutes later. A total of 14,607 simultaneous distances were calculated for 45 sheep-cow pairs for the entire period.

In addition to the GPS collar data collection, daily census of all the sheep in the park was performed and IDs, age, and sex of the sheep were recorded. Locations of the sheep were determined using hand-held GPS receiver (Garmin Legend C). This data for mid July-mid October period was collected on 76 sheep. As bighorn sheep often formed cohesive groups that moved together, I considered six sheep groups for the analysis to avoid pseudoreplication. A total of 54 cow-sheep group pairs were constructed and 562 simultaneous distances were calculated.

The distribution of distances between random locations of each sheep (or sheep group) and cow were also calculated. Locations of sheep were paired with locations of cows randomly with respect to time. I created pairs of random locations and used Hawth's Spatial Analysis Tools to calculate distances between these pairs (further referred to as random distances). I calculated 14,607 random distances from the ewe GPS collars and 562 random distances from census information.

The nearest-neighbour cow (GPS collared cow with the shortest average distance to the sheep) was identified for each sheep (sheep group). A total of 5 nearest-neighbour

pairs from GPS collar data and 6 nearest-neighbour pairs from census data were used to see whether simultaneous distances were greater than random distances, which would indicate avoidance behaviour.

Sometimes non-independence of spatial locations can result from normal daily movement patterns of the animals. For example, if both cattle and sheep move closer to the water during the day and further away at night, the locations of sheep and cows would appear to be closer together than expected from random distribution. In order to account for these patterns, I used information from GPS collars to calculate hourly average distances to the nearest body of water and average elevation for all collared sheep and cows during entire time period.

Statistical analysis

Bite rates and vigilance

SAS version 6 (1989) software was used to analyse the results and test data for normality and homoscedasticity. Means and standard errors (SE) of bite rates and vigilant frequency were calculated for each sex. I then carried out a repeated-measures mixed-model procedure to test for the effects of the cattle presence, sex of the sheep, interaction between the two, and time of day on the bite rates and vigilant rates of the sheep.

Avoidance behaviour

The average and minimum simultaneous/random distances for each sheep and cow pair were calculated for the entire period (15 June- 14 October). I compared the simultaneous and random distances between nearest neighbours (cow-sheep pairs with the shortest average distance) for each sheep (sheep group) using paired-sample t-tests.

To account for the daily movement patterns, I used General Linear Model that tested the effects of time of day (hour) and animal type (cow or sheep) on the average elevation and average distance to the nearest body of water.

Results

A total of 63 observations were made for bite rates and 62 observations for vigilance behaviour. Twelve female sheep were observed without cattle and 12 were observed with cattle, whereas 22 males were observed without cattle and 17 males were observed with cattle. The presence of cattle significantly decreased bite rates of the sheep ($F_{1, 19.2}=28.14$, $P<0.001$; Figure 3). Bite rates did not differ significantly between sexes of the sheep ($F_{1, 34.2}=0.01$, $P=0.928$) or time of day ($F_{1, 23.4}=0.52$, $P=0.479$). Presence of cattle significantly increased the number of vigilance postures per minute in sheep ($F_{1, 30.1}=4.81$, $P=0.036$; Figure 4). On average, males were less vigilant than females ($F_{1, 35.6}=13.87$, $P=0.001$) and vigilance did not differ significantly with the time of day ($F_{1, 39.8}=1.37$, $P=0.249$).

The average distance between sheep (or sheep group) and the nearest collared cow for the entire period was 2,125 m (calculated from sheep GPS collars) and 2,156 m (calculated from the sheep censuses). The minimum distance from the sheep (sheep group) to the nearest collared cow was 679 m (calculated from sheep GPS collars) and 694 m (calculated from sheep censuses).

The average simultaneous and random distances differed significantly for nearest neighbours (GPS collars: $t_4=3.739$, $P=0.020$; Census: $t_5=3.099$, $P=0.027$), however, in both cases average simultaneous distances were not greater than average random

distances (Figure 5 & Figure 6). Minimum random and simultaneous distances did not differ significantly between nearest neighbours (GPS collars: $t_4=1.668$, $P=0.171$; Census: $t_5=0.431$, $P=0.685$). The average elevation and average distance to the nearest body of water varied significantly with animal type (Elevation: $F_1=1756.89$, $P<0.001$; Distance to water: $F_1=29.30$, $P<0.001$), but not with the time of day (Elevation: $F_{18}=1.71$, $P=0.132$; Distance to water: $F_{18}=1.00$, $P=0.503$, Table II).

Table II. The average elevation and average distance to the nearest body of water for GPS-collared bighorn sheep and cows during the summer of 2006.

Hour	Sheep		Cows	
	Distance to Water (m)	Elevation (m)	Distance to Water (m)	Elevation (m)
0	167	1528.3		1482.5
1	200	1526.6	27	1484.8
2	111	1530.5	14	1485.2
3	83	1526.2	41	1488.9
4	91	1526.5	18	1487.6
5	36	1527.2	10	1489.1
11	46	1523.1	47	1485.9
12	26	1528.2	64	1492.7
13	34	1527.5	75	1493.6
14	102	1530.7	33	1488.9
15	139	1533.3	23	1490.9
16	149	1533.8	29	1492.9
17	167	1534.7	81	1494.4
18	174	1530	78	1491.4
19	143	1530.2	48	1490.7
20	156	1535.1	10	1491.3
21	137	1532.7	42	1483.9
22	108	1532	10	1483.5
23	122	1531.1	53	1484.2

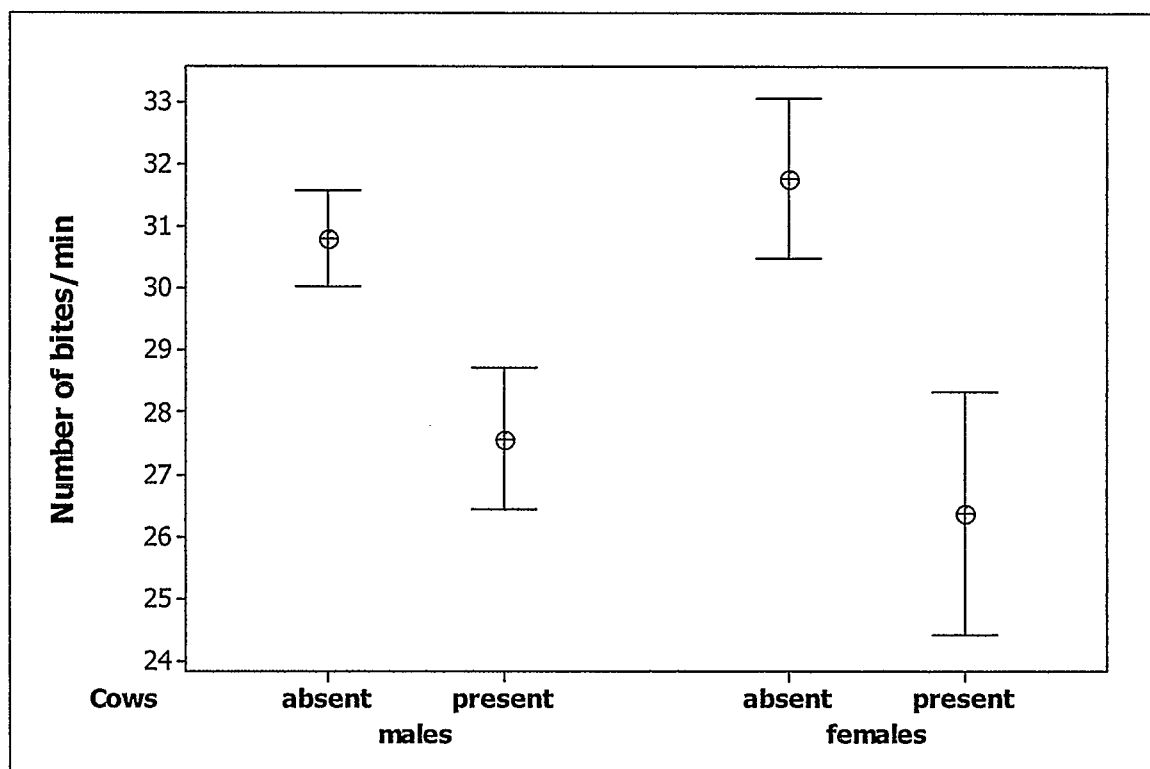


Figure 3. Effect of cattle absence or presence on the average (\pm SE) number of bites per min by male and female bighorn sheep in Sheep River Provincial Park from May to September 2006. Presence of cattle was defined as a herd of at least 10 cows and/or calves present within 500 m in a visible and audible (to humans) range of the sheep.

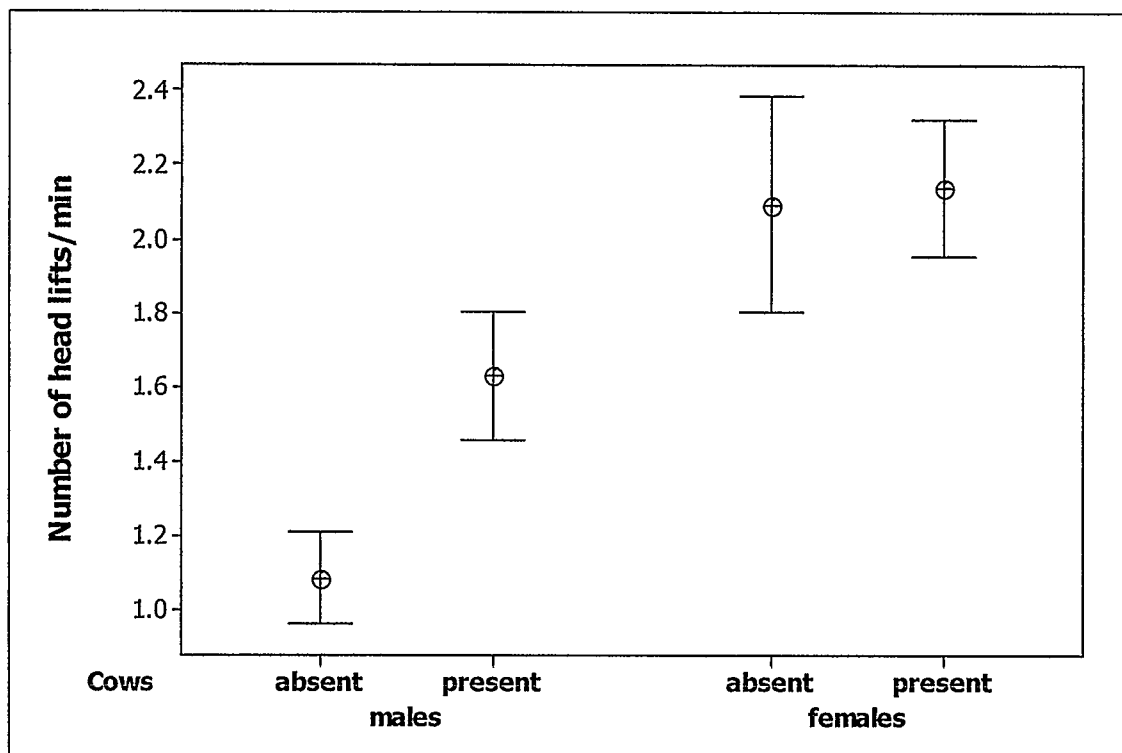


Figure 4. Effect of cattle absence or presence on average (SE) number of head lifts per min by male and female bighorn sheep in the Sheep River Provincial Park from May to September 2006. Presence of cattle was defined as a herd of at least 10 cows and/or calves present within 500 m in a visible and audible (to humans) range of the sheep.

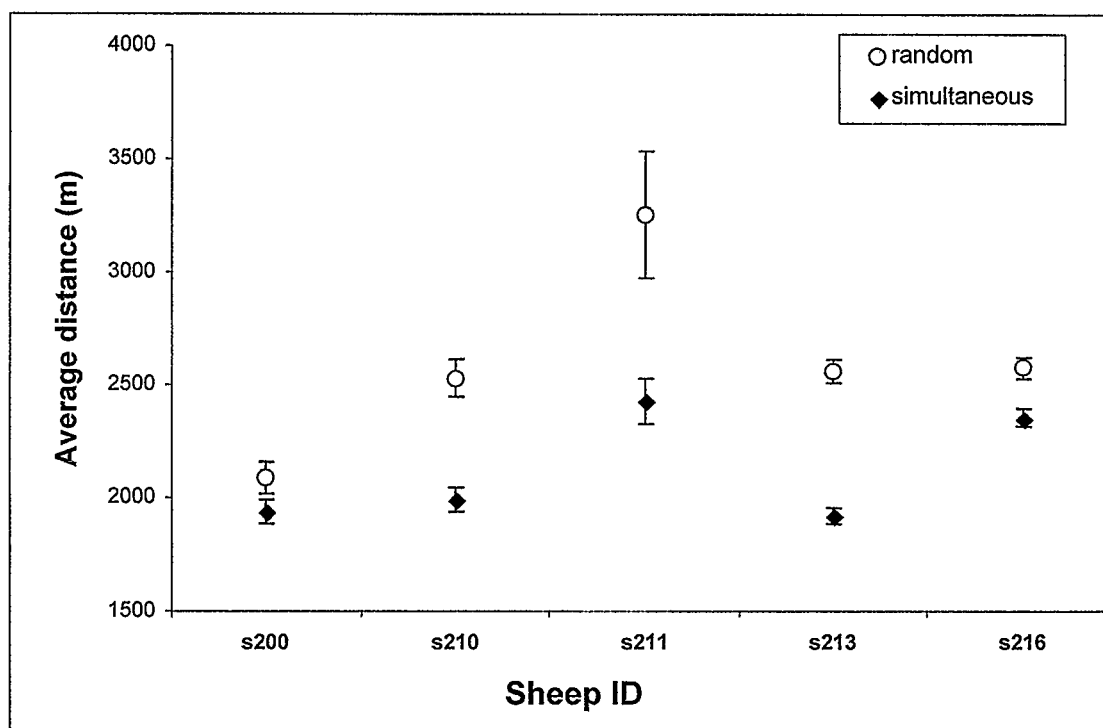


Figure 5. Average (\pm SE) random and simultaneous distances between nearest-neighbour bighorn sheep and cows for each of the five GPS-collared ewes during 15 June- 14 October. Calculated from location of 5 sheep and 9 cows obtained from GPS collars.

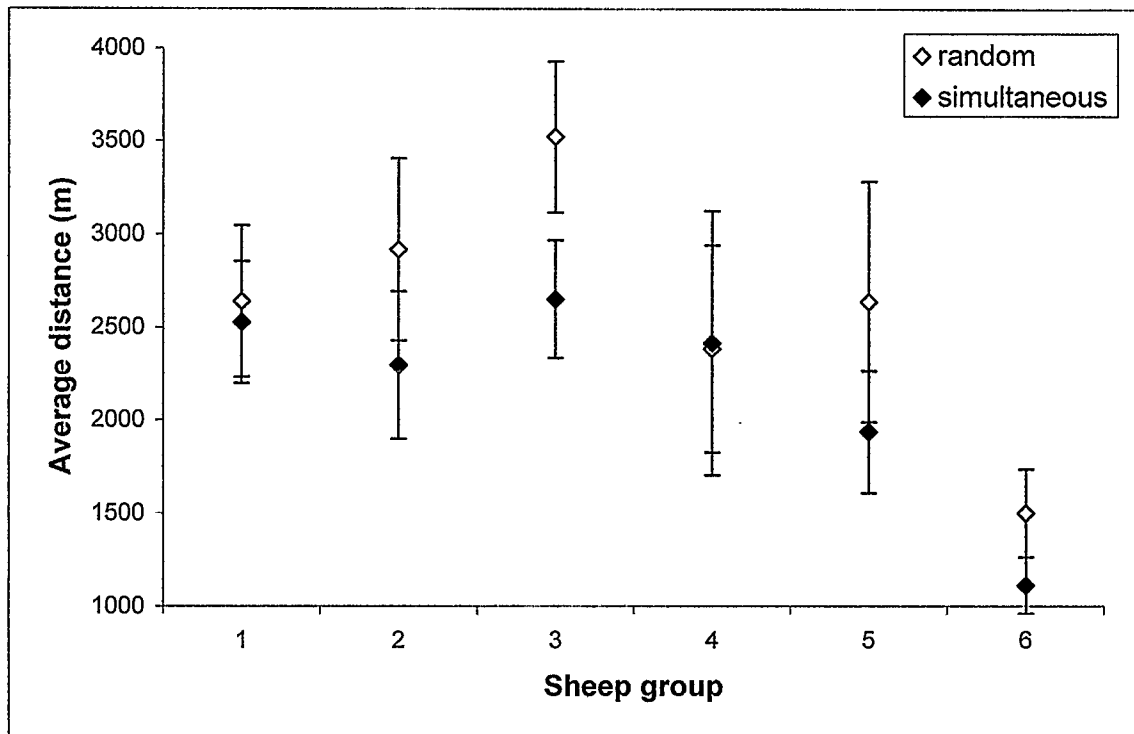


Figure 6. Average (\pm SE) random and simultaneous distances between nearest-neighbour bighorn sheep groups and cows for all sheep during 15 June- 14 October in the Sheep River Provincial Park, south-western Alberta. Calculated from census data on 6 sheep groups and information from 9 cows with GPS collars.

Discussion

The presence of cattle was associated with decreased bite rates and increased vigilance of bighorn sheep. These results support the hypothesis that the presence of livestock causes behavioural changes in some native ungulates. Females were more vigilant than males, which matched the results of Ruckstuhl et al. (2003) study on the same population. There is a trade-off between vigilance and bite rates, because sheep cannot forage and look around simultaneously (Ruckstuhl et al. 2003). Not only did the sheep increase the number of vigilant postures in the presence of cattle, but they also appeared to maintain alert postures longer. Future studies should investigate the duration of vigilant postures, as well as their frequencies. Overall, my results indicated that bighorn sheep might perceive cattle as a potential threat, similar to the results from Bissonette and Steinkamp (1996), who demonstrated that sheep moved closer to escape terrain when cattle approached. A study by Kie (1996) also showed that cattle grazing altered activity budgets of female mule deer, as deer rested less and fed more in the areas with heavy cattle grazing. Mattiello et al. (2002) found that elk spent less time resting and feeding and more time being vigilant with cattle nearby.

In addition to the changes in behaviour, my results showed that cattle and sheep were not located independently from one another. Interestingly, the average simultaneous distances were shorter than random distances, which suggested that cattle and bighorn sheep were not avoiding each other, but instead used similar locations at the same time. Some previous studies indicated a similar trend, although they did not use simultaneous locations for the analysis. Mattiello et al. (2002) showed that even though elk altered their behaviour in the presence of livestock, they spent more time foraging in the areas

previously grazed by cattle. Willms et al. (1979) also suggested that in spring deer preferred pastures that were cattle-grazed in the previous fall.

Minimal distances (shortest distances between sheep and cows) in our study were not statistically affected by the presence of cows. Thus, sheep appeared to neither avoid nor prefer cattle during closer encounters. On a few occasions when cattle and sheep came into close contact, I observed that the cattle always approached the sheep. If sheep were bedded prior to contact, they would get up and move away when the cows moved closer. No chasing or aggressive interactions were observed.

The results indicate that sheep were attracted to the general areas used by cattle, but not to the cattle themselves. This non-independence could possibly be explained by the similarity in the daily movement patterns of sheep and cattle, if both species use lowland areas or move closer to the water during same time of day. However, when I looked at the daily patterns of cattle and sheep locations, I found that average elevation and distance to water did not change significantly with time of day for either sheep or cows, but did differ between the species. Therefore, similarity in daily movements could not be used as an explanation for non-independence of animal locations.

Another reason for the apparent attraction may be that the vegetation quality was higher in the cattle-grazed areas (Ganskopp et al. 2006, Casasús et al. 2007) due to the decreased forage maturation caused by grazing (Fryxell 1991). The sheep may have faced a trade-off between avoiding contact with cattle and better foraging opportunities. Female Dall's sheep (*Ovis dalli*) have been shown to select areas of lower predation risk (closer to escape terrain) during years of high forage availability, and areas with more vegetation during the years of low forage availability (Rachlow and Bowyer 1998).

Further studies should investigate whether sheep group size and the presence of cattle have interactive effects, as Frid (1997) argued that factors such as sheep group size and distance to escape terrain interact to influence vigilance of Dall's sheep. Future research could also look at whether the size of the cattle group has an effect on sheep behaviour.

Our findings present some cause for concern, especially for female bighorn sheep. Lactating females have higher bite rates than non-lactating females (Ruckstuhl and Festa-Bianchet 1998) and males (Ruckstuhl et al. 2003), because they have higher energetic demands. Females are also more vigilant than males, perhaps out of concern for the safety of their lambs (Ruckstuhl et al. 2003). When cattle were present, females decreased their bite rates due to an increase in vigilance. This trade-off may place energetic constraints on females, as they require higher food intake and are more affected by the cattle than males.

The results indicate that presence of livestock has an effect on foraging behaviour of bighorn sheep, but does not result in avoidance behaviour. It is possible that the higher forage quality in the grazed areas compensated for the reduced bite rates in bighorn sheep.

Chapter 4: Effects of cattle grazing on vegetation and ungulate use of the exclosures and grazed plots

Introduction

The introduction of cattle can have a major influence on grassland communities affecting both producers and consumers (Dunham et al. 2003, Jenks and Leslie Jr. 2003, Casasús et al. 2007), yet little is known to fully evaluate the extent of these impacts. Competition between ungulates and domestic cattle remains an important concern (Vavra et al. 1999). Despite considerable research on this topic, the results are mostly inconclusive or controversial (Chaikina and Ruckstuhl 2006).

It remains unclear whether the interactions between livestock and wildlife are mainly competitive or facilitative. On the one hand, negative impacts of cattle grazing on native ungulates are well recorded (Dunham et al. 2003, Jenks and Leslie Jr. 2003, Mishra et al. 2004). Some diet overlap was reported between cattle and elk (Mackie 1978), as well as between cattle and white-tailed deer (Ortega et al. 1997). White-tailed deer altered their winter diets on sites that were continuously grazed by cattle by selecting more herbs and less browse (Thill and Martin 1986). Native ungulates have consistently been reported to prefer ungrazed or rested areas within rest-rotation systems (Ragotzkie and Bailey 1991, Yeo et al. 1993, Clegg 1994, Coe et al. 2001, Coe et al. 2004). Intensive grazing reduced vegetation biomass (Rhodes and Sharrow 1990) and decreased hiding cover for mule deer (Loft et al. 1987). Exclusion of cattle from an area decreased bare ground (Dobkin et al. 1998, Hoover et al. 2001) and increased vegetation biomass and litter layer (Casasús et al. 2007). Furthermore, Yeo (2005) reported that even with increased cattle management, health of sagebrush communities was still negatively

affected by grazing.

On the other hand, previous research has shown that moderate cattle grazing can benefit native ungulates (Anderson & Scheninger 1975; Bastian et al. 1991; Vavra & Sheehy 1996). Holechek et al. (2006) postulated that light to moderate grazing could improve vegetation survival and productivity under arid conditions. Light and heavy grazing reduced vegetation biomass in the fall, but elevated crude protein content and digestibility in fall and winter (Ganskopp et al. 2006). Clark et al. (2000) reported that grazing by domestic sheep during late spring increased protein content of bluebunch wheatgrass (*Agropyron spicatum*) and improved winter forage for elk. Casasús et al. (2007) also showed that moderate cattle grazing elevated protein content of forage. However, the increase in vegetation quality and nitrogen content was temporary and was lost during winter due to vegetation senescence (Wambolt et al. 1997). The degree of competition between cattle and native ungulates consequently varies throughout the year. Early summer grazing minimally reduced foraging efficiency of mule deer and elk (Damiran et al. 2003). Alternatively, Thill and Martin Jr. (1989) showed that cattle grazing during late fall decreased availability of deer forage, whereas moderate summer grazing did not have this effect. Good management plans can successfully increase both cattle production and ungulate density (Anderson and Scheninger 1975, Smith et al. 1979, Bastian et al. 1991, Vavra & Sheehy 1996), as well as reduce damage to range during drought (Holechek and Galt 2004). Because the effects of cattle grazing on native ungulates vary throughout the year, it is important to study changes in vegetation and ungulate range use on a month-to-month basis.

I investigated seasonal differences in vegetation quality, mainly crude protein and

acid detergent fibre (ADF), and biomass inside cattle exclosures and corresponding grazed plots. I also assessed changes in habitat use by bighorn sheep and other native ungulates in response to cattle grazing. Based on published research, I hypothesized that livestock would reduce vegetation quantity and increase vegetation quality. If the current grazing intensity in my study area (Sheep River Provincial Park, Alberta, Canada) is detrimental to native ungulates, the decrease in forage availability should cause native ungulates to prefer exclosures over the grazed areas. However, cattle grazing may temporally improve vegetation quality by increasing protein concentration and decreasing ADF concentration (lower ADF is an indicator of higher digestibility). The increase in forage quality would cause wildlife to preferentially select the grazed areas. This effect may be lost in the winter, when forage availability is limited and vegetation quality decreases due to senescence. I also predicted that the total crude protein and digestible energy of forage would be higher inside exclosures due to the higher vegetation biomass. Additionally, I compared my results to the vegetation samples previously collected from the same areas in 1994-95. As the stocking rates have decreased in the South Sheep Allotment Area (Dr. Gates, personal communication) from 5176.07 cow-calf pairs in 1994 to 4458.37 cow-calf pairs in 2006, I expected to see an increase in forage biomass, decrease in the proportion of live vegetation and change in proportion of live forbs, as indicated by previous research (Clark et al. 2000, Ganskopp et al. 2006). The effects of cattle grazing on the proportions of forbs vs. grasses are unclear. Dobkin et al. (1998) reported less and Loeser et al. (2005) reported more forb cover on the grazed vs. ungrazed areas, whereas Popolizio et al. (1994) found little difference in the forb density resulting from cattle grazing. The direction of change may depend on grazing intensity,

with moderate grazing removing enough competition from graminoids and increasing diversity (Hart 2001), and intense grazing decreasing forb density and allowing only the strongest competitors to thrive.

Methods

Study site

This study was conducted in Sheep River Provincial Park located near the Rocky Mountains in south-western Alberta (50°N and 114°W). The 18500 area is grazed by approximately 3400 cow-calf pairs from Mid-June to mid-October (Alberta Community Development 2006). The park was first subdivided into grazing allotments in 1917, which are currently leased to grazing (Alberta Community Development 2006). Different sections of the park are separated by fences and cattle gates. Ranchers practice grazing rotation to homogenize grazing throughout the park, and cattle herds are moved between allotments several times during the grazing season (May-October).

The terrain is characterized by hills, canyons and flat meadows. Due to mild weather and strong winds, ungulates have snow-free forage access on hill slopes during most of the winter. Vegetation varies from grass and shrubland communities to aspen and coniferous forests. Some sections of the park are dominated by native vegetation, such as rough fescue (*Festuca scabrella*), whereas others are overtaken by invasive species, such as kentucky bluegrass (*Poa pratensis*) and timothy (*Phleum pratense*). Altitude varies from 1420m to 1740m (Ruckstuhl and Festa-Bianchet 2001). The park is closed to vehicle access from 1st of December to 15th of May to protect native populations of elk, moose, bighorn sheep, mule deer, and white-tailed deer.

Exclosures

Exclosures are commonly used to study the effects of grazing on the vegetation (Sarr 2002). In May 2005, 24 35m×35m exclosures and 24 corresponding grazed plots of the same size were established in the Sheep River Provincial Park. Exclosures were located in areas used by both cattle and native ungulates. Eleven exclosures were placed on flat open meadows, 11 on open hill slopes and 2 in forested areas. Location of exclosures within a selected area was chosen randomly. Grazed plots were randomly positioned 35 m from the exclosures and clearly marked with wooden painted pegs. Each exclosure and grazed plot was assigned a unique Plot ID. Exclosures consisted of a 3-strand barbed wire fence with fence posts 3.5 meters apart. The timing of opening and closing of the fences (performed by taking down the barbed wire) controlled the timing and amount of cattle grazing inside the exclosures. I assigned exclosures into three grazing applications as follows: “no grazing” exclosures were closed to cattle for the entire grazing season, “summer” exclosures were open from June to mid August and closed from August to October and “fall” exclosures were closed from June to mid August and open between August and October. The numbers of exclosures assigned to these treatments differed between the years as follows: “no grazing,” 2005 n=13, 2006 n=15; “summer grazing,” 2005 n=6, 2006 n=9; “fall grazing,” 2005 n=5, 2006 n=0. At the end of each grazing season (October) when cattle were removed, all exclosures were opened to allow free access of native ungulates via removal of barbed wire, although the fence posts remained in place.

Vegetation

The summer of 2005 was unusually wet and resulted in greater vegetation growth in the park (total precipitation 566 mm during May-July compared to a 5-year average of 285 mm; Environment Canada 2007). In contrast, the summer of 2006 involved a moderate rainfall, which resulted in lower production of vegetation (237 mm during May-July; Environment Canada 2007).

I assessed plant biomass and quality through bi-monthly vegetation clippings during the spring and summer (April to August) and monthly clippings during fall and winter (September to March), whenever the range was free of snow. Three subplots (25cm×25cm) were randomly chosen for each exclosure and grazed plot and all vegetation was clipped at ground level. Samples were stored in paper bags, dried at 20 °C for 24 h and weighed. I then sorted selected samples into senescent and live vegetation, as well as into grasses and forbs and ground selected samples to 1 mm with a vegetation grinder (Figure 7). Bodycote Northwest Labs (Lethbridge, Alberta) analyzed dry matter for crude protein and acid detergent fibre (ADF). Prior to analysis, 5 samples were chosen randomly and divided in half to test the error in precision of lab analysis.

Crude protein is good indicator of digestible protein (Van Soest 1994) and is calculated as 6.25 times the percentage of total nitrogen. Crude protein concentration was analyzed via the Leco combustion method (reference number 990.03 in AOAC® Official Methods of Analysis, AOAC International 2003). The vegetation samples were combusted in oxygen inside a Leco FP-528 combustion analyzer and nitrogen was released as a gas. Emitted gases were collected and homogenized. A gas sample was then

passed through a detector, which measured gas thermal conductivity, used to calculate nitrogen concentration. I have also calculated total crude protein as crude protein concentration \times biomass of the sample.

Acid Detergent Fibre is the amount of cellulose and lignin in the plant cell walls, which take the longest time to digest; so elevated ADF corresponds to decreased net energy. ADF concentration was analyzed using the reflux method (reference number 973.18 in AOAC® Official Methods of Analysis, AOAC International 2003). Vegetation samples were boiled in sulphuric acid detergent solution to separate insoluble ADF from soluble vegetation components. The residue remaining after extraction was dried at 100 °C and weighed. The ADF concentration was then calculated as $100\% \times (\text{residue mass} / \text{sample mass})$.

Digestible energy content of the dry sample was estimated using crude protein and fibre concentration as $DE = (1.91 - (0.05 \times ADF)) + (0.0151 \times CP) + (0.00051 \times ADF \times ADF)$. Total digestible energy was calculated as digestible energy content \times biomass of the sample.

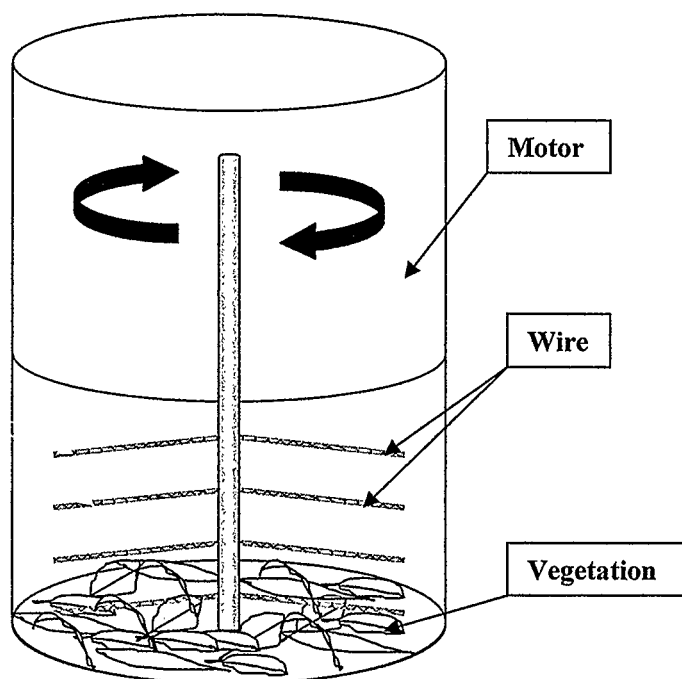


Figure 7. Vegetation grinder built and used to prepare vegetation samples for laboratory analysis. The motor from a household blender was connected to the metal rod with steel wires attached.

A total of 1578 vegetation samples were collected during the first year of the study and 834 samples were collected during the second year. I used 458 samples from the first year and 405 samples from the second year to measure the mass of live vegetation and forbs. A total of 750 samples in the first year and 420 samples in the second year were used for ADF and crude protein analyses.

Data were analysed separately for the two years because the assignment of grazing applications (summer, fall and no grazing) differed from one year to the other. The first year (2005-2006) was divided into 5 seasons: pre-grazing (May 2005-mid June 2005), summer (mid June 2005-mid August 2005), fall (mid August 2005-mid October 2005), winter (mid October 2005-March 2006), and spring (April 2006-mid June 2006). The spring season was analyzed as a part of the first year to assess the effects of the previous summer's grazing on the vegetation during the following spring. Consequently, the second year (2006) was divided into three seasons: summer (mid June 2006-mid August 2006), fall (mid August 2006-mid October 2006), and winter (mid October 2006-December 2006).

Not all areas in the park were grazed equally, as cattle spent more time in the meadows and less time on the hill slopes. To control for this difference, I performed weekly visual estimates of grazing intensity in areas with experimental plots. Grazing intensity during the previous week was scored from 1 to 4 (1 = no grazing signs, 2 = some trampling and grazing signs, but little vegetation removed, 3 = medium grazing with vegetation removed down to 5-10 cm, 4 = extensive grazing, with vegetation height below 5 cm). At the end of the grazing season (October) I estimated the average grazing intensity as either high (average score between 3 and 4) or light (average score between 1

and 2). Most of the exclosures and grazed plots in the hayfields and meadows were located in the highly grazed areas, whereas hill slopes and forests were lightly grazed.

Additionally, to evaluate long-term effects of grazing on vegetation, I used samples previously collected from eight locations during the springs and summers of 1994 and 1995 using same techniques. Biomass, proportion of live vegetation, and proportion of forbs in these samples were compared to the samples collected from the same locations during the springs and summers of 2005 and 2006.

Animal use of the exclosures

All fences were removed at the end of each cattle grazing period (October), so native ungulates had free access to all exclosures during winter and spring. During the summer ungulates could access exclosures because, unlike cattle, they could easily jump the fences (Figure 8). The native ungulates' use of exclosures and grazed plots was evaluated by performing year-round weekly observations of exclosures and grazed plots. During these observations I recorded the presence of all sighted native ungulates inside the exclosures and grazed plots and their activity at that time (grazing, lying, etc).

During the winter and spring of 2006, I performed monthly fecal pellet-group counts of all exclosures and grazed plots. Fecal transects were run from one side to the other side of the exclosures and grazed plots. Transect direction was determined randomly; however all exclosures and plots were sampled in a same way during one sampling period. Fecal groups within 1 m on either side of a transect were identified to the species and counted. Only fecal groups of native ungulates were sampled. Care was taken to count only fresh fecal groups to avoid repeated counts.

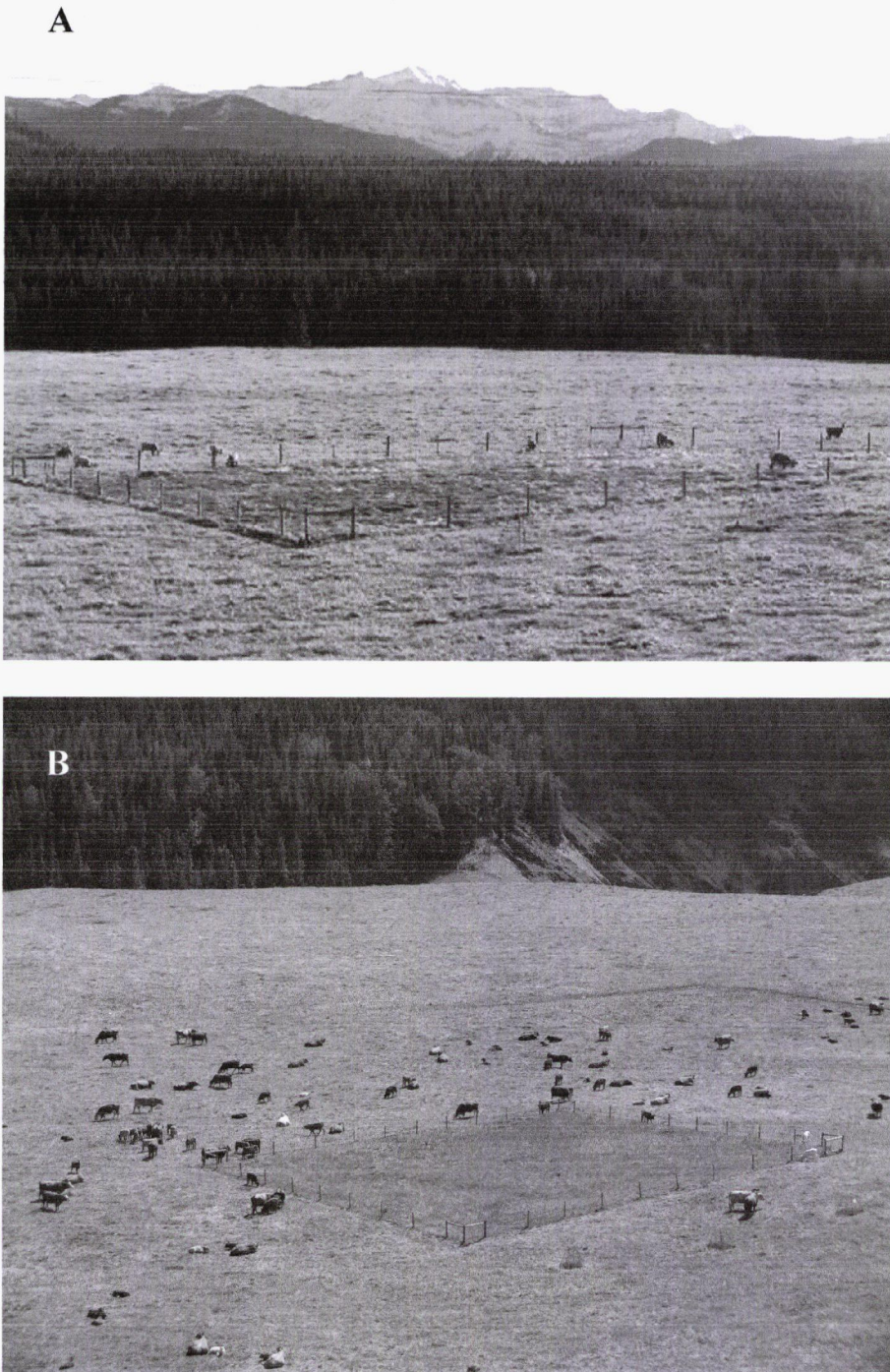


Figure 8. Cattle exclosure on the flat meadow with a) some bighorn sheep grazing inside and b) cattle grazing around the exclosure. Note the difference in vegetation inside and outside of the exclosure. Photos courtesy of G. Pelchat and K. Ruckstuhl.

Statistical analysis

Vegetation

SAS version 6 (1989) software was used to perform repeated-measures mixed-model analysis and Minitab version 14 (2003) software was used for all of the other statistical tests. Precision of lab analysis was tested with paired-sample t-tests that compared ADF and crude protein between split samples.

The averages of biomass, crude protein concentration and total crude protein, ADF, total digestible energy, mass of forbs and mass of live vegetation from the three vegetation samples from each enclosure and grazed plot were calculated and used for analysis. I analysed the pooled data from all three grazing applications (no grazing, summer and fall). Biomass was log-transformed to meet the assumptions of normality and homoscedasticity. Effects of grazing application, treatment (exclosure or grazed plot), season, date, and interactions of these factors on the biomass were analyzed using repeated-measures mixed-model procedure. A mixed-model was also used to test the effect of grazing intensity (high/light), grazing application (summer, fall, no grazing), treatment, date, and interactions of these factors on the proportion of acid detergent fibre (ADF), crude protein concentration, total crude protein and total digestible energy. Additionally, I analyzed the effects of grazing intensity (high/light), grazing application, treatment, date, sample mass, and interactions of these factors on the masses of live vegetation and of forbs. Whenever significant interactions were found, I used contrasts tests to further investigate specific effects. Linear regression analysis was performed to compare the proportions of forbs and grasses to ADF and crude protein concentration. To analyze the long-term impact of grazing, I used a repeated-measures mixed-model to test

for the effects of year and month on the biomass, proportion of live vegetation, and proportion of forbs.

Fecal data

Fecal count data were separated into two periods: February-May 2006 (4 repetitions) and December 2006 (3 repetitions). Average counts for each period and each exclosure were taken for sheep and elk. As there were only 6 sightings of moose fecal groups and one deer group, they were not considered for analysis. The average fecal group count was ln-transformed used to meet the assumptions of normality and homoscedasticity. I used a General Linear Model (GLM) to test for the effects of period, grazing application (summer, fall, no grazing), animal species (elk or sheep), plot ID (unique name assigned to each exclosure and grazed plot), and treatment type (exclosure or grazed plot) on the average number of fecal groups found per transect.

Ungulate use of exclosures and grazed plots

The average number of animal groups during two years in each exclosure and grazed plot was calculated. Because assumptions of normality could not be met, I used the non-parametric Wilcoxon Matched-Pairs Signed-Ranks test to test for the differences in animal counts between exclosures and grazed plots. A goodness of fit chi-square test was performed to investigate whether the animals grazed more often in the exclosures than in the grazed plots.

Results

Vegetation

Quality assurance tests of five samples showed that lab results differed by 0.62%

for ADF analysis and by 1.00% for crude protein analysis. The results from split bags did not differ statistically for either ADF ($t_4=0.054$, $P=0.960$) or crude protein ($t_4=0.074$, $P=0.945$). During the first year, grazing application ($F_{2, 43.9}=2.52$, $P=0.092$) and treatment ($F_{1, 43.8}=3.80$, $P=0.058$) had almost significant effects on the vegetation biomass. Biomass varied significantly among dates ($F_{7, 412}=4.98$, $P<0.0001$) and seasons ($F_{4, 412}=28.44$, $P<0.0001$) and treatment effects varied among seasons (Interaction: $F_{4, 412}=5.43$, $P<0.001$). The posteriori contrasts indicated significantly higher biomass in exclosures than grazed plots during the winter only ($F_{1, 68.9}=10.40$, $P=0.002$; Figure 9a). During the second year, biomass varied similarly among seasons ($F_{2, 211}=19.51$, $P<0.0001$; Figure 9b) and exclosures had higher biomass than grazed plots ($F_{1, 45.4}=12.12$, $P=0.001$). Higher biomass was found in the “no grazing” plots than in “summer” plots ($F_{1, 45.4}=7.42$, $P=0.009$; Figure 9). No significant interactions between factors were observed.

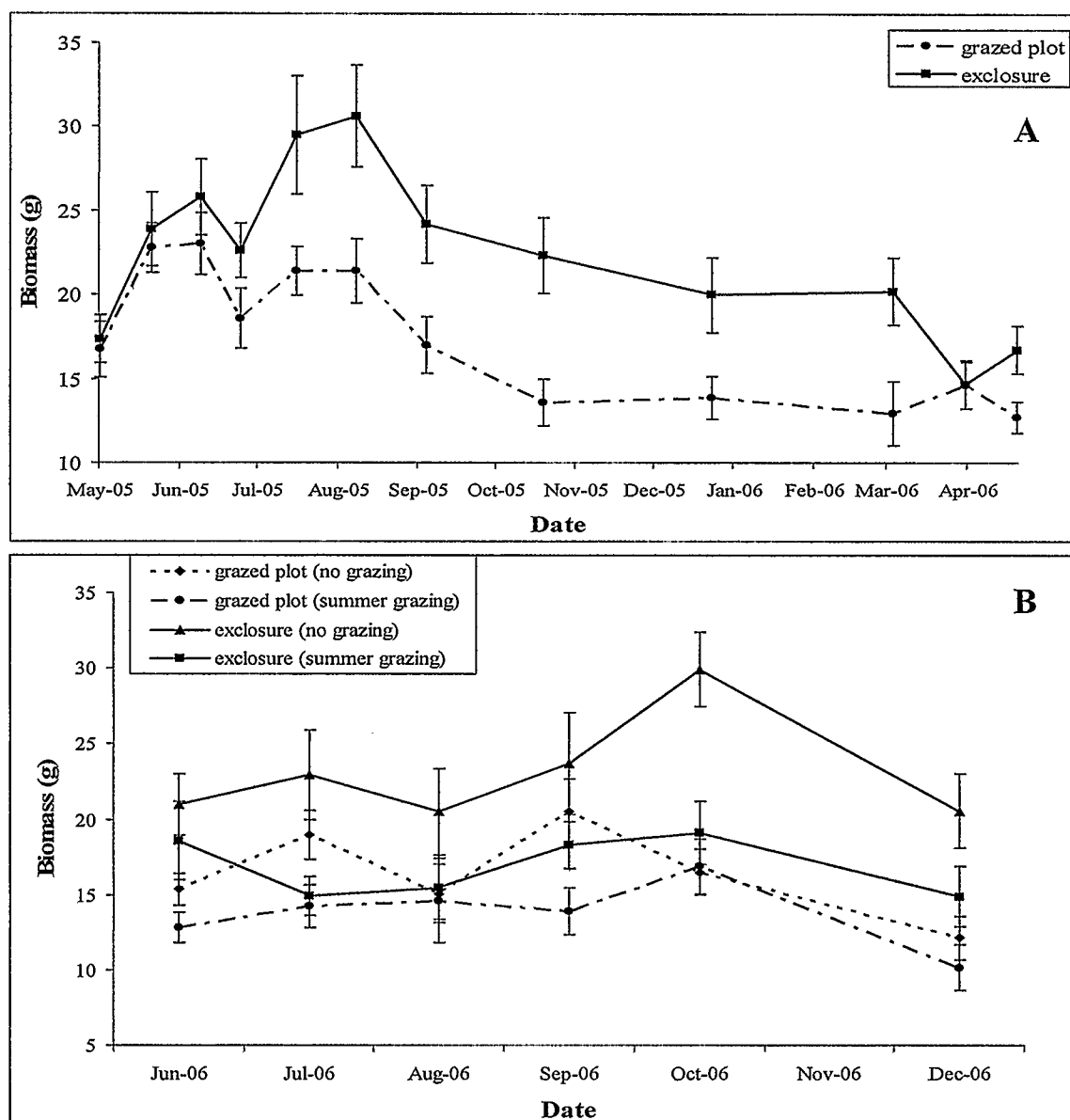


Figure 9. Average (\pm SE) vegetation biomass from 25×25 cm² subplots collected in 24 grazed plots and 24 exclosures from a) May 2005 to May 2006 (first year) and b) June 2006 to December 2006 (second year) in Sheep River Provincial Park, Alberta. Cattle had access to grazed plots from 15 of June to 15 of October. Summer, fall, and no grazing applications were pooled when grazing application had no significant effect.

During both years, ADF concentration was not significantly higher in exclosures than grazed plots, except for June 2006 ($F_{1, 97.9}=13.56$, $P<0.001$; Figure 10a). ADF concentration was significantly higher in areas of light grazing (Year 1: $F_{1, 41.8}=24.14$, $P<0.0001$; Year 2: $F_{1, 33.9}=23.90$, $P<0.001$) and varied with date (Year 1: $F_{8, 161}=28.47$, $P<0.0001$; Year 2: $F_{4, 83.3}=37.51$, $P<0.0001$). Total digestible energy was significantly higher in the exclosures than grazed plots (Year1: $F_{1, 11.5}=5.125$, $P=0.044$; Year2: $F_{1, 13.5}=6.828$, $P=0.021$; Figure 10b) and varied with date (Year 1: $F_{7, 151.7}=19.462$, $P<0.001$; Year2: $F_{5, 111.8}=6.350$, $P<0.001$).

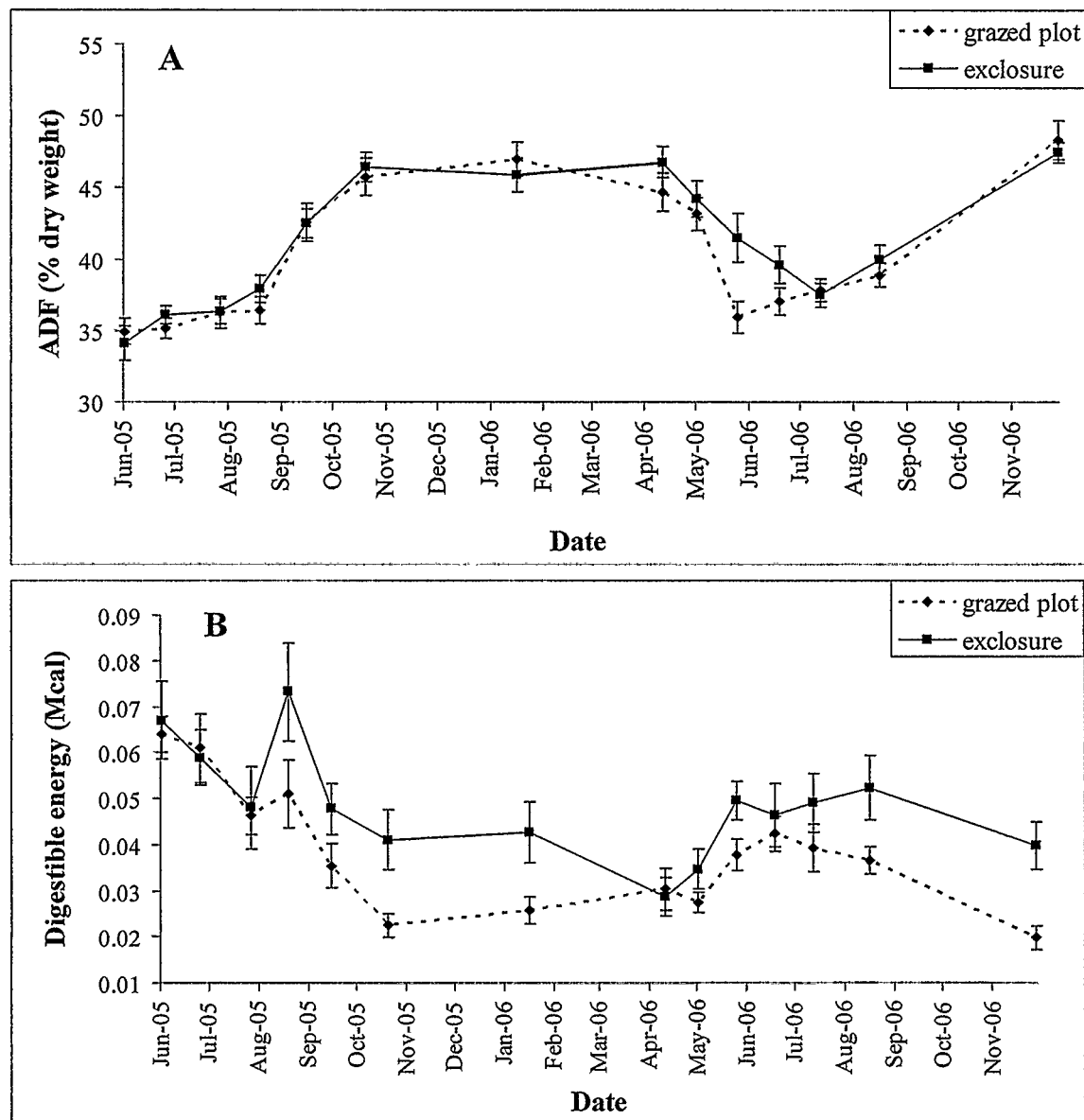


Figure 10. Average (\pm SE) a) Acid Detergent Fibre (ADF) concentration and b) total digestible energy of vegetation from $25 \times 25 \text{ cm}^2$ subplots collected in grazed plots and exclosures from June 2005 to December 2006 in Sheep River Provincial Park, Alberta. Cattle had access to grazed plots from 15 June to 15 October in 2005 and 2006. Summer, fall, and no grazing applications were pooled when grazing application had no significant effect.

During the first year, crude protein concentration varied significantly with date ($F_{8, 166}=33.36$, $P<0.0001$; Figure 11a) and grazing application ($F_{2, 20.3}=6.74$, $P=0.006$). Protein concentration was significantly higher in grazed plots than exclosures ($F_{1, 20.3}=4.61$, $P=0.044$) and grazing treatment interacted significantly with grazing application ($F_{2, 20.3}=3.47$, $P=0.050$) and grazing level ($F_{1, 20.1}=8.25$, $P=0.009$). Vegetation had higher protein concentration in grazed plots in highly grazed areas ($F_{1, 20.4}=15.40$, $P<0.001$) and for the “fall” grazing application ($F_{1, 20.9}=12.41$, $P=0.002$; Figure 12). During the second year, crude protein concentration was significantly higher in the highly grazed areas ($F_{1, 25}=4.31$, $P=0.048$) and significantly affected by date ($F_{4, 43.6}=24.63$, $P<0.001$; Figure 12a). Significant interactions were found between treatment and grazing level ($F_{1, 31.8}=2.43$, $P=0.1291$) and treatment and date ($F_{4, 43.4}=3.49$, $P=0.015$). Contrasts indicated that protein concentration was higher, although not significantly, in grazed plots than exclosures in highly grazed areas ($F_{1, 28.4}=3.29$, $P=0.080$) and significantly higher in grazed plots than in exclosures on June 2006 ($F_{1, 24.2}=9.68$, $P=0.005$).

On the contrary, there was a non-significant trend towards higher total protein inside the exclosures especially in the second year (Year 1: $F_{1, 11.7}=1.594$, $P=0.231$; Year 2: $F_{1, 13.6}=4.132$, $P<0.062$; Figure 11b). Total protein varied significantly between dates (Year 1: $F_{7, 152.0}=26.494$, $P<0.001$; Year 2: $F_{5, 112.3}=7.624$, $P<0.001$).

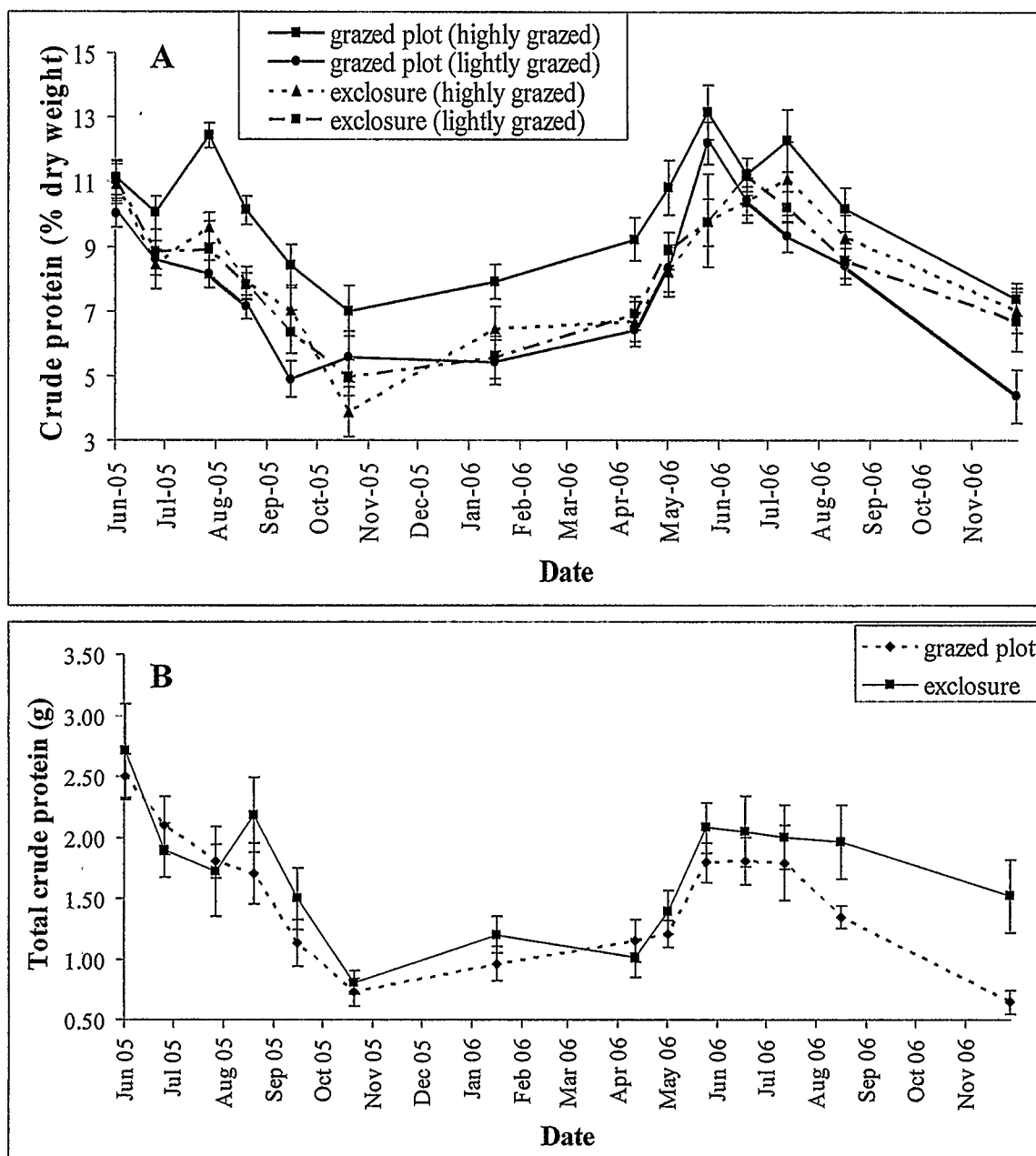


Figure 11. Average (\pm SE) a) crude protein concentration and b) total crude protein of vegetation from 25×25 cm² subplots collected in grazed plots and exclosures in high and low grazed areas from June 2005 to December 2006 in Sheep River Provincial Park, Alberta. Cattle had access to grazed plots from 15 June to 15 October in 2005 and 2006. Summer, fall, and no grazing applications were pooled for clarity of presentation.

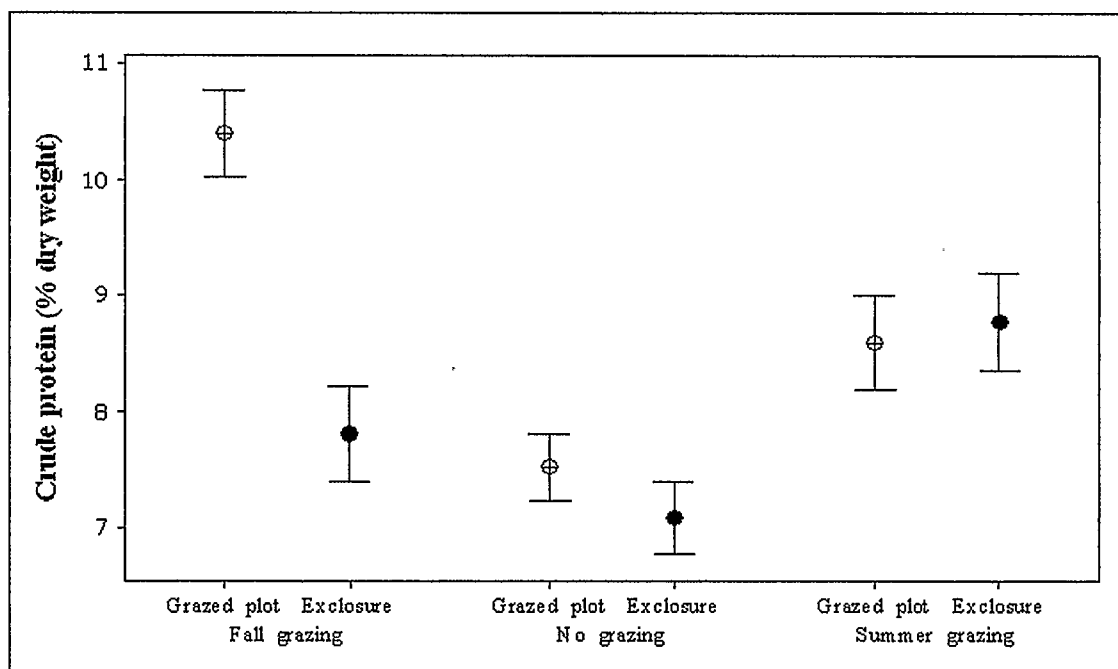


Figure 12. Average (\pm SE) crude protein content of vegetation from 25×25 cm² subplots collected in grazed plots and exclosures from June 2005 to May 2006 in Sheep River Provincial Park, Alberta. Cattle had access to grazed plots from 15 June to 15 October in 2005. Grazing was completely removed from the exclosures under “no grazing” application. “Summer grazing” exclosures were open from June 2005 to mid-August 2005, and closed to grazing from mid-August 2005 to October 2005. “Fall grazing” exclosures were closed from June 2005 to mid-August 2005, and open to grazing from mid-August 2005 to October 2005.

The mass of live vegetation during the first year varied significantly with date ($F_{2, 86}=88.66$, $P<0.0001$; Figure 13) and total biomass of the sample ($F_{1, 94.3}=331.59$, $P<0.0001$). During the second year, mass of live vegetation was higher in grazed plots than exclosures ($F_{1, 44.9}=5.12$, $P=0.029$), and was also affected by date ($F_{2, 86}=31.52$, $P<0.0001$) and total biomass of the sample ($F_{1, 89.9}=152.86$, $P<0.0001$). A significant interaction between treatment and date ($F_{2, 85.3}=5.41$, $P=0.006$) resulted because live vegetation mass was higher in the grazed plots than in exclosures on June 2006 ($F_{1, 120}=15.21$, $P<0.001$).

During the first year, the mass of forbs differed significantly among the grazing applications (lowest for “fall” grazing application, followed by “summer”, then “no grazing” application) ($F_{2, 52.6}=3.72$, $P=0.031$). Forb mass was higher in the low grazed areas ($F_{1, 52.3}=7.18$, $P=0.010$; Figure 14). Mass of forbs was also affected by date ($F_{4, 93.2}=9.47$, $P<0.001$; Figure 14), and total biomass of the sample ($F_{1, 123}=32.40$, $P<0.001$). Date and grazing intensity had interacting effects ($F_{4, 87.5}=2.29$, $P=0.066$), because lightly grazed areas had more forbs during September 2005 ($F_{1, 57.4}=6.41$, $P=0.014$) and June 2005 ($F_{1, 39.9}=5.81$, $P=0.021$). During the second year forb mass was higher in lightly grazed areas ($F_{1, 41.6}=6.21$, $P=0.017$) and varied with date ($F_{2, 53.4}=4.34$, $P=0.018$; Figure 15) and total biomass of the sample ($F_{1, 107}=21.00$, $P<0.001$).

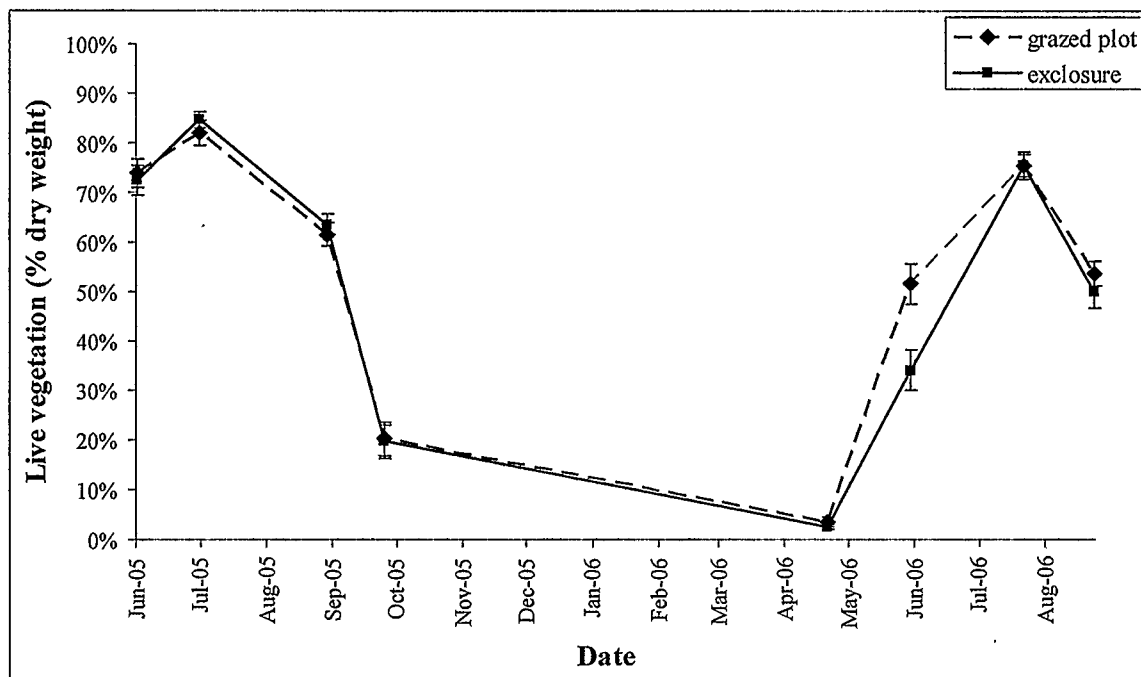


Figure 13. Average (\pm SE) proportion of live vegetation from 25×25 cm² subplots collected in grazed plots and exclosures from June 2005 to September 2006 in Sheep River Provincial Park, Alberta. Cattle had access to grazed plots from 15 June to 15 October in 2005 and 2006. Summer, fall, and no grazing applications were pooled when no significant effect of grazing application was found.

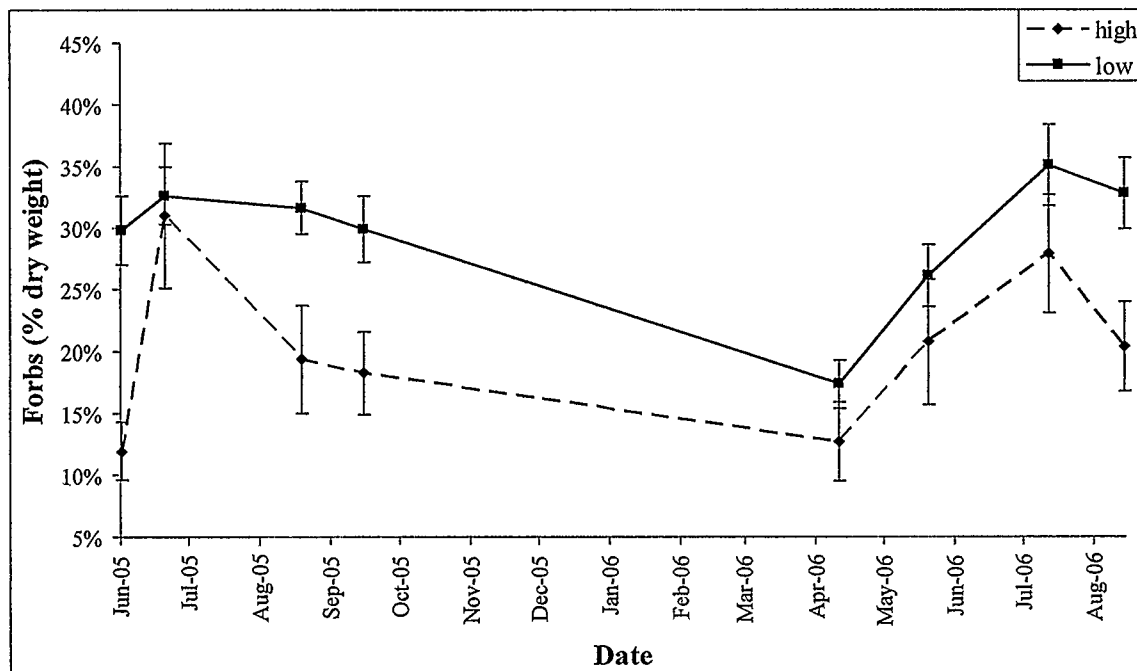


Figure 14. Average (\pm SE) proportion of forbs from 25×25 cm² subplots collected in highly and lightly grazed areas from June 2005 to September 2006 in Sheep River Provincial Park, Alberta. Cattle grazing was applied from 15 of June to 15 of October in 2005 and 2006. Intensity of grazing was estimated visually during weekly censuses. Summer, fall, and no grazing applications were pooled when no significant effect of grazing application was found.

The ADF concentration varied negatively ($ADF=45.5 - 14.2 \times \text{live vegetation}$; $T_{217}=-17.20$ $P<0.001$, $R\text{-Sq}(\text{adj})=57.7\%$, Figure 15a), whereas the crude protein concentration varied directly with the percentage of live vegetation ($CP=5.68 + 4.73 \times \text{live vegetation}$; $T_{217}=7.50$, $P<0.001$, $R\text{-Sq}(\text{adj})=20.4\%$, Figure 15b). No significant relationship between proportion of forbs and ADF or protein concentration was detected ($N=217$, $T=-0.80$, $P=0.425$, $R\text{-Sq}(\text{adj})=0.0\%$; $N=217$ $T=0.71$, $P=0.480$, $R\text{-Sq}(\text{adj})=0.0\%$). The proportion of live vegetation did not change significantly between 1994-95 and 2005-06 ($F_{1, 15.4}=1.51$, $P=0.237$), but it did vary significantly from month to month ($F_{7, 40.4}=68.41$, $P<0.001$). Overall biomass of the sample showed similar trends (Year: $F_{1, 15.3}=0.83$, $P=0.376$), (Month: $F_{7, 37.6}=2.81$, $P=0.019$). Proportion of forbs increased significantly from 1994-95 ($\bar{X}=21.47\% \pm 3.07\%$) to 2005-06 ($\bar{X}=35.57\% \pm 3.39\%$; $F_{1, 19.5}=14.99$, $P=0.001$) and changed from month to month ($F_{7, 24.3}=14.85$, $P<0.001$, Figure 16).

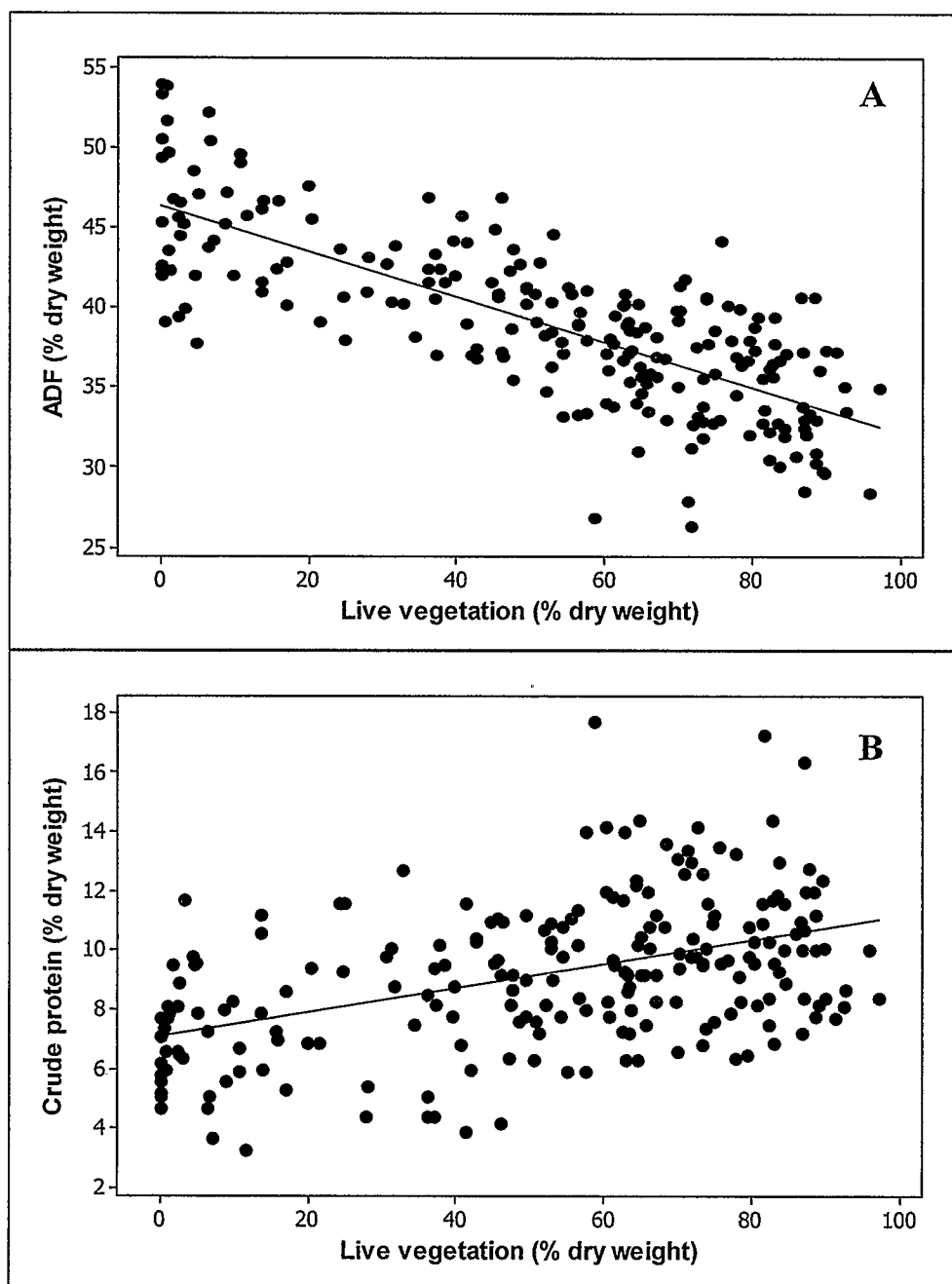


Figure 15. Relationship of a) ADF content and b) crude protein content to the proportion of live vegetation in samples from 25×25 cm² vegetation subplots collected from June 2005 to September 2006 in Sheep River Provincial Park, Alberta.

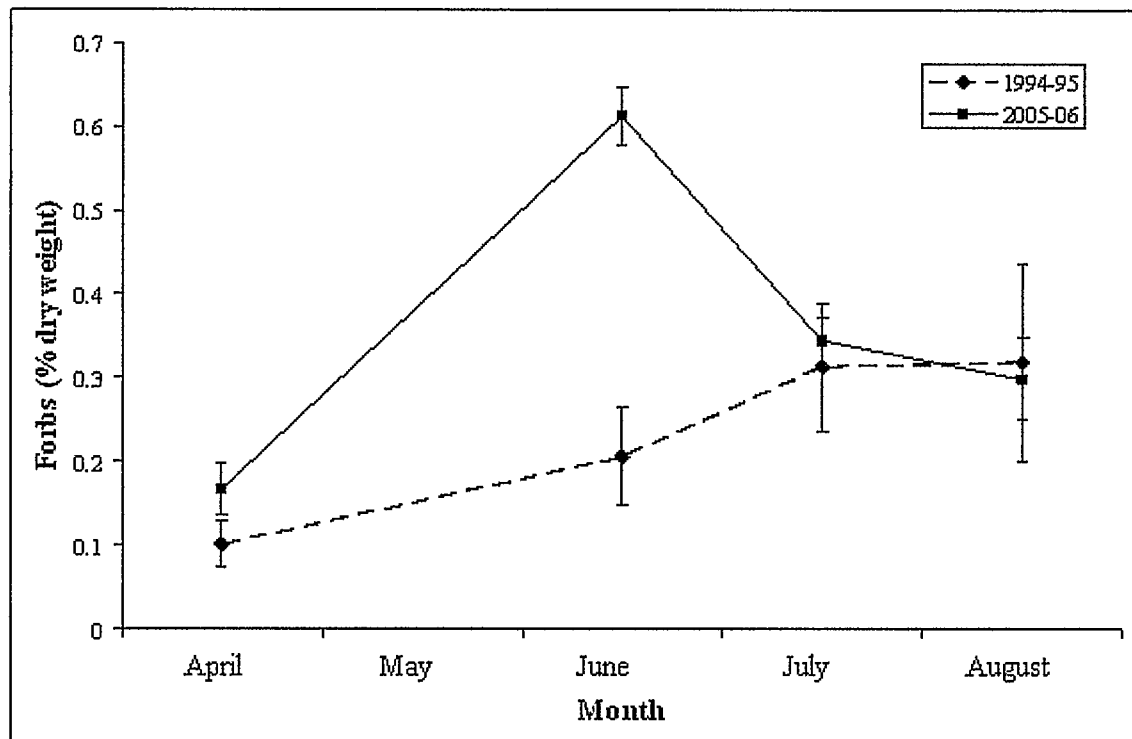


Figure 16. Average (\pm SE) proportion of forbs from 25×25 cm² subplots collected from April through August of 1994-95 and 2005-06 at the cattle grazed areas in Sheep River Provincial Park, Alberta.

Fecal data

Number of fecal groups was significantly higher for elk than sheep ($F_1=66.26$, $P<0.001$), and differed between the periods of collection ($F_1=4.72$, $P=0.031$), and the different plots ($F_1=2.99$, $P<0.001$) (Figure 17). Neither grazing application (summer, fall, no grazing; $F_2=0.03$, $P=0.971$) nor treatment (exclosure, grazed plot; $F_1=1.73$, $P=0.190$) significantly affected fecal density.

Ungulate use of exclosures and grazed plots

A total of 60 sightings of bighorn sheep groups were recorded in 14 grazed plots and 12 exclosures. Only 13 sightings of other ungulates (elk, mule deer and white-tailed deer) were recorded, so I only used bighorn sheep data (Figure 18). During the summer, sheep groups were observed more often in the grazed plots than in the exclosures ($W+=33.50$, $W-=2.50$, $N=8$, $P=0.023$). During the winter the difference between sheep groups in grazed plots and exclosures was not significant ($W+=6.50$, $W-=21.50$, $N=7$, $P=0.219$). Animal activity also did not differ significantly between exclosures and grazed plots ($\chi^2=1.164$, $P=0.281$, $df=1$).

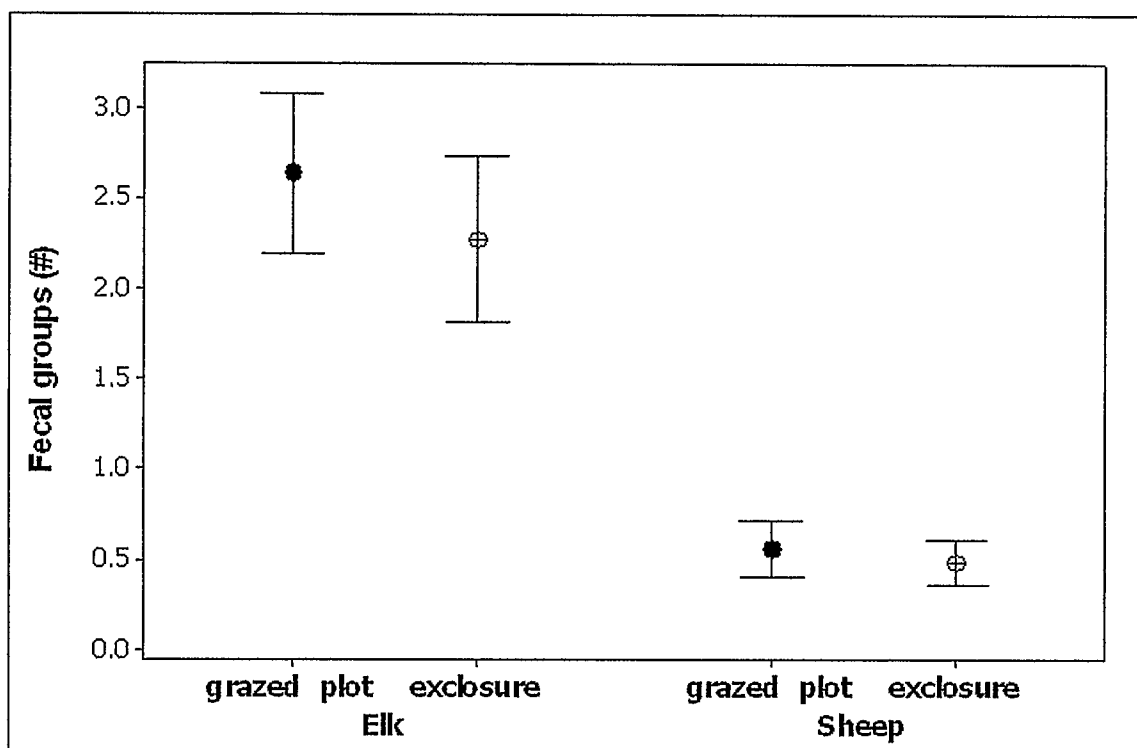


Figure 17. Average (\pm SE) number of elk and bighorn sheep fecal groups collected by monthly sampling of exclosures and grazed plots during winter and spring of 2006 in Sheep River Provincial Park, Alberta.

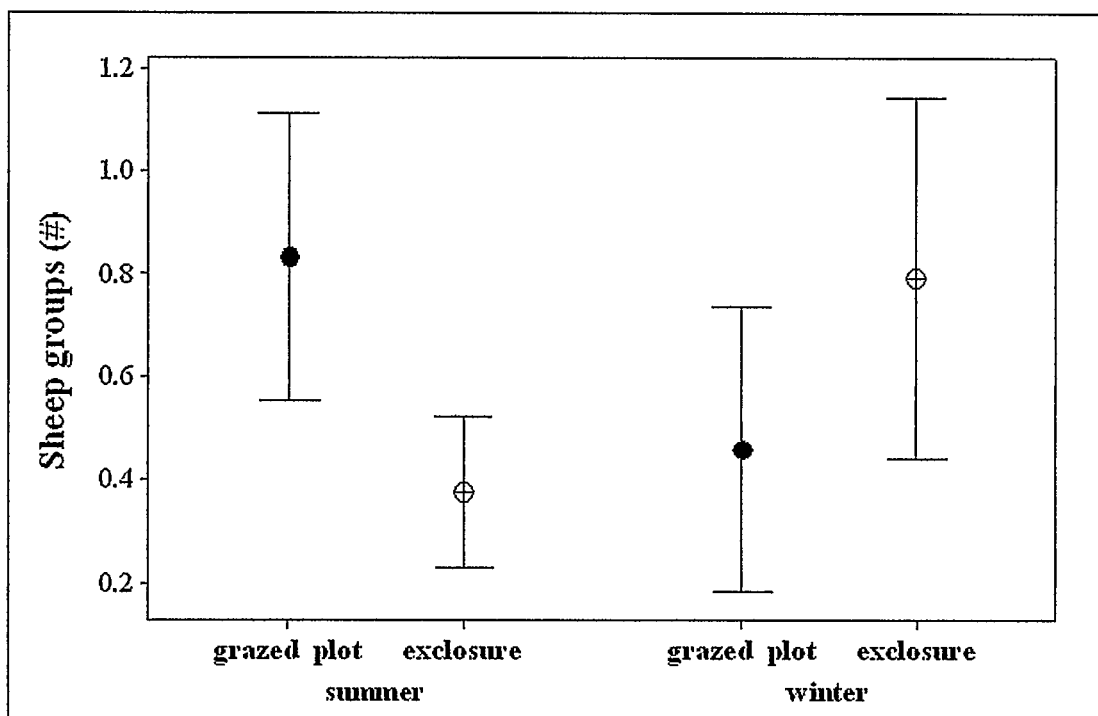


Figure 18. Average (\pm SE) number of bighorn sheep groups observed inside grazed plots and exclosures during June 2005-December 2006 in Sheep River Provincial Park, Alberta.

Discussion

Biomass

Not surprisingly exclosures contained more biomass than grazed plots, as Casasús et al. (2007) and Ganskopp et al. (2006) also reported. During both years, the difference between exclosures and grazed plots was highest during the winter, when the forage supply can be critical for native ungulates. During the second year, exclosures that were closed for the entire season had more biomass than exclosures that were open during the summer.

The effect of treatment and grazing application changed from near significant during the first year to significant during the second year. This increased effect could have arisen because vegetation biomass took more than one year to increase after reduction or removal of cattle grazing. The relatively heavy precipitation during the summer of the first year may also have offset the grazing impact by increasing vegetation growth in both exclosures and grazed plots. Vegetation biomass was indeed higher during the first than during the second summer. Additionally, biomass was highest during August of the first year and during October of the second year. This difference may also reflect contrasting precipitation patterns between the years.

Protein, ADF, and Digestible Energy

ADF concentration was higher in the exclosures located in lightly grazed areas during the early summer. Because high ADF indicates lower digestibility of the vegetation, cattle grazing appears to increase forage quality, although not significantly for most of the year. As expected, the biggest difference in ADF concentration between

exclosures and grazed plots occurred during early summer, but not during late fall or winter. On the other hand, crude protein concentration was higher in the plots subjected to intense grazing even during fall and winter. These results do not correspond to the findings of Wambolt et al. (1997) who argued that increase in protein due to cattle grazing becomes non-significant during the following winter. However, their experiment investigated the effect of spring grazing only, whereas I looked at summer and fall grazing, the effects of which may continue through the winter. Ganskopp et al. (2006) similarly found that summer cattle grazing increased crude protein and digestibility of vegetation during fall and winter. It is possible that cattle grazing delayed maturation of forage which led to production of more immature and highly nutritious stages of vegetation (Fryxell 1991).

I did not anticipate that the difference in crude protein concentration between grazed plots and exclosures would be significant only in exclosures open to grazing during the fall of the first year. I expected this difference to be greater between the exclosures that were closed for the entire season and the associated grazed plots. Closer examination of the data indicated that the grazed plots associated with “fall” exclosures had higher protein concentration than other grazed plots from the beginning of the study. The cause for this difference, however, remains an open question.

Although vegetation quality was higher in grazed plots, total amount of digestible energy and crude protein was higher inside the exclosures. This could be explained by the higher biomass inside the ungrazed areas that offset any gains in vegetation quality. The exclosures, therefore, were more profitable for the sheep especially during the second year.

In general, livestock grazing increased forage quality, which is well supported by previous studies (Wambolt et al. 1997, Clark et al. 2000, Ganskopp et al. 2006, Casasús et al. 2007). However; these patterns were irregular and changed between years. Biomass decreased substantially on the grazed plots, and total digestible energy was higher in the exclosures. It would be interesting to extend this study to see whether the differences in quality and biomass between exclosures and grazed plots accentuate over time, due to litter accumulation in the ungrazed areas.

Mass of live vegetation

Fibre content varied negatively, whereas crude protein content varied directly with the percentage of live vegetation, showing that new vegetation provides the most nutritional value to the ungulates. As expected, the amount of live vegetation was highest during summer and lowest during winter. Grazed plots had more live vegetation, but only during the second year, and mainly during June. Grazing during the previous year appeared to increase new growth and nutrition during the following early summer, possibly by increasing access to sunlight through the removal of old layers of vegetation. However, I expected that livestock grazing would affect the amount of live vegetation during the entire year, not just during the spring. Previous studies consistently found more litter inside exclosures, which would correspond to a lower proportion of live vegetation (Gordon 1988, Schulz and Leininger 1990, Willms et al. 2002). Even though cattle reduced litter mass, they may also have removed live vegetation in similar proportions. The proportion of live vegetation mass did not differ between 1994-95 and 2005-06. It is possible that the decrease in stocking rates was offset by the increase in

mass of cows and calves that has been occurring over the decade.

Forbs

The dry biomass of forbs did not differ between grazed plots and exclosures in contrast to expectation. It is unclear whether the livestock grazing increases or decreases the proportions of forbs and grasses and the effects of grazing on community composition vary with grazing intensity. Dobkin et al. (1998) reported higher forb cover inside long-term exclosures, whereas Loeser et al. (2005) found fewer forbs inside cattle exclosures, and Popolizio et al. (1994) showed that forb cover did not vary much with long-term grazing. Removal of grazing may also change vegetation composition more slowly than would be detected by a two-year study (Loeser et al. 2007).

Forbs were more abundant in the lightly grazed areas. However, I cannot exclude the effect of other factors in addition to cattle grazing, such as elevation and hill steepness, as cattle preferred to graze on low meadows with close access to water (Bailey 2005). Proportionally fewer forbs were found during 1994-95 than in 2005-06. Unfortunately, I cannot separate the effect of the decrease in long-term grazing from shifts in vegetation composition due to other factors. It is possible that high rainfall during the summer of the 2005 caused an increase in forb production, resulting in the observed difference. Future studies should consider vegetation composition in more detail and differentiate between plant species. Comparisons of long-term changes inside and outside the exclosures are also needed to separate the effects of cattle grazing from other factors.

Ungulate use of exclosures and grazed plots

Based on fecal group counts wild ungulates used grazed plots and exclosures equally during the winter. This result was unexpected, as previous studies reported that elk preferred ungrazed areas to the grazed sites (Knowles and Campbell 1981, Skovlin et al. 1983, Frisina 1992, Clegg 1994). On the other hand, Halstead et al. (2002) found minimal impacts of cattle grazing on elk distribution. Lack of visible differences in this experiment might also be attributed to the size of the exclosures. Fecal counts were performed during the winter when barbed wire fences were removed, so exclosures themselves were unlikely to deter animals from ungrazed patches. However, 35×35 m exclosures might have been too small to affect sheep and elk. Gross and Knight (2000) argued that an exclosure must be at least 4 hectares to observe changes in elk use due to vegetation differences.

Visual counts indicated that sheep used grazed plots more often than exclosures during the summer, but not during the winter. This result could be due to the barbed wire around some exclosures during summer that might have deterred sheep. Sheep may have also selected grazed plots during early summer because of the higher availability of live vegetation. Bighorn ewes have previously been shown to forage mainly on new vegetation during the spring, because of its higher nutritional value (Goodson et al. 1991). During the winter period, when barbed wire was down, sheep use of exclosures did not differ, so sheep either did not preferred grazed over ungrazed areas, or exclosures were too small to show this preference.

Summary

As predicted, the livestock grazing caused some increase in vegetation quality and decreased the amount of forage and digestible energy. The reduction in forage availability was most significant during winter. From a management perspective the increase in digestibility might not make up for the decrease in the forage quantity, total protein, and digestible energy during the periods of forage shortage. It is important to consider the impacts of grazing throughout different seasons and not just overall annual changes to recognize most critical periods for native ungulates. This study shows that the extent of impacts of cattle on forage supplies can change through the year. Although grazing induces increase in quality, sheep may still experience a nutrient deficiency. Even though grazed plots had higher proportion of live vegetation during June 2006, more of the total biomass and digestible energy was found in the exclosures during the same month.

Long-term cattle grazing may alter vegetation composition. I found more forbs now than 10 years ago. More detailed studies are needed to recognize whether this change resulted from cattle grazing or other factors (i.e. rainfall). Moderate livestock grazing has been previously associated with greater vegetation diversity than either lack of grazing or high stocking levels (Hart 2001). However, if vegetation composition changes, we need to ensure that it is not driven by the introduction of invasive species. Native ungulates, such as elk and bighorn sheep, did not prefer either grazed or ungrazed areas when fences were removed. Either the ungulates may not have been constrained by forage availability or the larger cattle exclosures are necessary to observe this effect.

Chapter 5: Summary and conclusions

Goals of the study

The overall purpose of this thesis was to investigate the impact of summer and fall livestock grazing on the behaviour and range use of bighorn sheep. Furthermore, this study looked at the differences in vegetation quality and quantity between cattle exclosures and grazed plots, as well as ungulate use of these areas. This research was separated into five following parts.

The first part of this study investigated whether the physical presence of cattle altered behaviour of bighorn sheep. It was expected that the presence of cattle would result in decreased bite rates and increased vigilance of the sheep. The second part looked at whether sheep avoided cattle within the park. It was expected that minimum and average simultaneous distances between sheep and cows would be greater than random. The third part of this research focused on the differences in biomass, crude protein, ADF, mass of live vegetation and mass of forbs between vegetation in cattle exclosures and grazed plots on a month-to-month basis. It was expected that more biomass, total protein and digestible energy would be found inside cattle exclosures, while higher crude protein concentration and lower fibre concentration would be found in the grazed plots. It was also expected that more live vegetation would be found in the grazed plots and mass of forbs would vary between grazed plots and exclosures. The fourth part of the study looked at the difference in ungulate use of exclosures and grazed plots. I predicted that ungulates would use exclosures more than grazed plots during the times of forage limitation. The fifth part investigated changes in vegetation biomass, percentage of live vegetation and percentage of forbs from 1994-95 to 2005-06. Due to the reduction in

stocking rates, I expected that more biomass, lower percentage of live vegetation and different percentage of forbs would be found in 2005-06 than 1994-95.

Summary of major findings

The first part of our research revealed that cattle presence was associated with decreased bite rates in male and female bighorn sheep. Male bighorn sheep also showed an increase in vigilance when cattle were present. Sheep did not show avoidance behaviour towards cows. The simultaneous distances between nearest sheep and cows were smaller than expected but on average still around 2000m. Minimal simultaneous distances did not differ from random, which did not indicate avoidance behaviour at closer encounters.

The second part of our research indicated that cattle grazing decreased vegetation biomass and total digestible energy, especially in the winter season. Grazing also caused an increase in vegetation quality that was most prominent during the spring and early summer. No differences in ungulate use between exclosures and grazed plots were observed. A significant increase in proportion of forbs from 1994-95 to 2005-06 was recorded, but no significant changes in biomass or proportion of live grass were found.

The results of this research provided evidence that the presence of cattle influenced sheep behaviour and range use. For the first time, our study showed that bighorn sheep preferred to use similar areas as the cattle.

Strengths and weaknesses

As with any Master of Science work, this study was greatly limited by time and budget. Because this research was only carried out for two years, I was able to observe

only short-term changes and not subtle yet equally important long-term changes in vegetation. Grazing-induced shifts in community composition that are recorded during long-term studies (Hayes and Holl 2003, Manier and Hobbs 2007) can play an important role in changing ecosystem productivity (Kahmen et al. 2005), and therefore, forage availability for native ungulates. Another problem with the short duration of this research was the high variation in precipitation over the two years. Longer studies are not as strongly impacted by fluctuating variables, such as temperature or rainfall that could affect vegetation growth and composition.

Another potential limitation of this research was the enclosure size. It would be ideal to exclude the cattle from the entire grazing allotment to truly see the difference in ungulate area use and eliminate the effect of enclosures. Unfortunately, this was not possible, as ranchers would not have been agreeable to this.

On the positive side, this research was one of the few that involved a large number of enclosures, and therefore had a bigger sample size. Most of the previous vegetation studies did not use more than 5 enclosures (Dobkin 1998, Schulz and Leininger 1990, Valone and Sauter 2005, Casasús et al. 2007). Having 24 plots throughout the park located in different habitats (hill slopes, meadows, and forests) allowed us to be more confident in our results. Furthermore, month-to-month collection of the vegetation helped us to look at the seasonal dynamics and revealed the critical times in forage availability. The majority of the previous vegetation research did not address the continuous effects of grazing throughout different times of the year (Westenskow-Wall et al. 1994, Dobkin 1998, Mishra et al. 2004). Additionally, our research considered the combination of different cattle grazing effects in one area, which helped us to obtain a more complete

picture of how wild ungulates are impacted by the livestock.

Another strong point of this research was the ability to use GPS collars on both sheep and cows. Collars provided us with a large amount of data that also gave us more confidence in the observed trends. Finally, the opportunity to work with a well-studied and tagged bighorn sheep population helped us to eliminate the unwanted pseudoreplication that is inevitable when studying untagged populations.

Suggestions for future research

Before introducing livestock into new areas or increasing stocking rates, managers should ensure that nutritional requirements of native ungulates are met during the winter. It was previously shown that the lack of sufficient forage opportunities or poor forage quality during the winter can lead to a decrease in the number of micro-organisms in the rumen of the animals. Ruminants depend on bacteria and protozoa for digestion of cellulose and they can die after a period of winter starvation even as forage becomes more available in the spring, literally starving with stomachs full of grass (Pearson 1969, Giles and McKinney 1968). Goodson et al. (1991) calculated daily energy consumption and compared it to daily energy requirements of bighorn ewes. They calculated daily vegetation intake by multiplying total daily feeding time (estimated from energy budgets) and vegetation intake rate (estimated from bite rates and bite size data). Daily digestible energy intake was then calculated as $1.54 \times \text{dry matter intake}$ (Goodson et al. 1991). This thesis provides more precise calculations of digestible energy content of the vegetation in Sheep River Provincial Park. Goodson et al. (1991) estimated that daily energy requirements of ewes ranged between approximately 3000 to 4000 Kcal/day in Jan-Mar

and increased to about 3500 to 4500 in Apr-May due to lactation. It would be possible to calculate protein and energy intakes of bighorn sheep in the Sheep River Provincial Park by estimating the bite size and number of bites per day and using vegetation information provided in this thesis.

The presence of cattle in grassland ecosystems can have additional effects that were not covered in this study. Future studies could have an even more extensive approach and investigate the above effects to obtain a full picture of the ecosystem responses to cattle grazing. More extended samplings of the exclosures are also required to look at the long-term changes in vegetation and community composition.

The use of new technology can bring an improvement in data collection and reveal previously hidden patterns. For example, GPS collars on cattle showed that cows were located more uniformly throughout the park and crossed the river more often than I expected. Future research could use GPS collars on other ungulates, such as elk and deer, to study their movement patterns and avoidance behaviour. Additionally, establishment of motion sensor cameras on exclosures and grazed plots would help to collect more data regarding animal presence, especially during the night time when censuses are difficult.

Cattle grazing, mutualism, and competition

Perhaps the main reason that we still do not fully understand the impacts of cattle grazing on native ungulates is because of the complicated mix of positive and negative roles that these herbivores play in the ecosystem. The results of this study revealed a number of different beneficial, neutral and antagonistic effects. Grazing by cattle reduced vegetation biomass but increased protein content and digestibility of vegetation. These

results were not surprising, as similar effects on vegetation were previously reported by Westenskow-Wall et al. (1994), Clark et al. (2000), and Alpe et al. (1999) elsewhere. In addition to this, cattle presence caused sheep to be more vigilant. However, sheep were not actively avoiding cattle and showed preference for general areas used by cattle. It should be kept in mind that the minimal distance between cattle and sheep was still around 700 meters, which means they were never in very close contact with each other. Our findings somewhat contradict the study by Bissonette and Steinkamp (1996) who showed that bighorn sheep avoided cattle. On the other hand, Mattiello (2002) reported that elk also preferred to forage on livestock grazed areas, but were more vigilant in the presence of cattle.

Our results indicate that the strength of interactions between cattle and native ungulates varies with season, even if the grazing is only applied during the summer and fall. Similarly, the strength and direction of cattle impacts were previously shown to depend on the timing of the grazing application. For example, early summer grazing was found to be beneficial or resulted in a minimal impact, while late summer or fall grazing was shown to have adverse effects on native ungulates (Smith and Doell 1968, Alpe et al. 1999, Damiran et al. 2003).

Domestic cattle are not the only species whose effect on other organisms changes with different conditions. Other grazers also have a range of antagonistic or mutualistic interactions between each other and the strength of these relationships varies with different spatial and temporal scales. Arsenault and Owen-Smith (2002) suggested that facilitation among herbivores is highest during the growing season because of the improvement of forage quality due to grazing. On the other hand, competition between

herbivores is strongest during the dormant season when the effects of forage removal are greatest. For example, wildebeests (*Connochaetes spp.*) in Africa may improve vegetation quality for other grazers during the rainy season, but cause resource depletion during the dry season (Arsenault and Owen-Smith 2002).

This interesting overlap of mutualism and antagonism is not unique to grazers. There are other systems where the interactions between two species change from facilitative to antagonistic. A famous example of a friend-enemy relationship is found in figs and fig wasps, wherein the figs require pollination by the wasps to reproduce. However, while doing a fig tree a favour, wasps also lay eggs inside the flower that hatch into larvae and cause a reduction in seed production (Herre and West, 1997). Such patterns of species interactions are constantly shifting from mutualistic to antagonistic and back, driven by the arms race of organisms that try to gain the most benefit from each other. These shifts sometimes result in complicated interactions where one of the players acts as the facilitator, while the other one takes the role of the competitor. For example, grazing by European brown hares (*Lepus europaeus*) increased vegetation quality, which benefited barnacle geese (*Branta leucopsis*); while vegetation depletion by geese negatively affected foraging patterns of hares (Stahl et al. 2006). Similarly, the presence of snails (*Lymnaea stagnalis*) had positive effects on growth and weight of tadpoles (*Rana temporaria*) through removal of the competition between different algae, which resulted in a higher abundance of the algae preferred by the tadpoles. Tadpoles, on the other hand, negatively impacted the snails by depleting food resources (Brönmark et al. 1991).

The interactions between species are not always black and white and there is a

hidden complexity behind many of the connections. We cannot assume that just because one organism influences the other in a certain way, that the strength or direction of this connection will remain the same when the conditions change. It is possible that this ongoing change is the answer behind the “plankton paradox” (Hutchinson 1961) and the incredible abundance of life on this planet. Perhaps as we, humans, learn more about the complexity of our interaction with other species, we will be able to better evaluate and change the consequences of our actions, by shifting away from antagonism towards a more peaceful coexistence.

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Appendix A: Previous publications

Chaikina, N.A. and K.E. Ruckstuhl. 2006. The effect of cattle grazing on native ungulates: the good, the bad, and the ugly. *Rangelands* 28: 8–14.

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