University of Alberta

Ungulate guild dynamics: mechanisms and consequences for aspen-parklands

by

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PREVIEW

Canada

...the sky is clear and spacious, the earth is solid and full, all creatures flourish together, content with the way they are, endlessly repeating themselves, endlessly renewed...

– Lao Tzu

But honest men do not pretend to know; they are candid and sincere; they love the truth; they admit their ignorance and they say, "We do not know."

– Robert Green Ingersoll

Dedication

For my parents, who told me to go play outside.

And

For those who have sat upon the shore of the northern lakes, looked into the starlit sky, and fallen asleep to the haunting cry of the loon. For those who have wandered the fjords and mountains, watching the deepening twilight as the moon rises high amid the heavens. Your steadfast love and understanding are the stars that guide my path, the lapping waves that soothe my soul, and the makwag that guard my heart. You are my wilderness . . . and you have my eternal gratitude. Miigwetch.

Abstract

Multi-ungulate communities can be structured by competition and facilitation, but few studies explore the interactions by which these processes occur or the subsequent implications for plant communities. Using paddock experiments conducted in central Alberta, I evaluated how previous and concurrent grazing influences resource selection and intake in a native assemblage containing bison (*Bison bison*), wapiti (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*). Bison were unaffected by concurrent grazing, whereas previous grazing reduced daily intake. By altering the activity and resource selection of wapiti and deer, bison facilitated the daily intake of wapiti and displaced deer. When foraging simultaneously, behavioural interactions reduced forage utilization and homogenized the spatial distribution of forage. Although sequential grazing decreased the spatial heterogeneity of graminoid biomass in most scenarios, sequential grazing generally increased the patchiness of forbs. My research demonstrates that behavioural interactions have implications for ungulate assemblages and forage biomass in aspen parklands.

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1.1 Ecological context and background

Competition creates selective pressure by altering the fitness of individuals (Darwin 1859). Over time, this process may restrict niche availability or broaden niche breadth (Abrams 1990), steer the evolution of species, and ultimately form and maintain community structure. Although ecologists often overlook facilitation (Boucher et al. 1982, Bruno et al. 2003), like competition, it influences individual fitness by altering the abundance and distribution of resources. Competition occurs when one species reduces the fitness of another by limiting a shared resource via exploitation or interference (Darwin 1859, Crombie 1947, Birch 1957, Case and Gilpin 1974), whereas facilitation occurs when one species increases the fitness of another by improving access to resources (Allee et al. 1949). Although competition and facilitation are mutually exclusive, both outcomes depend on the condition of communities. Understanding the mechanisms by which these two outcomes occur is therefore critical to population and community ecology (Strong et al. 1984, Diamond and Case 1986).

Much of our theory on competition and facilitation in multi-species grazing systems comes from research conducted in the Serengeti-Mara, where ungulates migrate in a predictable progression (Gwynne and Bell 1968). At the end of the rainy season, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), topi (*Damaliscus lunatus*), and Thomson's gazelle (*Gazella thomsoni*) migrate into the tall-grass sward in order of decreasing body mass (except topi, which precede wildebeest). Some ecologists hypothesized that this progression was driven by facilitation (Gwynne and Bell 1968, Bell 1971) and, indeed, early work indicated that large-bodied zebra migrate into the sward to forage on grass stems, medium-bodied wildebeest follow to forage on the leaves exposed by zebra, and small-bodied Thomson's gazelle follow to forage on the herbs and young grass shoots left by wildebeest (Bell 1971). Subsequent studies found that wildebeest facilitate the intake of Thomson gazelle by creating grazing lawns (McNaughton 1976, 1985), but have no demographic effect (Sinclair and Norton-Griffiths 1982, Dublin et al. 1990). Other ecologists proposed that narrow incisor breadth permits-small bodied ungulates to be more selective than larger-bodied ungulates, allowing them to remove high quality forage (Illius and Gordon 1987). Succeeding experiments demonstrated that wide-muzzled wildebeest could forage on shorter swards than narrow-muzzled topi but that topi could forage more selectively (Murray and Illius 2000), indicating that topi may be able to reduce the quality of tall-grass swards enough to displace wildebeest.

The same mechanisms are believed to have driven evolutionary grazing patterns in North America (Hudson et al. 2002). Prior to the arrival of industrial agriculture, bison

(*Bison bison*), wapiti (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) were the dominant ungulates on the northern Great Plains (Allen 1877, Murie 1951, Soper 1964). Research has shown that summer grazing by cattle improves winter forage conditions for wapiti (Anderson and Scherzinger 1975) and that grazing lawns created by bison (Vinton et al. 1993, Coppedge and Shaw 1998) increase the intake of wapiti by increasing bite rates (Didkowsky 2006). Although studies have shown that wapiti depress cattle production by decreasing intake (Hobbs et al. 1996a, 1996b) it remains unclear whether wapiti also compete against bison. Similarly, despite evidence of competition between elk and deer (Stewart et al. 2002) research has not demonstrated whether or not competition is related to the higher selectivity of deer.

Competition and facilitation are equally important from a practical viewpoint, as land managers have expressed interest in the application of multi-ungulate communities. Multi-species foraging is believed to result in more balanced utilization than single-species foraging (Nolan and Connolly 1989) via the complementary use of forage (Bell 1970, Jarman and Sinclair 1979). Multi-species foraging can also increase economic output by increasing animal performance and permitting increased stocking rates (Telfer and Scotter 1975, Nolan and Connolly 1989, Wright et al. 2006, Fraser et al. 2007). These economic effects have the additional benefit of increasing output using energy optimization rather than energy input (Briske and Heitschmidt 1991). Increased gains are therefore not offset by the cost of increasing management intensity.

Despite the theoretical and practical importance of competition and facilitation, identifying the mechanisms by which they occur is challenging. Ecologists often infer competition and facilitation from resource overlap (Jenkins and Wright 1988, Jenks et al. 1996, Voeten and Prins 1999, Kuiters et al. 2005, Wegge et al. 2006). However, because ungulates can alter foraging behaviour at multiple scales, ecologists must evaluate changes in spatial, temporal, and dietary behaviour. For example, Stewart et al. (2002) demonstrated that mule deer and wapiti in eastern Oregon avoid one another during 6-hour intervals, but do not maintain spatial separation over 7-day intervals. Although such studies are easily quantified, most provide little insight into the processes by which competition and facilitation occur and do not demonstrate altered performance (Putman 1996). Identifying the foraging processes that alter performance is difficult in natural settings where performance may change in response to predation, disease, and variable resource availability (Connell 1983). In contrast, experimental settings allow researchers to control for environmental variability and isolate the mechanisms that drive competition and facilitation.

The hope that rangelands can be restored and maintained by evolutionary grazing patterns (Fuhlendorf and Engle 2001) highlights the practical and theoretical importance of identifying the mechanisms that drive competition and facilitation. Observations within the aspen-parkland ecoregion of central Alberta suggest that native ungulates persist at higher densities than cattle due to complementary forage use (Telfer and Scotter 1975), but little is known about the competitive and facultative interactions. The fact that this ecoregion is a valuable livestock production zone (McCartney 1993) and has been promoted as a potential site for native ungulate production (Telfer and Scotter 1975), prompted the foundation of the Precision Ranching Initiative.

1.2 Precision Ranching Initiative

The Precision Ranching Initiative (PRI) was established to evaluate whether evolutionary grazing patterns can improve the efficient and sustainable use of rangelands, and provide practical management recommendations. Driven by the belief that *grazing the right animal at the right place at the right time* is fundamental to rangeland management (Hudson et al. 2002), PRI explored how multi-species grazing influenced foraging behaviour and landscape characteristics. Field studies at the University of Alberta Kinsella Research Ranch were designed to answer two questions. First, is the multi-species grazing of native ungulates more productive and sustainable than cattle? Second, is the sequential grazing of native ungulates more productive than simultaneous grazing?

PRI conducted research at the University of Alberta Kinsella Research Ranch (53 °01'N, 111 °34'W), located 150km east-southeast of Edmonton, Alberta. Climate at the ranch is continental with 115 to 125 frost-free days (Chetner et al. 2003). The mean annual temperature averages 2.3 °C and total annual precipitation averages 414mm (Environment Canada 2005). Mean summer (June and July) and autumn (September and October) temperatures are 15.8 °C and 7.4 °C and total precipitation averages 204mm. The ranch is located within the Viking Upland physiographic district (Howitt 1988), where it overlies moderately calcareous bedrock (Mossop and Shetsen 1994). The area is characterized by knob and kettle terrain dominated by the Elnora soil group, a well-drained assemblage of Chernozemic soils interspersed with poorly drained Gleysolic depressions and small portions of Solonetzic soils (Howitt 1988). Vegetation on the ranch is representative of the aspen parkland ecoregion (Strong 1992), consisting of a grassland-forest mosaic with graminoid-dominated uplands, interspersed with lowland forests and riparian meadows.

Four grazing treatments were imposed for two 45-day periods, one in summer (1 June to 15 July) and another in autumn (1 September to 15 October). Treatments were replicated in 3 paddocks (n=12) and consisted of (1) cattle grazing for 45 days; (2) bison, wapiti, and mule deer grazing simultaneously for 45 days; (3) a sequence of bison, wapiti, mule deer grazing for 15 days each; and (4) a sequence of mule deer, wapiti, and bison grazing for 15 days each.

Paddocks varied in size (Appendix I), but the average proportions of six vegetation communities were similar across the replicate paddocks. The number of individuals within each 15-day period was constrained to ensure there was equal forage removal across paddocks given *a priori* 45-day stocking rates (Society for Range Management 1998; Appendix II.B). As a result, the number of individuals within each paddock differed among the four treatments (Appendix II.D). Study animals were primarily non-pregnant adult and sub-adult females, but bison and cattle that gave birth during the experiment and were allowed to remain within the study with their calves (Appendix III). Animal handling was conducted according to University of Alberta animal ethics protocols HUDS 2004-33B and HUDS 2004-33C.

1.3 Thesis overview

The primary objective of my thesis was to evaluate the effect that multi-species foraging had on its members and the forage they consumed. Within the scope of PRI, I evaluated how three native ungulate species, bison, wapiti, and mule deer, altered the vegetation community selection and foraging behaviour of one another and assessed how such interactions influenced the utilization and distribution of forage. Evaluations were conducted in a series of foraging trials, each consisting of three 15-day periods: (1) bison, wapiti, and mule deer foraging simultaneously; (2) a sequence of bison, wapiti, mule deer foraging for 15 days each; and (3) a sequence of mule deer, wapiti, and bison grazing for 15 days each.

First, I examined the selection, intake, diet composition, and fecal nitrogen of species and showed that species interactions were both competitive and facilitative and primarily driven by changes in selection and activity (Chapter 2). Next, I demonstrated that species interactions affected forage utilization and resulted in differential changes to spatial pattern (Chapter 3). Finally, I discussed the implications of my findings for management and conservation (Chapter 4).

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The influence of ungulate guild dynamics on resource selection and intake

2.1 Introduction

The ability of ungulates to influence ecosystem structure and function (reviews by Fleischner 1994, Hobbs 1996, Augustine and McNaughton 1998, Kie and Lehmkuhl 2001, Cote et al. 2004) has generated interest in the formation and maintenance of ungulate communities. Ungulates alter ecosystems through selective removal of forage (review by Augustine and McNaughton 1998), trampling (Naeth et al. 1991, Donkor et al. 2002), and nutrient redistribution (McNaughton 1985, Day and Detling 1990, Frank et al. 1994, Bokdam and Gleichman 2000, Augustine and Frank 2001). However, the nature of these ecosystem relationships depends on the evolutionary history of the ecosystem (Milchunas and Lauenroth 1993) as well as current environmental conditions. Intact multi-species communities can be structured by competition (review by Schoener 1983, Sinclair 1985, Murray and Illius 2000) and facilitation (Gwynne and Bell 1968, McNaughton 1976, Didkowsky 2006), but few studies have tested the conditions under which these two processes occur (however see Sinclair and Norton-Griffiths 1982).

Competition occurs when shared resources are limited by exploitation (Illius and Gordon 1987, Murray and Illius 2000) or interference (Park 1962, Stewart et al. 2002), resulting in reduced performance. Animals may respond to reduced resources by increasing search time, which may result in decreased bite rates (Spalinger and Hobbs 1992). Alternatively, animals may forage less selectively, resulting in increased chewing times and lower diet quality (Balch 1971, Shipley and Spalinger 1992). Finally, species may reduce activity to conserve energy (Schoener 1971) or broaden their diets to include less preferred forages (MacArthur and Pianka 1966, Van Soest 1982, Demment and Van Soest 1985). Ungulates can, however, mitigate competition by altering foraging behaviour at any one scale. For example, species whose resources are limited by an interfering competitor may maintain intake by foraging in a new location or altering diet composition. However, because mitigating strategies are constrained by resource availability, animals may not be able to fully compensate when forage is most limiting (Sinclair 1975, Wiens 1977).

Facilitation occurs when an animal improves the foraging opportunities for another. For example, an herbivore may open vegetative structure (Vesey-Fitzgerald 1960) or promote the nutritive regrowth of a shared resource (McNaughton 1976, Gordon 1988), improving performance of a second herbivore. Because of growing season dynamics, facilitation resulting from plant regrowth occurs during the growing season when plants can compensate for tissue removal (Maschinski and Whitham 1989, Tiffin 2002). In contrast, increased forage access may be most important early in the growing season when residual forage from the previous year is most abundant, or at the end of the growing season when most current annual growth has senesced. Animals may respond to increased resources by reducing search time, which may either decrease time-spent active (Schoener 1971) or increase bite rates (Spalinger and Hobbs 1992). Alternatively, species may increase feeding time in an attempt to maximize energetic input (Schoener 1971, Belovsky 1986, Kie 1996).

Ecologists often infer competition and facilitation from resource overlap (Jenkins and Wright 1988, Jenks et al. 1996, Voeten and Prins 1999, Kuiters et al. 2005, Wegge et al. 2006). However, because ungulates can alter foraging behaviour at multiple scales, such changes must be evaluated in terms of spatial, temporal, and dietary behaviour. For example, Stewart et al. (2002) demonstrated that mule deer and wapiti in eastern Oregon avoid one another during 6-hour intervals, but do not maintain spatial separation over 7-day intervals. Although such studies are easily quantified, most provide little insight into the processes by which competition and facilitation occur and do not demonstrate altered performance (Putman 1996). Identifying determinants and dynamics of performance is difficult in natural settings where performance may change in response to predation, disease, and variable resource availability (Connell 1983). Controlled grazing experiments allow researchers to control these factors and expose the processes that result in competitive and facilitative relationships (Hobbs et al. 1996a, 1996b; Didkowsky 2006).

To assess when competition and facilitation occur during summer and autumn, I conducted three experiments comparing the spatial distribution and foraging behaviour of a focal species grazing in a mixed-species assemblage to the same species (1) foraging alone, (2) foraging alone following another species, or (3) foraging alone following two other species. My research was conducted in the aspen parklands of Alberta where I used an ungulate guild comprised of bison (*Bison bison*), wapiti (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*; Allen 1877, Murie 1951, Soper 1964, Telfer and Scotter 1975). Comparisons took place during three 15-day periods, with the focal species changing depending on the period. I estimated daily intake (kg/day) and fecal nitrogen (%) and assumed that competition occurred when one or both decreased, and that facilitation occurred when one or both increased. I repeated evaluations in summer and autumn because I predicted that species would respond differently as the availability of high quality resources declined.

I hypothesized that behavioural interactions would be driven by body size and gut constraints (reviews Hanley 1982, 1997). Because large-bodied organisms have absolutely high metabolic requirements (Kleiber 1961) and are socially dominant (Schoener 1983, Berger 1985, Persson 1985), I predicted that bison would not be affected by the foraging of other species. Because large-bodied ungulates increase access to high-quality forage (Vesey-Fitzgerald 1960, Gordon 1988), I predicted that wapiti, an intermediate forager that feeds on a mixture of forbs and graminoids in summer (Cook 2002, Gibbs et al. 2004), would increase intake and diet quality (Hanley 1982, Merrill 1994) by selecting areas previously grazed by bison. Furthermore, because I expected plant senescence would negate the benefit of following bison, I predicted that wapiti would maintain intake by selecting independent of bison in autumn. Rather I predicted that wapiti would increase selection for shrubs, whose leaves breakdown faster than graminoids (Spalinger et al. 1986) allowing more efficient energy accumulation. Because I expected wapiti would deplete high-quality forage revealed by bison in summer, I predicted that deer would increase intake and diet quality by selecting areas preferred by bison but not wapiti. Finally, as plants senesced and wapiti depleted high-quality forage in autumn, I predicted that deer would maintain intake and diet quality by avoiding areas selected by bison and wapiti. Consequently, I expected facilitative interactions in summer, when resources were abundant, and competitive interactions in autumn, when resources were more limiting.

2.2 Methods

2.2.1 Study area

Research was conducted at University of Alberta Kinsella Research Ranch (53 °01'N, 111 °34'W), located 150km east-southeast of Edmonton, Alberta. Climate at the ranch is continental with 115 to 125 frost-free days (Chetner et al. 2003). The mean annual temperature averages 2.3 °C and total annual precipitation averages 414mm (Environment Canada 2005). Mean summer (June and July) and autumn (September and October) temperatures are 15.8 °C and 7.4 °C and total precipitation averages 204mm. The ranch is located within the Viking Upland physiographic district (Howitt 1988), where it overlies moderately calcareous bedrock (Mossop and Shetsen 1994). The area is characterized by knob and kettle terrain dominated by the Elnora soil group, a well-drained assemblage of Chernozemic soils interspersed with poorly drained Gleysolic depressions and small portions of Solonetzic soils (Howitt 1988). Vegetation on the ranch is representative of the aspen parkland ecoregion (Strong 1992), consisting of a grassland-forest mosaic with graminoid-dominated uplands, interspersed with lowland forests and riparian meadows. Within the study area, I distinguished six vegetation communities: mixed prairie grassland, fescue grassland, shrubland, aspen forest, riparian meadow, and riparian edge.

2.2.2 Experimental design

I examined spatial distribution, forage intake, diet composition, and fecal nitrogen of three ungulate species during two 45-day foraging trials, one in summer (1 June to 15 July 2005) and another in autumn (1 September to 15 October 2005). Each foraging trial consisted of three 15-day periods, during which, species were deployed in three replicated sequences (n=9): (1) bison, wapiti, and mule deer foraging simultaneously; (2) a sequence of bison, wapiti, mule deer foraging for 15 days each; and (3) a sequence of mule deer, wapiti, and bison grazing for 15 days each.

To control for phenological changes in vegetation, my study consisted of three experiments. Individual experiments were composed of one or two intra-specific comparisons, each of which contained two or three treatments (Table 2.1). In the first 15-day trial, I compared the behaviour and daily intake of both bison (B1) and deer (D1) foraging alone to the same species foraging simultaneously in a mixed group of bison, wapiti, and deer (S1). In the second 15-day trial, I compared wapiti foraging alone in paddocks previously grazed by either deer (WD2) or bison (WB2) to wapiti foraging simultaneously with bison and deer in paddocks previously grazed by the same mixed group for 15 days (S2). Finally, in the last 15-day trial, I compared both bison (B3) foraging alone in paddocks previously grazed by deer followed by wapiti, and deer (D3) foraging alone in paddocks previously grazed by bison followed by wapiti, to the same species foraging simultaneously in a mixed group of bison, wapiti and deer previously grazed by the same group for the previous 30 days (S3).

Paddocks varied in size (Table 2.2), but the average proportions of six vegetation communities were similar across the triplicate paddocks (nonparametric MANOVA, df =12, χ^2 =13.12, P<0.36). The number of individuals within each 15-day period was constrained to insure there was equal forage removal across paddocks given the *a priori* 45-day stocking rate of 2.4 animal unit months/ha (Society for Range Management 1998; Appendix II.A). As a result, the number of individuals within each paddock differed between the sequential and simultaneous foraging sequences (Appendix II.D). The two sequences contained six bison, four wapiti, and three deer, whereas the simultaneous sequence contained three bison, three wapiti, and two deer.

The study was comprised primarily of non-pregnant adult and sub-adult females, but four bison gave birth and were allowed to remain within the study with their calves. The mean body mass of adult and sub-adult bison, wapiti, and deer differed between species at the beginning of both the summer (Appendix III; ANOVA, df=3, F=101.42, P<0.01; Bonferroni *post hoc*, P<0.01) and autumn (ANOVA, df=3, F=70.69, P<0.01; Bonferroni *post hoc*, P<0.01) trials. Animal handling was conducted according to University of Alberta animal ethics protocols HUDS 2004-33B and HUDS 2004-33C.

2.2.3 Diet composition and fecal nitrogen

Feces were collected during the summer and autumn to compare the diet composition and fecal nitrogen of each species. Feces were collected at the end of each 45-day trial and therefore reflected species' diet during each 15-day trial when grazed alone and during each 45-day trial when grazed simultaneously. Six composite samples were collected in each paddock for every species, each consisting of 2-3 pellets collected from 5 individual fecal samples. The six samples were pooled into two independent composites and oven dried for a minimum of 48 hours at 50 °C.

Diet composition (Appendix IV) was estimated at the Wildlife Habitat Nutrition Laboratory, Washington State University. Botanical composition was determined by modifying existing microhistological techniques (Sparks and Malechek 1968, Holechek and Vavra 1981, Holechek and Gross 1982). The relative cover of plant fragments was quantified at 25 randomly located microscope views on each of eight slides per sample (Korfhage 1974, Davitt 1979). Botanical composition was calculated by dividing the cover of each genus by the total cover and multiplying by 100. Genera were collapsed into three forage classes (graminoids, forbs, shrubs). Treatments were compared with nonparametric MANOVA, which tests the equality of mean ranks using the chi-square distribution (Puri and Sen 1971, Finch 2005). Nonparametric MANOVA was also used to evaluate diet composition within each forage class. The inability to consistently identify forb genera prevented analyses from being conducted on forbs, but genera within the graminoid (*Agrostis*, *Bromus*, *Calamagrostis*, *Carex*, *Dactylis*, *Deschampsia*, *Elymus*, *Hesperostipa*, *Juncus*, *Poa*) and shrub (*Populus*, *Rosa*, *Salix*, *Shepherdia*/*Eleagnus*,