University of Alberta

Estimating Winter Carrying Capacity for Bison in Wood Buffalo National Park

by

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Abstract

Bison (*bison bison*) in the Peace-Athabasca Delta (PAD) of Wood Buffalo National Park have been fewer than the neighbouring Hay Camp since the late 1990s despite being greater in the 1970-80s. I compared the winter nutritional carrying capacity (K) of the PAD to the Hay Camp, assuming varying snow depth and forage preferences, to determine whether K was restricting in the PAD. I sampled plant cover and biomass to estimate forage availability and quality within five vegetation types, and estimated K for the extent of these types. The PAD had more biomass of preferred species, *Carex atherodes* and *Calamagrostis* spp., than the Hay Camp, resulting in 4 to 12 times the K of the Hay Camp. I simulated the effect of non-native plants on K assuming a 65% average reduction in preferred forage. Non-natives were more widespread and abundant in the PAD, but did not reduce K below that of Hay Camp.

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CHAPTER 1

Bison Populations, Management, and Research in Wood Buffalo National Park

Wood Buffalo National Park (WBNP) is Canada's largest national park and one of the largest national parks in the world. Established in the early 1920s, it is now home to the most genetically diverse herd of wood bison in the world (Wilson and Stroebeck 1999). The park is located in the northeastern portion of Alberta, crossing into the Northwest Territories, and was established in 1922 to protect a declining herd of wood bison (*Bison bison athabascae*) in a 26 800 km^2 area north of the Peace River (Carbyn et al. 1993). Ferguson (1990) believed the decline in wood bison in this area began in the 1840s due to the heavy demand for meat by local trappers and forts, while Raup (1935) believed the bison decline was most rapid between 1860 and 1893 due to severe winters and deep, crusted snow. Nevertheless, though about 1500 bison were reported in the WBNP by 1983 (Carbyn et al. 1998), by the turn of the century bison numbers may have gone as low as 300 animals (Graham 1923). While the reasons for the decline in bison at the turn of the century remain unknown, the decline was reversed with a controversial introduction of over 6600 plains bison (*Bison bison bison*) into WBNP in 1925, primarily at sites near Hay Camp along the Slave River. During the winter of 1925-26, about 400 of the introduced bison crossed the Peace River and moved into the Quatre Fourches and Sweetgrass regions of the Peace-Athabasca Delta (PAD) (Carbyn et al. 1993), and in the same year an additional 17,408 km^2 south of the Peace River were added to the Park.

While there were many references to bison in the PAD prior to the introduction of plains bison (Gates et al. 1992), large numbers of bison were not reported there and the importance of the PAD as bison range in the era of the fur trade remains in debate. Nevertheless, it is unlikely that numbers of bison were ever as high as observed after the introduction of the plains bison in the early 1920s (Carbyn et al. 1993). Several explanations have been offered to explain why bison populations may not have been as high in the PAD prior to introductions (Carbyn et al. 1993). First, vulnerability to hunting in the open PAD relative to the wooded area has been proposed, but little data, other than rough estimates of potential annual bison take (Carbyn et al. 1993, FEARO 1990) exist to address this hypothesis. Second, Delta conditions may have been different from those during the high bison numbers of the mid 1900s; yet again there is little information to support this. Third, wood bison may have preferred small prairies interspersed by woodlands whereas plains bison may have preferred larger more open meadows. However, more recent studies on wood bison in the McKenzie Bison Sanctuary have not supported this explanation since wood bison also tend to concentrate in open meadow areas (Larter and Gates 1991).

With the introduction of plains bison, the number of resident and introduced bison increased and likely numbered between 10 000 and 12 000 animals between the 1930s and 1960s (Soper 1941, Fuller 1950, Novakowski 1961). This was a period of initially low wolf populations, although wolf predation was considered significant by the 1940s leading to intensified poisoning. Aerial surveys also were conducted at this time on primary bison ranges across the Park, although they were not always flown regularly (Carbyn et al. 1998). The increase in bison during this time occurred despite the presence of tuberculosis (*Mycobacterium bovis*), known to be present in the released bison because the herd had tested positive for the disease prior to arrival at WBNP. Further, the presence of brucellosis (*Brucellus abortus*) in the population was confirmed in 1956 and the first outbreak of anthrax (*Bacillus anthracis*) occurred in 1964.

By the 1970s, the bison numbering ~10 000 in WBNP started to decline. From the aerial survey data collected between 1971-1998, Carbyn et al. (1998) showed a decline in the bison herd south of the Peace River (Area I) that was not evident north of the Peace River (Area II). Joly and Messier (2004) suggested that the population grouping used by Carbyn et al. (1993, 1998) relative to the Peace River obscured trends of five populations they identified based on bison movements from telemetry studies conducted between 1997 and 2000. In their analysis of trends among these five populations Joly and Messier (2004) concluded that the decline in the PAD bison population was not distinct from Hay Camp, the PAD and Hay Camp being the two areas from which numbers are most reliable (95% confidence intervals overlap). This contradicted Carbyn et al. (1993:240, 1998), who concluded that bison south of the Peace River declined more precipitously. More recently, Bradley (2002), based on his analysis of aerial total count data through 2002, reported that Hay Camp subpopulations identified by Joly and Messier (2001) had been increasing slightly while the PAD population continued to decline. The most recent survey data (2001-2003) may indicate a possible leveling off of this decline (Bradley 2002).

Several hypotheses have been proposed to explain the decline in the abundance of bison in the PAD subpopulation. First, Gates et al. (1997) formalized the ideas of Carbyn et al. (1993) in the *habitat dispersion hypothesis*. This hypothesis proposed that where bison concentrate with high spatial and temporal predictability, such as the use of the large meadows in the PAD, they are more vulnerable to predation than in less predictable locations, as has been suggested for other areas of the Park. Habitat changes in the park blamed on the W.A.C. Bennett dam, constructed upstream along the Peace River, were considered to have forced the PAD bison into these higher concentrations, but such changes and their cause have been contested (Timoney et al. 1997, Timoney 2002).

Second, since the discovery of tuberculosis and brucellosis in WBNP bison in the late 1940s, it has been suggested that the debilitating effects of these diseases may directly influence bison demography by reducing reproduction or indirectly predisposing bison to other mortality factors (Carbyn et al. 1993, Joly and Messier 2001). For example, tuberculosis can weaken animals, reduce conception, and impede mobility especially because arthritis is a common complication; yet bison infected with TB can often survive for long periods (Carbyn et al. 1993). Similarly, brucellosis can cause reproductive failure through several means including abortion and reduced milk production. However, while an individual may harbor brucellosis, it may not impair physiological functioning (Williams et al. 1993). Estimates of disease prevalence in WBNP were obtained in conjunction with the slaughtering program with a major focus on disease status occurring more systematically after the mid-1950s.

Joly and Messier (2001) completed a comparison of current disease status in the PAD, Hay Camp and Nyarling River areas in WBNP. They found in their study (1997-2000) that 30.9% (107/346) of animals were seropositive for brucellosis which was related to age and sex of the animal. After controlling for age and sex, bison in the Hay Camp were 1.5 times as likely to be seropositive than bison in the PAD. Forty-nine percent of the bison (n =342) captured tested positive for tuberculosis and incidence of infection was again a function of age and sex; prevalence in the Hay Camp also was higher than in PAD. Further, they found that body condition and an interaction between brucellosis and tuberculosis were important factors for predicting bison pregnancy rate. While the results of disease prevalence were not directly comparable to earlier disease surveys, if the assumption that the age and sex classes of the two samples were similar is correct, the data indicate that prevalence of both diseases have not changed in the last 40 years. Nor did they find evidence indicating that disease prevalence was density dependent (Joly and Messier 2001), although they cautiously interpreted these results because if TB reduced pregnancy rates in the survivors prevalence rates may actually increase.

As a result, Joly and Messier (2004) proposed the *disease-predation hypothesis*. This hypothesis holds that the presence of tuberculosis and brucellosis reduces the productivity and survival of bison thus shifting bison populations from a high density equilibrium where food competition is regulatory to a low density equilibrium where predation by wolves is regulatory. They suggested this shift would be substantially greater than would be expected from the effects of disease alone, or more simply put, the combination of predation and disease would exceed bison population growth resulting in a decline in numbers while predation alone would not. Using a stochastic simulation model of bison population growth based on field data, their hypothesis was supported in that they found the probability was high that infected bison in the presence of wolf predation would stabilize populations at a low density (< 0.83 bison/km^2) where the probability of stabilizing at low density was low (< 10%) that uninfected bison, even considering anthrax and drowning. Without disease, they found that the majority of simulations resulted in densities within 33% of ecological carrying capacity, which they assumed to be 12 500 bison.

Nudds (1992) proposed a third hypothesis for the decline in the WBNP bison by suggesting that a large number of bison introduced in the 1920s are following a simple decline to a density more appropriate for large mammalian herbivores in the area after an eruption. Based on allometric relationships, Nudds (1992) proposed a null model against which to compare current bison declines. Using the interspecific relationships of 326 species ranging in weight between 0.01 and 2500 kg, Peters and Raelson (1984) found that body weight explained 67% of the variation in population density. Based on typical body masses for bison of different age and sex classes (~372 kg), and 5500 km^2 of principal bison habitat (Oosenburg and Carbyn 1985;69) as compared to 44 800 km^2 in WBNP, Nudds (1992) estimated a carrying capacity of 2035 bison in WBNP (0.37 bison/km^2 x 5500 km^2). However, given the high body weight of bison, the 95% confidence limits in this number included both 0 and the 14 000 bison estimate proposed previously by Novakowski and Choquette (in FEARO 1989:168-169). Nudds (1992) argued that the lower K value is corroborated by data on bison densities in the Mackenzie Bison Sanctuary, including actual bison densities of 0.2-0.5 bison/km^2 and the bison dispersal threshold of 0.5-0.8 bison/km^2 (Gates and Larter 1990). Further, he likened this density to those present prior to the introduction of bison to WBNP in the 1920s, and, based on the population trend data, suggested that the population decline was slowing. He also suggested that while the bison may have declined for reasons related to diseases, mass drownings, slaughter, predators and even habitat loss, the ultimate reason was "no other reason than it is attaining a new, appropriate equilibrium with available resources."

At first glance, Nudds' (1992) conclusion is not supported by the simulation modeling of Joly and Messier (2004), who suggest that a high equilibrium ecological carrying capacity could be maintained in the absence of disease. However, in Joly and Messier's simulations they assume an ecological carrying capacity of 12 500 bison. There are several reasons why using the pre-decline population estimates for ecological carrying capacity may not be justified. First, following the reasoning of Nudds (1992), bison may be following the decline of an eruptive sequence whereby they modify vegetation, decline, and then converge to a carrying capacity as is described in Caughley's plant-herbivore models (Caughley and Lawton 1976, Caughley 1979). No such dynamics in bison-vegetation interaction is represented in the stochastic model of Joly and Messier (2004), although bison can influence their environments through grazing and non-grazing habits (Campbell et al. 1994). Moreover, bison are not indiscriminate grazers (Knapp et al. 1999) and, as such, their habits can influence the growth patterns of plant communities (Vinton et al. 1993, Damhoureyeh and Hartnett 1997).

Second, the long-term carrying capacity of the Peace-Athabasca Delta (PAD) may have been altered due to environmental change. The PAD is the confluence of the Peace River, the Athabasca River, and the Birch River deltas, and is characterized by a complex of stream channels and perched basins forming a multitude of lakes. These lakes went through a reduction in areal extent in the early 1970s (Dirschl 1973). In order to curb the changes in the PAD and preserve the ecosystem, the governments of Canada, Alberta, and Saskatchewan built a dam in the Quatres-Fourches Channel in 1971 to set water levels back to those similar to before dam construction, but this was only a temporary measure because it impeded fish movement. Two control weirs were put in place in 1976 to replace the dam and continue the regulation of water levels. Hydrologic models suggested while peak water levels in summer were similar to those before dam construction, the amplitude of water level fluctuations would be lower (PADIC 1987).

If hydrological changes have occurred, forage availability for bison is likely to have been altered. For example, reduction in flooding events may reduce forage availability due to successional progression of the vegetation communities, normally kept at bay by repeated spring flooding. Dirschl (1973) outlines the expected succession of plant communities as they move from aquatic communities to emergents, meadows, shrubs, and eventually forests. He noted rapid colonization of newly dried areas by *Carex atherodes* and *Salix* spp., among others and speculated that competition between *Carex atherodes* and *Calamagrostis canadensis* leads to meadow communities. Monitoring of vegetation cover from 1993-2002 suggests this model of succession is overly simplified, however. For example, changes do not occur uniformly across the Delta, with some areas changing from wet to dry locations while others do the opposite in the same period of time (Timoney 2004).

In addition to changes from flooding, fire may have been responsible for keeping woody plants from overgrowing the various meadows important to bison. *Salix* spp. growth is impeded by occasional fire, though the precise impacts on vegetation as a whole is often dependent on the timing of the burn (Coppedge and Shaw 1998, Quinlan 1999). Unburned meadows accumulate litter over time that can impede growth and reduce production, especially in *Carex*-dominated wet medows (Quinlan, 1999). Recent fire suppression may be the cause of grasslands being overgrown by shrubs (Schwarz and

Wein 1997). Furthermore, freshly burned areas are attractive to bison (Coppedge and Shaw 1998). In Alaska, a herd was seen to expand its winter range for several years following a fire as grasslands replaced the shrub communities (Campbell and Hinkes 1983).

Finally, the influence of non-native species on preferred bison forage has not been addressed. Non-native species have been expanding in northern Canada (Wein et al. 1992). Peterson (2001) reported 60 unique non-native species in WBNP in disturbed areas, primarily along major roads and other human-disturbed areas. The dispersal of these species is a concern in the park and is recognized as being an increasing threat to native species (Peterson 2001). In particular, the invasion of non-native species has been evident in disturbed areas such as roadways and historical residences (e.g., Hay Camp, Peace Point) (Wein et al. 1992). Timoney (2004) also suggested that human activity and bison grazing influenced the presence of weeds in the Sweetgrass area of the PAD with an increase in some weedy species and a decrease in others between 1993 and 2001. Of the non-native species that have been found, broad-leaved plantain (*Plantago major*) and Kentucky bluegrass (*Poa pratensis*) are known to invade disturbed areas (Stearman 1983, Vallentine 1989). Other species such as Canada thistle (*Cirsium arvense*) and perennial sow thistle (*Sonchus arvensis*) have been established in the park and are regarded as persistent and competitive plants responsible for the loss of yield in agricultural fields in many parts of Alberta (Stearman 1983, AAFRD 1995, Grekul and Bork 2004). Continued invasion of non-native species may alter plant community composition and thus has implications for bison carrying capacity if these invasive species were to restrict the growth of preferred bison forage.

It seems clear that an understanding of the dynamics of ecological carrying capacity has important implications for the bison of WBNP. To date, various attempts have been made to estimate ecological carrying capacity using a forage-supply approach. For example in WBNP, Allison (1973) estimated the number of bison that could be supported by in a 2391 km^2 area of the PAD assuming a third of the forage was accessible and intake requirements were 5454 kg of dry matter per year per average bison. She calculated a carrying capacity of 19 788 bison or a density of 8.3 bison/km^2, which is considerably greater than the 0.37 bison/km^2 estimated by Nudds (1992) from allometric relationships, greater than the 0.5-0.8 dispersal threshold (Carbyn et al. 1993), and greater than observations of bison in the area, which ranged from 5500 to 9263 bison. Similarly, Reynolds et al. (1978) calculated bison carrying capacity for the Slave river lowland based on the following estimates: an average 4400 kg/ha and 2280 kg/ha in wet and dry meadows; 1083 and 3720 ha of wet meadow and dry meadow; 33% and 50% of the forage available in wet and dry meadow; and a bison requiring 4307 kg/yr (11.8 kg dry matter/day). This resulted in 1350 bison supported by 48 km^2 or 28 bison/km^2 of meadow habitat only. Both studies concluded that food was not the limiting factor for existing bison populations.

Current models of nutritional carrying capacity incorporate several explicit nutritional constraints that illustrate the simplicity of the above estimates (Hanley and Rogers 1989). For example, from studies of the functional responses of ungulates, animals typically will not forage in areas where biomass availability is below a threshold. Deer stop feeding when forage biomass drops to approximately 25 kg/ha (Wickstrom et al. 1984, Spalinger et al. 1988). Range-supply calculations may overestimate forage-based carrying capacity when they include consumption of forage with sub-maintenance quality. When explicit nutritional constraints can be modeled, these biases can be minimized (DeYoung et al. 2000). Although several studies have quantified the nutritive value of important bison forage (Reynolds et al. 1978, Larter and Gates 1991), these have not been incorporated into estimates of bison carrying capacity in WBNP. Even with these improvements, however, important assumptions remain about requirements of free ranging animals, averaged age and sex class effects on body sizes, and constraints due to interference that may lead to a higher threshold at which animals starve or disperse. This has led to the belief that nutritional approaches are adequate to provide relative comparisons between areas rather than absolute estimates of forage-based carrying capacity (McCall et al. 1996).

Research Objectives

Bison in WBNP have undergone a tremendous fluctuation in population over the past century. Studies to date have considered the effects of predation and disease, but only postulated on the impacts of habitat change and its influence on available forage quantity and quality. The major objective of my research was to determine food-based carrying capacities (K) for the Hay Camp and PAD areas of the park and to ascertain whether forage quality and quantity is limiting existing bison populations given a variety of environmental factors including winter severity and the presence of non-native species.

I specifically address the following research questions:

(1) How much forage is available to bison in the Hay Camp and PAD, and what is its quality?

(2) What is the winter nutritional carrying capacity of the Hay Camp and PAD areas in the park, and is it limiting the existing bison population?

(3) Are non-native species abundant in the study areas, and what, if any, impact do they have on preferred bison forage and thus on the nutritional carrying capacity?

In chapter 2, I assess the nutritional requirements and constraints of bison and the quantity and quality of available forage across five vegetation types. I use the approach of Hanley and Rogers (1989) to define K as the number of animals of a given species that can be supported per unit area of habitat based on the availability of forage biomass and its quality relative to the animals' nutritional requirements. I evaluate the model's sensitivity to the nutritional constraints by varying the quality and quantity inputs independently. I compare the results between the two study areas given scenarios in which I alter the available forage based on assumptions about environmental effects on forage. Finally I assess the impact non-native species in the park have on preferred bison forage and thus on K. In Chapter 3, I evaluate my findings in light of past research and discuss the implications of my results given historical trends in bison numbers.

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CHAPTER 2

Estimates of Winter Carrying Capacity for Bison in Wood Buffalo National Park

Introduction

Carrying capacity (K) is a term that has numerous definitions. In terms of population dynamics, Begon et al. (1986) define K as the population density at which intraspecific competition leads to birth rates equalling death rates (i.e., no population growth). Similarly, Caughley (1979) defined ecological carrying capacity as the equilibrium between herbivores and their plant resources without interference from predators or humans. In contrast, others have defined economic carrying capacity as the population size held in place by managers, most often for economic or social purposes (Caughley 1979, MacNab 1985, Xie et al. 2001). In contrast to these demographic approaches, a number of alternatives have been developed to quantify the *nutritional carrying capacity* of an area, defined as the number of animals that can be supported based on the availability of nutrients and the ability of animals to assimilate those nutrients (Wallmo et al. 1977, Hobbs and Hanley 1999, DeYoung et al. 2000). Here I compare estimates of the nutritional carrying capacity for two areas of Wood Buffalo National Park to provide a frame of reference upon which to interpret my results.

Several past attempts have been made to estimate carrying capacity for bison in Wood Buffalo National Park. Nudds (1992) used a general allometric relationship between animal density and body size developed across a number of ecosystems (Peters and Raelson 1984) and estimated bison densities of 0.37 bison/km^2 but with confidence intervals inclusive of 0 and over 1500 individuals/km^2. The poor precision of his estimate resulted from bison's weight being at the high end of the body masses used to develop the allometric relationship to predict K, and from including density estimates of herbivores across the globe.

As part of the Peace-Athabasca Delta Project, Allison (1973) reported a nutritionally based K from estimates of preferred forage species in several habitat types. While Allison's approach was based on estimates of forage biomass from the nearby Slave River Lowlands, her assessment of carrying capacity was based only on quantity of accessible forage and daily intake and did not consider the quality of available forage, which can lead to overestimates of true carrying capacity (DeYoung et al. 2000). Furthermore, nutritional carrying capacity is not a static property of the habitat and without a long-term history of availability of resources this approach is best used to compare habitat quality between areas (Hobbs et al. 1982).

In their study of the effects of predation and disease on bison, Joly and Messier (2004) assumed carrying capacity in the park was equal to the maximum number of bison ever recorded, i.e., 12 500 bison in 5000 km^2 of prime habitat (Campbell and Hinkes 1983). However, it is not clear whether this is a reasonable assumption given the extensive human intervention that has occurred in this ecosystem in the past century and because bison can modify their own habitat (Campbell et al. 1994, Nudds 1992). In fact, Nudds (1992) suggested that the introduction of plains bison in the 1920s was a human-caused eruption in population and the observed decline in wood bison reflected a typical return to a food-based equilibrium. Furthermore, the establishment of non-native species has been recorded throughout the park, especially in disturbed areas (Wein et al. 1992, Peterson 2001a). Many non-native species have been known to colonize in disturbed soils and compete with native plants (Stearman 1983, Vallentine 1989), but some are particularly competitive. Plants such as *Cirsium arvense* and *Sonchus arvensis* are responsible for a loss in herbage yield in many pastures in Alberta (Stearman 1983, AAFRD 1995, Grekul and Bork 2004), and have been identified in abundance in the PAD (Timoney 2004). Furthermore, *Sonchus arvensis* appears to be increasing in the PAD over the last decade (Timoney 2004). These factors make identifying the extent of colonization an important goal for the park (Peterson 2001a). If invasive species replace native forage but are not preferred species in bison diets, or are unavailable in winter, changes to winter forage and thus K may have been occurring over time.

In this study, I use a comparative approach to assess two adjacent areas within Wood Buffalo National Park, specifically the Peace-Athabasca Delta (PAD) and Hay Camp, and determine the *winter nutritional carrying capacity* for bison within and between those areas. I used the approach of Hanley and Rogers (1989) to determine nutritional carrying capacity because of their model's ability to simultaneously consider both dry matter digestibility (DMD) and digestible protein (DP). They define K as "the number of animals of a given species that can be supported per unit area of habitat" over time based on the availability of biomass and its quality relative to the animals' nutritional requirements (Hanley and Rogers 1989). The model calculates the maximum biomass available for consumption given constraints on the minimum observed DMD and DP. It also constrains the diet such that no one forage species constitutes greater than a user-defined amount of the total biomass consumed. Further refinement of the model in terms of availability due to environmental effects (e.g. snow, drought) can be assessed by modifying the inputs as necessary.

My estimates represent the *maximum* number of animals based on food limitation without consideration of predation or other direct effects such as extreme flood events. My principal objective was to determine food-based carrying capacities (K) for the Hay Camp and PAD areas of the park and to ascertain whether forage quality and quantity could be limiting current bison populations. I chose the PAD and Hay Camp because existing bison numbers have been well-documented for decades and because these two areas were more accessible than the rest of the park.

Methods

Study Areas

Wood Buffalo National Park is a 44 800 km^2 natural area in the northwest of Alberta and southwest of the Northwest Territories. Mean annual temperature in the area is –3.3°C and precipitation is 349.3 mm (Peterson 2001b). For this study, I used the designations of Hay Camp and Peace-Athabasca Delta regions provided by Joly and Messier (2001a) and Bradley (2002) that were defined based on bison movements (Fig. 1). The Hay Camp study area is a largely forested, 6565 km^2 region east of the Slave River with major meadow complexes throughout (Jensen 2003). Human activity has been present in the area for many decades (Parks Canada 2001). Since the early 20th century several "hay camps" were established along the Slave River as sources of winter feed for horses. Currently, access to the area includes one all-season road between Fort Smith and the Peace River, several walking trails, a day-use area at the Salt Plains in the northwest, and a base camp for fire fighters and private cabins at Pine Lake.

In contrast, the PAD is an area of 8614 km^2 that is comprised largely of major water bodies (23%) including the Peace, Birch, and Athabasca River deltas, and Lakes Mamawi and Claire (Jensen 2003). The delta region itself, 36% of the total PAD study area (Allison 1973), is primarily an open meadow-shrubland complex dominated by sedges, grasses, and willows (Timoney 1996). The delta meadows are more expansive than meadow complexes in Hay Camp (Carbyn et al. 1993). Access is primarily by boat or helicopter, with the only roads limited to winter use.

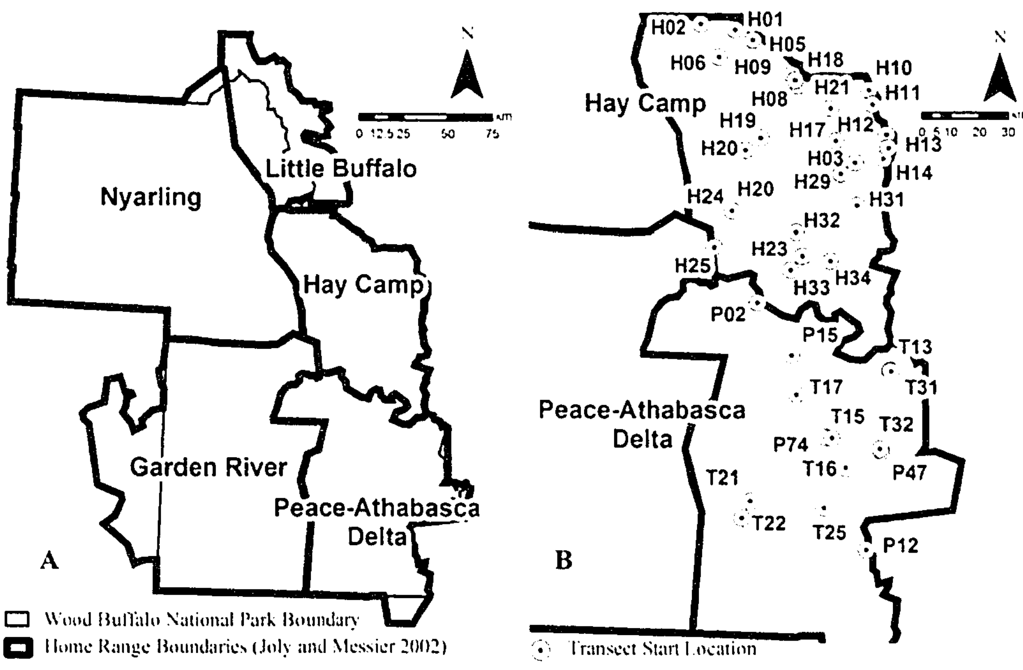

Fig. 1. (A) Map of the Hay Camp and PAD study areas as defined by Joly and Messier (2001) based on the ranges of the bison herds in Wood Buffalo National Park. (B) Distribution of transects sampled in the Hay Camp (H) and PAD (P) areas during the summer of 2003. Transects denoted by 'T' are a subset of Timoney's transects in the PAD established between 1993 and 1996 (Timoney 1996) and sampled as part of this study in summer 2003.

Forage Availability

I calculated total forage availability (kg/ha) for the PAD and Hay Camp by estimating the average forage biomass within 5 vegetation types weighted by their areal extent within each region. The areal extent of vegetation types in each of the PAD and Hay Camp were obtained from a vegetation classification of a Landsat 7 ETM+ image (Jensen 2003). The five vegetation types were derived by grouping 40 ecosite classes (80.2% overall accuracy) into five vegetation types (coniferous forest, deciduous forest, shrubland, graminoid meadows, and sedge meadows) and one non-vegetative type (including water, clouds and shadows, mud) (Appendix A). In the original classification (Jensen 2003), the 1999 forest burn was classified as *recent burn* (329 km^2, 72% in Hay Camp), which did not correspond to my 5 vegetation types. Based on helicopter reconnaissance of the area in the summer of 2003, and an unsupervised classification of the vegetated area within the burn area, I was able to estimate and map residual conifer forests, deciduous forests/shrublands, and graminoid/sedge meadows within the burn, but could not distinguish within these types further. As a result, I assumed the ratio of deciduous forest to shrublands (9:10 in Hay Camp, 7:5 in PAD) and grassland to wet meadow (9:5 Hay Camp; 2:1 PAD) within the burn was the same as in each study area to calculate the extent of my 5 types within the burn for my analysis.

Plant biomass was estimated along 25 transects in the Hay Camp and 14 transects in the PAD between 3 July and 15 August 2003 by post-stratifying sample plots along the transects into each of the 5 vegetation communities (Appendix B). Vegetation during this time was assumed to represent the maximum available biomass in winter. Transects ranged from 30 m to over 800 m in length, averaging 347 ± 217 m (mean ± SD) and sample plots were located systematically along the transects every 10 to 15 m. In the Hay Camp, sites were picked by delineating 1-km^2 grid cells within accessible areas (walking distance of roads) and randomly establishing transects in 16 cells with at least 3 vegetation types present. Because graminoid and sedge meadows were under-represented in this sample due to their relatively small extents, I established an additional 9 transects accessible by helicopter within the large meadow complexes in Hay Camp. In the PAD, I re-sampled 9 transects established by Kevin Timoney in 1993 as part of his efforts to monitor changes in vegetation composition (Timoney 1996) that had the most number of vegetation types intersected by the transect, and that were accessible (within walking distance or access by boat). I chose transects from throughout the PAD, including areas on the north and east portions of Lake Claire, the Birch River, Prairie River, Lake Mamawi, Sweetgrass, and the Revillion Coupee, to account for spatial variation. In addition, because Timoney's transects did not adequately sample the forests, I selected an additional 5 transects representative of forest types in the PAD in a manner similar to that of the Hay Camp with 1-km^2 grids primarily dominated by forest.

Percent cover for each plant species (forbs, graminoids, sedges, shrubs < 25cm in height) and others (bare ground, water, graminoid, leaf, and twig litter, mosses and lichens) was sampled in 0.25m^2-plots (353 in Hay Camp, 185 in PAD) located along each transect at 5-m intervals in open meadows or 15-m intervals in forests and shrublands. Cover was estimated on a per-species basis (i.e. the sum of per-species cover in a plot can exceed 100%). Herbaceous biomass (graminoids and sedges) was clipped to either 3 cm above the ground (even in standing water) or litter layer (where litter was sufficiently thick to indicate a threshold to grazing depth in the past several years, from personal observation). Thus, my estimates of vegetative biomass do not represent plant production *per se* but forage considered available to bison in winter. I assumed a linear relationship between biomass and species canopy cover in a plot. Biomass on a per species basis was estimated by multiplying the species' relative portion of total vegetated cover in a plot by the mean biomass within the 5 vegetation types. The resulting biomass estimate of a species per plot was averaged for each vegetation type in each study area.

At every fifth plot along the transects, the number of shrub stems of each individual > 25 cm height and a basal diameter (BD) for an average stem was recorded in each of the 4 quadrants of a 10-m^2 circle. Shrubs smaller than 25 cm were considered unavailable as forage in winter (Larter and Gates 1991). I used the general relationship derived by Visscher et al. (2004) between BD and woody current annual growth (CAG) for willow species to estimate biomass for an average stem in a quadrant. Four of the six willow species used to derive the relationship were present in my study area. I then estimated the woody CAG for each quadrant from total stem densities and the average CAG/stem and summed the values of each quadrant within the 10-m^2 plots. Additional information on other shrubs was collected (Appendix 3) but only willow biomass was an input into the carry capacity model because it was the only woody forage to make up a significant proportion of bison winter diet (Reynolds 1976, Larter and Gates 1991). I compared biomass between study areas by vegetation type using a t-test ($\alpha = 0.05$).

Forage Quality

Estimates of forage quality were limited to a subset of plant species based on known bison diets in similar environments, and plant species abundance in the study areas. Plant species considered as *major* forages (> 5% of bison diet during any winter month, Reynolds 1976) included all species in the genus of *Calamagrostis*, and the sedge species *Carex atherodes*. However, because there were substantial amounts of *Carex aquatilis*, other *Carex* spp., *Elymus innovatus*, *Agrostis scabra*, *Poa palustris*, and particularly *Scolochloa festucacea* in the PAD, I collected these species for analysis as well (Appendix 4). Samples for each species were collected from 15-20 plants from at least 8 locations in the Hay Camp and 4 locations in the PAD. Samples of herbaceous forage species were collected in the Hay Camp and PAD in early fall after a frost to represent forage quality in winter. I used a Wilcoxan ranked sums test (α=0.10) to determine whether the quality of samples between the two study areas differed.

All forage quality samples were dried at < 60°C for 48 hours. *In vitro* dry matter digestibility (IVDMD) was determined at the Agriculture Canada Laboratory in Lethbridge, Alberta using Ankom Daisy incubators with cattle innoculum (Ankom Technology, Macedon, NY, Cherny et al. 1997). Crude protein (CP) was estimated for the samples using the IVDMD analysis, then indexed by the amount of nitrogen multiplied by a factor of 6.25 (Van Soest 1982) and converted to digestible protein (DP) using the relationship between dietary protein and biological value reported by Robbins (1983: Fig.13.12).

Carrying Capacity Model

I used the original model of Hanley and Rogers (1989:Fig. 1) to predict nutritional K (Fig. 2) modified to select iteratively the inputs for 4 variables (species IVDMD, DP, biomass, and daily intake/average bison) randomly within 1 standard deviation of the estimated mean value assuming a normal distribution. Thus, model results are expressed as the mean $\pm$ SE for 1000 model runs based on variation of these 4 inputs (Appendix 5).

Read list of species in habitat, available biomass, and mean and SD DMD and protein concentrations.

Select values for DMD and protein concentrations for each species from the distributions provided.

Read animal DM intake and minimum DMD and protein requirements.

STEP 1. Ignore protein constraint and assume all biomass available for each species. Rank species from high to low DMD.
1a. Add available biomass until DMD constraint reached.
If species contributes > 75% total biomass then reduce amount available for that species by 0.3%, reset totals, and repeat at **1a.**
Otherwise calculate protein concentrations for resulting mix.

STEP 2. Ignore DMD constraint and assume all biomass available for each species. Rank species from high to low protein.
2a. Add available biomass until protein constraint reached.
If species contributes > 75% total biomass then reduce amount available for that species by 0.3%, reset totals, and repeat at **2a.**
Otherwise calculate DMD concentrations for resulting mix.

STEP 3. If resulting total biomass is < 25 kg/ha for either **STEP 1** or **STEP 2** then there is no solution, carrying capacity is zero.

STEP 4. If only **STEP 1** satisfies both constraints then **STEP 1** is the solution; subtract 25 kg/ha from total biomass, compute carrying capacity for that mix.
If only **STEP 2** satisfies both constraints then **STEP 2** is the solution; subtract 25 kg/ha from total biomass, compute carrying capacity for that mix.
If both **STEP 1** and **STEP 2** satisfy both constraints then the step with greatest biomass is the solution; subtract 25 kg/ha from total biomass, compute carrying capacity for that mix.

STEP 5. If neither **STEP 1** or **STEP 2** satisfy both constraints then the solution is somewhere in between. Assume all biomass is available for all species.
5a. Add in available biomass of each species that had 100% included in **both STEP 1** and **STEP 2.** Add in additional biomass for each species in the order of the greatest amount that can be added while still satisfying both DMD and protein constraints. Continue adding biomass until constraints are reached.
If a species contributes > 75% to total biomass then reduce amount available for that species by 0.3%, reset totals, and repeat at **5a**;
Otherwise calculate DMD and protein concentrations, subtract 25 kg/ha from total biomass, and compute carrying capacity for resulting mix.

Fig. 2. Flow diagram of the nutritional carrying capacity model, adapted from Hanley and Rogers (1989).

Model constraints. I constrained diets so that no one species could exceed more than 75% of the total biomass consumed based on previous work on winter diets of bison in the Slave River lowlands (Reynolds 1976). The model further limited consumption to species that contribute at least 25 kg/ha of biomass assuming bison would not forage in areas with lower forage availability.

Animal requirements. The daily intake rate of an average bison was based on body weight. An average body weight of 550 kg was derived based on (1) the age distribution of bison counted in spring surveys across the Hay Camp and PAD between 2000 and 2002 (Table 1), (2) assuming a sex ratio of 1:1 for adults (M. Bradley, Parks Canada pers. comm.) and (3) body weights of bison reported by Soper (1964) and Meagher (1973). I used a daily intake rate of 10.4 $\pm$ 1.7 kg dry matter per day based on average intakes of 1.6-1.8% of body weight in winter during a 10-15% body weight loss (Feist 2000). I also assumed a minimum of 48% forage digestibility (Feist 2000), and 5.5% digestible protein (Mould and Robbins1981) as a minimum requirement. A sensitivity analysis was conducted to understand the effect of the assumed minimum required DMD and DP and the minimum required intake by an average bison holding all other variables constant and changing the baseline value by $\pm$ 5%, 10%, 25, and 50%.

Model Scenarios. The duration of winter was set at 180 days corresponding to the period from October to March. A total of 4 scenarios were run in the HC and PAD to represent different potential carrying capacities under differing environmental conditions

Table 1. Sex ratios and average body weights of bison in Wood Buffalo National Park.

	Bull	Cow	Yearling	Calf
Herd Ratios	100	100	41	40
Body Weight (kg)	907.0	453.5	272.5	158.5

and dietary preferences. The first scenario, representing the maximum potential of the landscape to support bison, allowed all available biomass of all forage species to be consumed. In the second scenario, I limited the amount of potential herbaceous forage accessible to bison due to snow and ice cover to one third of the available herbaceous forage to be comparable to Allison (1973) and by 10% of woody CAG (W. Olsen, Parks Canada pers. comm.). The third scenario considered nutritional K in terms of preferred forage species only. The fourth and final scenario limited both available forage (as in Scenario 2) and assumed diets as in Scenario 3.

Non-native Species

To assess the effects of potential invasion by exotic species on K, I selected species that I encountered in my transects (Appendix 6) from the list of known non-native species in the park (Peterson 2001a). First, I used a Mann-Whitney test ($\alpha = 0.10$) to determine if non-native species cover was greater in the PAD than Hay Camp. Then, to ascertain whether the presence of non-native species had an impact on the percent cover of preferred bison forage species I compared the percent cover of the preferred forages between plots with and without at least one exotic species present using a Mann-Whitney test ($\alpha = 0.10$). Because I did not collect biomass samples for forbs I assumed that changes in percent cover reflected changes in percent biomass. Finally, I used the average percent difference in mean cover of preferred forage between plots where non-native species were present and absent to recalculate the carrying capacity. Because I was interested in the impact of changes to preferred bison forage on K I used both Scenario 3 (preferred forage, all biomass) and Scenario 4 (preferred forage, limited biomass) as the basis for my results.

Results

Vegetation Types

Forest was a major component of both the Hay Camp and PAD regions, but was a relatively larger portion of the vegetation extent in Hay Camp (67%) than in the PAD (42%). Areal extent of graminoid and sedge meadows in Hay Camp was limited (7% of total area) while in the PAD graminoid and sedge meadows were more abundant (21%) (Fig. 3).

Forage Availability

Forage biomass was greatest in the sedge and graminoid meadows with the amount of forage 3 to 6 times more abundant ($P < 0.01$) in the PAD than the Hay Camp (Table 2). As a proportion of total forage, the two primary bison forages (*Calamagrostis*

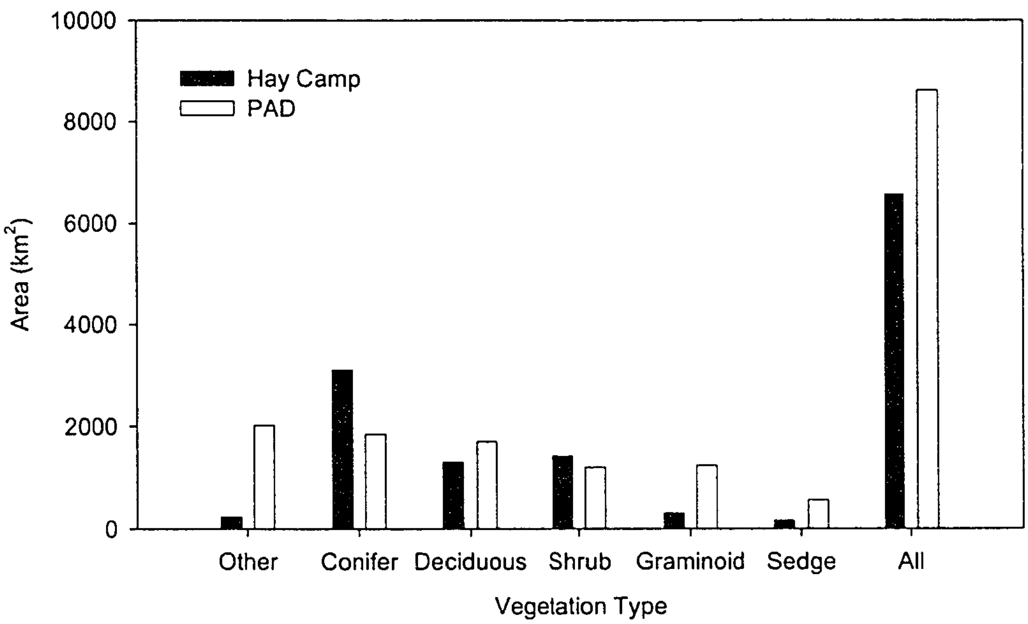

Fig. 3. The amount of area in Wood Buffalo National Park's Hay Camp and PAD regions by vegetation type. 'Other' consists primarily of water bodies but also clouds, shadows, roads, and other anthropogenic features.

Table 2. Mean ± SD of biomass (kg/ha) of selected forage species in the Hay Camp and PAD regions of Wood Buffalo National Park. Values in parentheses represent sample sizes within vegetation types (n).

Species	Conifer	Deciduous	Shrubland	Graminoid	Sedge
Hay Camp	(72)	(41)	(98)	(98)	(44)
Calamagrostis spp.	1.03±11.53	4.21±41.24	50.36±274.62	230.61±912.48	72.96±449.63
Carex aquatilis	0.31±2.61	0.00±0.00	51.24±113.56	4.32±25.59	192.46±359.29
Carex atherodes	0.00±0.00	0.00±0.00	20.94±67.98	24.51±104.61	201.00±383.35
Scolochloa festucacea	0.47±3.94	1.74±11.09	0.00±0.00	21.57±109.10	0.00±0.00
Other Grass	13.76±51.57	23.70±100.28	48.65±277.82	288.12±1008.39	43.65±399.80
Other Sedge	8.96±15.91	19.48±35.47	118.24±175.80	62.61±158.07	247.07±419.58
Salix spp.	3.26±14.22	21.12±29.75	80.20±133.06	6.34±40.50	22.40±115.34
TOTAL	*27.79±57.18*	*70.25±111.01*	*369.64±378.56*	*638.07±1032.90*	*779.55±790.72*
PAD	(36)	(13)	(57)	(47)	(32)
Calamagrostis spp.	0.00±0.00	0.00±0.00	55.41±216.27	1153.96±4269.93	160.84±924.11
Carex aquatilis	0.00±0.00	0.00±0.00	0.00±0.00	3.21±21.92	79.51±352.38
Carex atherodes	0.00±0.00	0.00±0.00	16.67±42.38	531.25±879.94	1404.36±1764.97
Scolochloa festucacea	0.00±0.00	0.00±0.00	2.62±14.07	427.39±1052.74	39.27±159.38
Other Grass	0.07±0.55	1.67±10.57	55.41±147.50	795.01±3136.74	43.38±308.12
Other Sedge	0.02±2.10	0.00±0.00	0.35±2.59	120.46±513.38	374.54±933.24
Salix spp.	0.00±0.00	0.00±0.00	68.91±115.78	0.17±0.87	13.93±55.85
TOTAL	*0.09±2.17*	*1.67±10.57*	*199.37±192.77*	*3031.44±3462.04*	*2115.93±2057.93*

spp. and Carex atherodes) constituted less ($P < 0.01$) of the available forage in graminoid meadows (mean ± SE: 40 ± 5%) and sedge meadows (36 ± 7%) in the Hay Camp than the same two species in graminoid (56 ± 7%) and sedge meadows (74 ± 7%) of the PAD. In contrast, forage abundance was 2 times greater ($P < 0.01$) in shrubland and was substantially higher ($P < 0.01$) in the forest communities in the Hay Camp than in the PAD, although forage in forests was relatively low in both areas. When averaged across the area, total available herbaceous forage (kg/ha) was 5.5 times greater ($P < 0.01$) in the PAD than Hay Camp while willow biomass was similar between the two areas ($P = 0.57$) (Fig. 4).

Forage Quality

There was a significant difference in the dry matter digestibility (DMD) of *Calamagrostis* spp. ($P < 0.01$) and in DP of *Carex atherodes* ($P = 0.02$) between the Hay Camp and

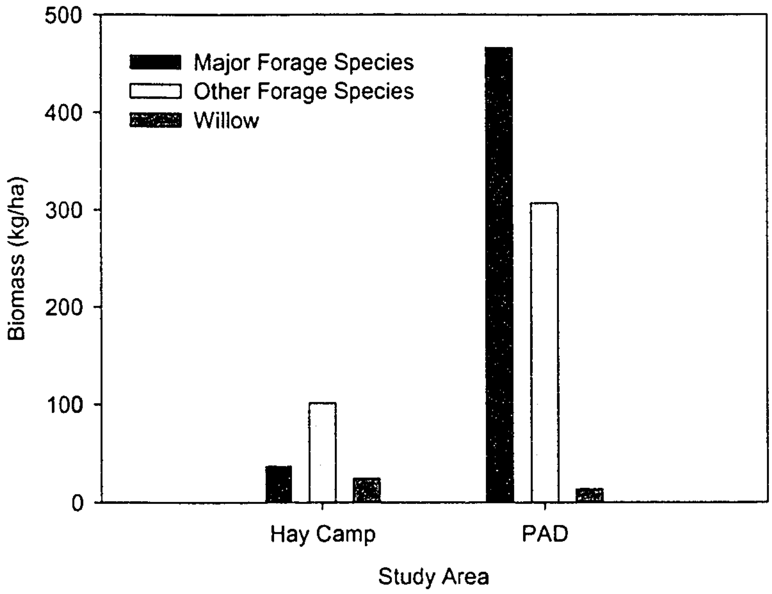

Fig. 4. Average biomass (kg/ha) of major bison forages, other potential forages and willow (*Salix* spp.) in Wood Buffalo National Park's Hay Camp and PAD regions.

PAD but no significant difference in DMD ($P = 0.40$) or DP ($P = 0.29$) for *Salix spp.* (Table 3). Comparisons could not be made for *Carex aquatilis* or *Scolochloa festucacea* because samples were not collected in both study areas. Other grasses and sedges also could not be compared because the species within these categories were not the same between study areas. Because of the small sample sizes (n=4) and inconsistency across plant species and measures, I did not include the differences found in *Calamagrostis* spp. and *Carex atherodes* between study areas in my analysis to keep my comparisons between areas conservative (Table 3). Instead I assessed the effect of this decision by comparing the model results assuming quality is different and not different.

Nutritional K for Bison

Bison nutritional carrying capacity was 3.8 – 12.1 times greater in the PAD than in the Hay Camp across all scenarios (Table 4). Furthermore, the variation in K among scenarios was greater in the Hay Camp than the PAD. Carrying capacity for Hay Camp in the most constrained scenario (preferred forage, limited species) was 4% of the least constrained (all forage, all species) while the comparable value for the PAD was 11% (Fig. 5). Differences in K between areas resulted not only because of higher overall biomass availability in the PAD, but because Carex atherodes, a high-quality forage, was more abundant in the PAD than Hay Camp. Because the major forage species were more abundant in the PAD relative to the Hay Camp, constraining K by the species considered to be preferred forages (Scenarios 3 and 4) had less effect on carrying capacity in the PAD than the Hay Camp (Fig. 5). Carrying capacity in the PAD was relatively higher than in Hay Camp whether DMD or DP of Calamagrostis spp. and Carex atherodes were

Table 3. Mean ± SD dry matter digestibility (DMD) and digestible protein (DP) for major forage species for bison in Wood Buffalo National Park. Samples were collected in the Hay Camp and Peace-Athabasca Delta (PAD) study areas in late summer and early fall of 2003. Other grass consists of *Elymus innovatus* in Hay Camp and *Agrostis scabra* and *Poa palustris* in the PAD. Other sedge consists primarily of *C. norvegica, C. concinna, and C. rostrata* in Hay Camp, and *C. sychnocephala* in the PAD.

	Hay Camp			PAD			Both		
Species	n	%DMD	%DP	n	%DMD	%DP	n	%DMD	%DP
Calamagrostis spp.	10	52.4±3.5	5.6±1.2	3	36.7±3.8	4.6±1.2	13	48.8±7.7	5.3±1.3
Carex aquatilis	4	49.4±2.6	5.6±0.6	--	--	--	4	49.4±2.6	5.6±0.6
Carex atherodes	4	53.4±6.6	5.3±3.0	4	55.4±3.4	7.2±1.4	8	54.4±5.0	6.0±1.6
Scolochloa festucacea	--	--	--	4	44.1±3.4	4.7±1.3	4	44.1 ± 3.4	4.7 ± 1.3
Other Grass	4	60.8±4.0	6.2±0.3	6	48.3±8.6	6.4±1.9	10	53.3±9.4	6.4±1.5
Other Sedge	4	52.1±5.6	8.9±2.4	1	36.9	6.9	5	49.0 ± 8.3	6.0 ± 0.9
Salix spp.	2	41.2±4.0	8.0±2.0	3	43.6±1.8	6.4±2.7	5	42.6 ± 2.7	7.5 ± 0.4

Table 4. Area-weighted mean ± SE (n=1000) values of nutritional carrying capacity (bison numbers) in the Hay Camp and PAD areas of Wood Buffalo National Park. Estimates using equal quality are based on assuming no difference in forage quality between Hay Camp and PAD, while unequal quality estimates assume there is a difference between study areas.

Scenario	Equal Quality		Unequal Quality	
	Hay Camp	PAD	Hay Camp	PAD
1. All Forage, All Spp.	47,862 ± 901	204,771 ± 6138	51,845 ± 982	151,497 ± 4172
2. Limited Forage, All Spp.	17,513 ± 332	66,425 ± 2040	19,932 ± 423	52,216 ± 1464
3. All Forage, Limited Spp.	4913 ± 238	70,005 ± 2748	4572 ± 244	63,219 ± 1939
4. Limited Forage, Limited Spp.	1682 ± 78	22,556 ± 933	1601 ± 77	20,768 ± 626

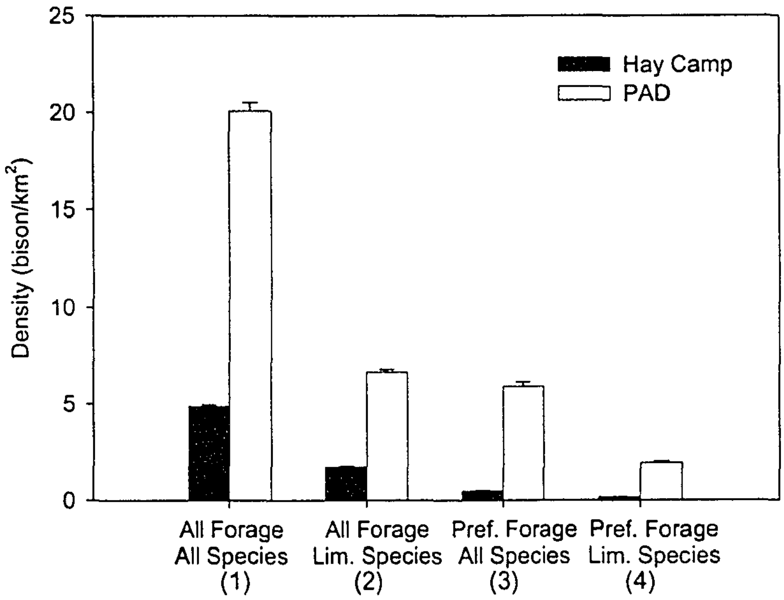

Fig. 5. Overall estimates of nutritional K for bison in the Hay Camp and PAD areas in Wood Buffalo National Park. In (1) all biomass of all species is available for consumption. In (2) biomass is limited by 1/3. In (3) and (4) only preferred forage species (*Calamagrostis* spp. and *Carex atherodes*) are available with all biomass available in (3) and 1/3 biomass in (4).

assumed different or not different between study areas (see Table 3, 4). Thus, I assumed estimates of forage quality between study areas to be equal for all further analyses.

Sensitivity of K to Model Constraints

Estimates of carrying capacity declined as constraints in forage quality became more restrictive, but were asymptotic because as one forage quality constraint was sufficiently relaxed the other constraint became limiting. The switch in constraints is reflected in the flat segment of the curve on the left-hand side of the graph (Fig. 6). Raising the DMD constraint by 10% decreased K more in the Hay Camp (48 ± 2%) than in the PAD (33 ± 4%), although because of the differences in the magnitude of K the change in actual bison numbers in the PAD was 3 times that in the Hay Camp (Fig. 6a). This difference occurred because *Carex atherodes* abundance was greater in the PAD than Hay Camp, and the DMD of this species was substantially greater than the minimum DMD assumed in the model. In contrast, raising the DP constraint 10% decreased K more in the PAD (31 ± 5%) than in Hay Camp (21 ± 3%), although the change in actual bison numbers remained higher in the PAD by a factor of 6 (Fig. 6b). Changes due to constraining DP are explained because the DP of species in the Hay Camp, such as *Salix* spp. and other grasses and sedges was relatively high. Changes in intake did not affect the relative comparisons in K between areas because the relationship between intake and K is determined primarily by available biomass (Fig. 6c).

Non-native Species

Four non-native species listed in the park's non-native plants management plan (Peterson 2001a) were found in plots in my study areas, only two of which were in the Hay Camp. *Plantago major* was the only major non-native species in the Hay Camp, being present in 1.7% of sampled plots, with just one incidence of *Sonchus arvensis* in Hay Camp (Table 5). *Cirsium arvense*, *Plantago major*, *Poa pratensis*, and *Sonchus arvensis* were located throughout the PAD with particularly high frequency in the Sweetgrass area north of Lake Claire (Fig. 7). The greatest frequency of non-native species was in graminoid meadows in both study areas, though shrublands had the second highest frequency in Hay Camp while sedge meadows were second in the PAD (Table 6). The PAD had more occurrences of non-native species than the Hay Camp both in terms of the number of plots and transects,despite fewer samples from the PAD than Hay Camp. Furthermore, percent cover of non-native species in the PAD was significantly greater than the Hay Camp in graminoid and sedge meadows ($P < 0.05$) but not in

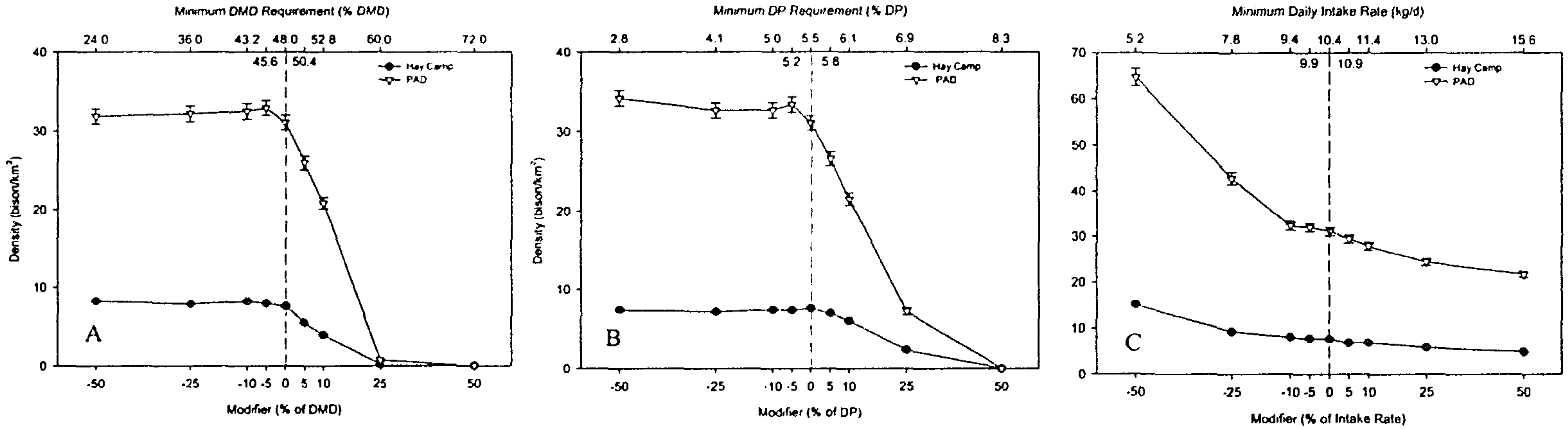

Fig. 6. The change in the nutritional carrying capacity relative to changes in minimum required DMD, DP, and daily intake rate constraints in the Hay Camp and PAD areas of Wood Buffalo National Park. Values are presented in % change from baseline constraints and in densities of animals (bison/km^2).

Table 5. Mean and SD percent cover of non-native species in the Hay Camp and PAD areas of Wood Buffalo National Park. Results are given across all plots in the study areas as well as only those plots where non-natives were found.

	Hay Camp					PAD				
	All Plots (% Cover)		Where Present (% Cover)			All Plots (% Cover)		Where Present (% Cover)		
	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD	n
Cirsium arvense	-	-	-	-	0	2.38	8.36	26.67	11.72	16
Plantago major	0.23	2.17	13.41	10.69	6	0.04	0.60	8.00	-	1
Poa pratensis	-	-	-	-	0	0.49	2.13	6.21	4.89	14
Sonchus arvensis	0.02	0.36	6.78	-	1	6.48	16.78	35.14	22.96	32
Any	0.25	2.20	0.34	2.55	7	9.39	22.19	13.13	25.31	37

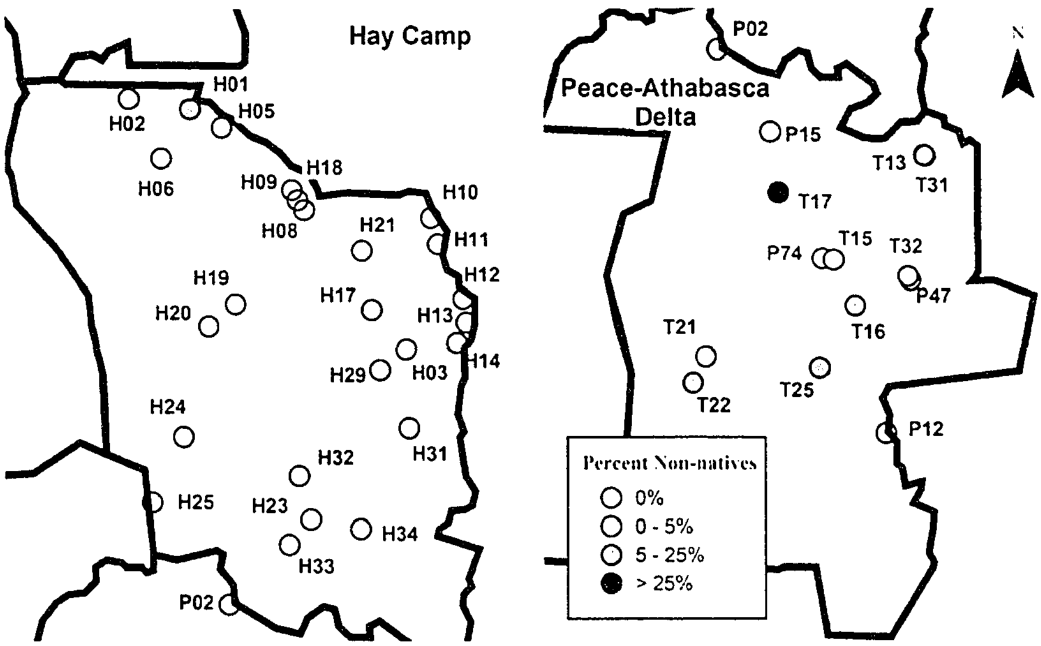

Figure 7. Locations of transects with non-native species by percent of plots within a transect in Hay Camp and PAD.

shrublands (P = 0.80), though the sample size for shrublands was very small (3 plots in Hay Camp and 6 in PAD).

The mean cover of preferred bison forage (*Calamagrostis spp.* and *Carex atherodes*) in the Hay Camp was lower in the presence of non-native species by 84% (P = 0.04) but the sample size of plots with both bison forage and non-native species was very small (n = 3). In the PAD preferred bison forage cover was 65% lower ($P < 0.01$) in plots where at least one non-native was present than in plots where non-native species were absent (Table 7). Differences within vegetation types could be compared only in the PAD due to the low number of plots with exotics (n = 7) in HC. In the PAD, bison forage in sedge meadows was 55.2% lower in the presence of non-native species (P = 0.06) and 17.6% lower in the graminoid meadows ($P < 0.01$). There was no significant

Table 6. Frequency of any non-native species (*Cirsium arvense*, *Plantago major*, *Poa pratensis*, and *Sonchus arvensis*) occurring in plots and transects throughout the Hay Camp and PAD areas of Wood Buffalo National Park.

	Number of Plots		Percent of Plots		Number of Transects		Percent of Transects	
	HC	PAD	HC	PAD	HC	PAD	HC	PAD
Conifer	1	0	4.2	0.0	1	0	4.0	0.0
Deciduous	0	0	0.0	0.0	0	0	0.0	0.0
Shrub	3	6	3.1	10.5	2	4	8.0	28.6
Graminoid	3	24	3.1	51.1	3	5	12.0	35.7
Sedge	0	7	0.0	21.9	0	3	0.0	21.4
All	7	37	2.0	20.0	4	8	16.0	57.1

Table 7. Mean ± SD percent cover of major bison forage (*Calamagrostis spp.* and *Carex atherodes*) when non-native species are not present in the plot and when they are present. ($\alpha = 0.10$)

	Hay Camp					PAD				
	Not Present		Present			Not Present		Present		
Species	Mean ± SD	n	Mean ± SD	n	*p*	Mean ± SD	n	Mean ± SD	n	*p*
Cirsium arvense	42.5 ± 33.5	122	-	0	-	50.3 ± 39.8	79	20.4 ± 14.5	14	0.05
Plantago major	43.4 ± 33.4	119	7.1 ± 3.8	3	0.04	46.2 ± 38.5	92	6.4	1	0.23
Poa pratensis	42.4 ± 33.5	122	-	0	-	51.9 ± 38.7	79	11.4 ± 6.3	14	<0.01
Sonchus arvensis	-	-	-	-	-	57.8 ± 39.6	64	19.3 ± 17.0	29	<0.01
Any	43.4 ± 33.4	119	7.1 ± 3.8	3	0.04	59.0 ± 39.9	61	20.5 ± 17.9	32	<0.01

difference between bison forage cover with or without non-natives in shrublands, but the number of samples was low (n = 4). From the above data, I assumed that any plots with non-native species would have 65% less preferred bison forage than otherwise for both Hay Camp and PAD and assessed this potential reduction on further expansion of non-native species could have on bison carrying capacity. To be conservative in my estimates

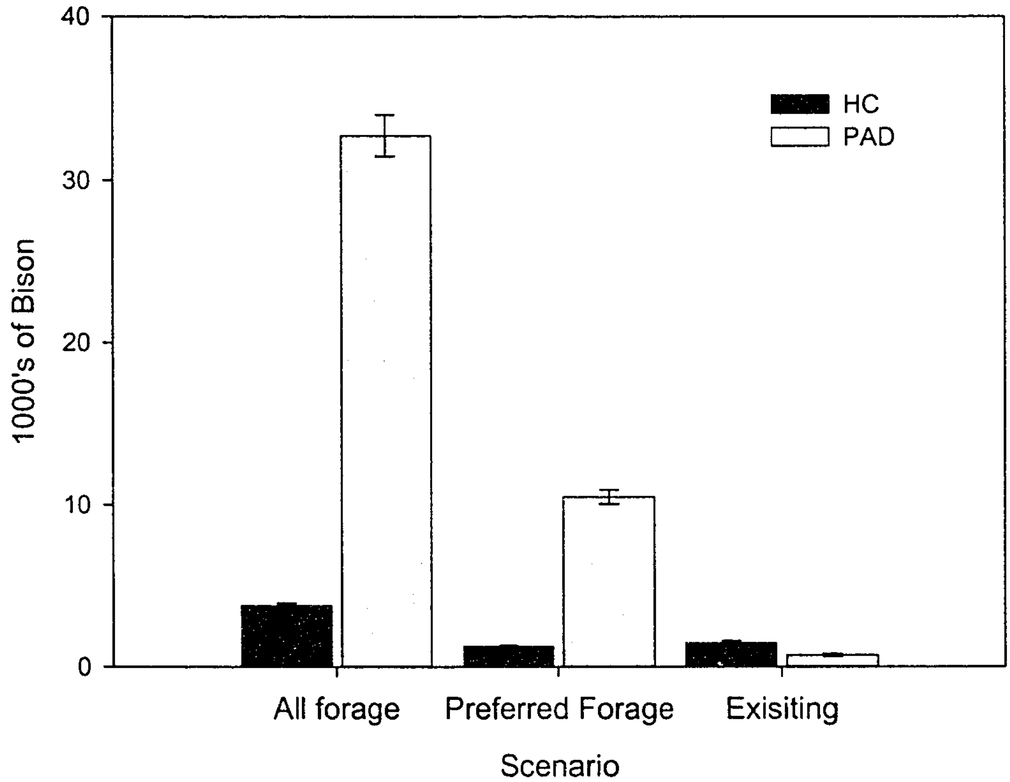

Figure 8. Nutritional K in the Hay Camp and PAD assuming non-native species exist in all plots. "All forage" assumes *Calamagrostis spp.* and *Carex atherodes* only are consumed but 100% of it is available, and "Preferred Forage" assumes that biomass is limited to one-third. Existing numbers are based on aerial surveys (Bradley 2002).

I disregarded the 84% difference between means in the Hay Camp because of the minimal sample size. Notably, I found that K in the PAD would not fall below existing bison numbers even if 100% of the area were assumed to have non-native plants present (Fig. 8). In the Hay Camp non-natives species do not cause K to fall below existing bison numbers either except in severe winter conditions, which is no different from model results not accounting for non-native species. Nevertheless, comparing the non-natives present to non-natives absent scenarios, K in the Hay Camp fell by 23% while K in the PAD fell by 46%. This is because there is less preferred forage in Hay Camp to influence by increasing non-native cover than in the PAD.

Discussion

My results provide quantitative support for the hypothesis that existing bison herds are not limited in winter by food in the PAD, but under some environmental conditions, they may be in the Hay Camp. Indeed, if bison were limited only by food there is the potential for the PAD to support over 4 to 12 times the population of the Hay Camp. The greater nutritional carrying capacity in the PAD relative to the Hay Camp was primarily the result of the difference in the extent of the open meadows in which there was 4 to 7 times as much available biomass. Only in the forests and shrublands of the Hay Camp was forage more abundant than in similar vegetation types in the PAD, but major forages preferred in winter were not generally abundant in the forest. In fact, forage biomass in the forest averaged below the model constraint of 25 kg/ha so that forest types generally did not contribute to bison habitat. However, Reynolds (1976) reported that bison in the Slave River lowlands used the forests and shrublands for up to

10% of their winter-feeding time. Given the assumptions of my analysis, shrublands, but not forests, contributed substantially to winter forage in both the PAD, but especially in Hay Camp.

The differences in forage availability between the PAD and Hay Camp were based on several important assumptions. First, I assumed that the error in the areal extents extrapolated from the original vegetation map were low and did not differ between areas. Jensen (2003) assessed his classification as 80.2% accurate. Based on my field observations, the greatest error occurred between sedge and graminoid meadows but open meadows themselves were well defined from other classes. Also, in the Hay Camp, mud was misclassified as sedge meadows occasionally. Second, I assumed my estimates of forage availability within vegetation types were representative of the 5 vegetation classes across the landscape. Access was a major concern in selecting my sampling sites and I cannot eliminate the possibility that selecting sites near access points biased the estimates of forage composition and biomass. Nevertheless, my relative abundances of bison forages in the PAD agreed with Timoney (1996) who identified *Carex atherodes*, *Calamagrostis canadensis*, and *Scolochloa festucacea* as three of the most common terrestrial plants based on occurrence, and with Raup (1935) who identified *Carex aquatilis*, *Calamagrostis inexpansa* and other sedges as abundant based on occurrence in uplands across Wood Buffalo National Park. However, to my knowledge there are no past estimates of plant biomass in either study area for comparison. In her estimates of winter K, Allison (1973) used only subcomponents of forage composition reported by Pringle (1971) that were obtained in the Slave River lowlands and, as such, may not be directly comparable to my results. The estimates of Reynolds et al. (1978:Table 2) of total vascular and non vascular biomass in wet and dry meadows in Hook Lake in the Slave River Lowlands were 6 - 7 times greater than in the sedge and graminoid meadows in Hay Camp, but were similar to my estimates in graminoid meadows in the PAD, and only 2 times greater than sedge meadows in the PAD. Their measurements were expected to be higher than those I presented because my estimates do not include forbs, bryophytes and *Juncus* spp.. In the Mackenzie Bison Sanctuary, Larter and Gates (1991) estimated total green biomass of herbaceous forage in August for wet sedge meadows about twice my estimates for the Hay Camp, but only about half as much as my PAD estimates. In the studies of both Reynolds et al. (1978) and Larter and Gates (1991), clippings were taken 3 cm above the ground. In contrast, I did not clip biomass below the litter height (mean ± SE: 7.1 ± 0.4 cm in Hay Camp; 8.2 ± 0.5 cm in PAD) because my observation in summer was that bison did not eat plant biomass beneath this thick, accumulated litter layer.

Third, I assumed biomass per species was linearly related to percent cover of those species, which may not have been true. This was less likely to have been a confounding factor in the PAD than the Hay Camp because the majority of plots had less diversity in grass or sedge species. Nevertheless, the total biomass available in a plot was directly measured and I used the standard error of the mean biomass iteratively in my simulations to account for some of this uncertainty. While the high number of iterations used resulted in a low standard error, given the vast differences in biomass between the two study areas and the high percentage of the biomass consisting of the preferred species, it is unlikely that this error would have altered the relative estimates of K in the PAD when compared to the Hay Camp.

Fourth, I assumed cured forages collected in late August and September represented winter forage quality, which may be an overestimate. Hawley et al. (1981) found February collections of *Calamagrostis inexpansa* were 43% lower than ours, while *Carex atherodes* were similar (8% lower) and willow were 23% higher. Differences among values may result from the timing of forage collections though the magnitude of difference in *Calamagrostis* spp. is difficult to explain. For shrubs, Dietz (1971) reported that some shrub twigs actually increase in DMD in winter, and this may include *Salix* spp. (Renecker and Hudson 1988). If winter dietary DMD is, in fact, lower than my estimates, this could result in an overestimation of carrying capacities. For example, from my sensitivity analysis, an overall increase in DMD requirements of even 5%, analogous to a decrease in dietary DMD, would reduce K by 25% in the Hay Camp and by 15% in the PAD. This would happen because the DMD of *Calamagrostis* spp. in my study was on the threshold of the bison's minimum requirements. Nevertheless, K in the PAD would remain higher than in Hay Camp, although the difference between the areas would be exaggerated. Further, even if quality of the same forages did differ between areas, which my data minimally support, my conclusions that bison in the PAD, and except under severe conditions in the Hay Camp, are not food-limited would not be altered. Nevertheless, if quality were lower, overall my estimates of K would more closely match existing bison densities.

Differences in nutritional carrying capacity between the PAD and Hay Camp were primarily due to the relative abundance of *Carex atherodes* and its high nutritive value. When I restricted the plant species that were available to only the major bison forages, there was a reduction of 10% in K in the Hay Camp and 25% in the PAD. *Carex* *atherodes* has consistently been found to constitute a major proportion of winter diets of bison in several areas (Raup 1935, Reynolds 1976, Larter and Gates 1991, Carbyn et al. 1993). *Carex atherodes* may be a primary forage species in winter not only due to its nutritive value (Hawley et al. 1981, Larter and Gates 1991, this study), but because it is a more robust plant than many other species (personal observation), making it more accessible under snow accumulation. The stature of *Carex atherodes* may be particularly important in meadows and shrublands where snow builds up more than under closed canopied areas. However, Carbyn et al. (1993) indicated that snow must exceed a critical depth estimated at 65 cm for adult bison and 55 cm for calves to have a noticeable effect on forage accessibility and movement. Forage height in my meadow plots averaged (mean ± SE) 81 ± 3 cm in the PAD in late summer but only 45 ± 2 cm in Hay Camp, indicating higher depths of snow might be necessary in the PAD to bury the same proportion of available forage. Carbyn et al. (1993) reported that for a 25-year period in Fort Smith snow depths never reached critical levels for bison foraging during the winter. In contrast, snow depth at Fort Chipewyan (PAD) over 13 years surpassed 55 cm, the critical levels for calves, for an average of 2 winter months each year. Although these snowpack data suggest that the reductions in forage availability I assumed may be extreme, interacting factors such as wind and topography make understanding the spatial variation in forage availability due to snow cover complex.

In addition, until sufficient ice has built up on some wet meadows, bison may be limited in their choices of meadows to graze (Larter and Gates 1991). Alternatively, forage availability can be reduced in winter because it is locked up by ice in very wet meadows (C. Gates, University of Calgary, pers. comm.). Hydrological effects on winter forage availability may be important, but are difficult to assess, especially in the PAD. Average rainfall between May and September 1993-2002 was not significantly different between Fort Smith and Fort Chipewyan in any month, but complexities of drainage patterns and the influence perched basins in the delta make hydrological predictions speculative. Recent efforts to map areas of flooding using a combination of remote sensing techniques (Pietronero and Toyra unpublished report) may provide some insight into these dynamics.

Finally, my model of nutritional carrying capacity ignored the spatial distribution patterns in forage. Access to certain forage areas may be restricted at several scales. First, in the PAD, some levees had willow stands thick with both live and dead plants making access to individual plants difficult. Further, long ridges of thick willows may hinder direct movement paths among foraging areas. In contrast, the Hay Camp meadows are more isolated within a forest matrix than in the PAD (Carbyn et al. 1993). Small, isolated meadows contribute equally to the available biomass in the model, but high isolation may reduce the likelihood of being grazed by bison. A resource selection function approach reflecting bison habitat use patterns from survey or telemetry data (Jensen in prep.) could be applied to remove habitats with low probabilities of bison use. However, the behaviour of animals may change as the population approaches carrying capacity.

Despite these uncertainties, my estimates of bison density when forage availability is restricted (mean ± SE: between 1.94 ± 0.08 and 6.65 ± 0.14 bison/km^2 in the PAD and 0.17 ± 0.01 and 1.74 ± 0.03 bison/km^2 in Hay Camp) are generally comparable to past studies. Nudds (1992) suggested that 0.37 bison/km^2 was a reasonable carrying capacity while the highest recorded density observed in the park was 2.5 bison/km^2 (Campbell and Hinkes 1983). The 2.5 bison/km^2 calculated by Campbell and Hinkes (1983) is based on the assumption that 12,500 bison used only 11% of the park's habitat while my estimates are based on all areas weighted by forage availability. Allison (1973) on the other hand predicted the PAD could support up to 8.78 bison/km^2 when 30% of the forage was available, which is higher than my estimates under a similar 30% reduction in forage availability. Applying my forage quality and dietary constraints and using her estimates of forage abundance resulted in a reduction in K by 24% to 6.67 $\pm$ 0.14 bison/km^2 in the PAD, which is similar to my own estimates.

The presence of non-native species was related to a lower-than-average cover of native bison forage by 65% in the PAD, which constitutes a potential threat to native biological resources in the park. The goal of Wood Buffalo National Park's non-native vegetation management plan is: "To prevent the introduction of non-native plants and to eliminate or control them as much as possible in support of maintaining biodiversity" (Peterson 2001a). Based on my sampling, non-native species were more widespread and abundant in the PAD than in the Hay Camp. However, it is important to note that my data do not contradict Wein et al. (1992) or Cody (1995) with regards to the number of non-native species in the park. Their studies focused on areas where non-natives were expected to be found (i.e., near disturbed sites) whereas my focus was away from such areas in the Hay Camp. Of the 25 transects I sampled in Hay Camp, 75% of the sites where non-native plants were present were near recreational day-use areas, though one case was found in the Hay Camp meadows far from any anthropogenic activity. In the Sweetgrass meadows of the PAD, an area with a long history of human activity and bison grazing (Wein et al. 1992, Carbyn et al. 1993) and typically used by bison throughout winter (Bradley 2002), had the highest frequency of plots with non-native species along a transect. Other sites with non-native plants were often near shores of either the delta lakes or the channels between them. Further, Wein et al. (1992) predicted that non-native species would expand into the PAD due to the seed source increasing alongside agricultural expansion upstream on the Peace River, and that this process would be aided by climate warming. Though I only examined the four species in my study that coincided with Peterson (2001), my findings are consistent with those of Timoney (2004) in that both studies found the area just north of Lake Claire (especially Sweetgrass) had the highest concentration of non-native plants while other shorelines exhibited a lesser presence, though his findings offer a more complete record both over time and space of non-native species in the PAD.

Non-native species can adversely influence crop yields in agricultural operations (AAFRD 1995) and, from this study it is evident that it also interacts with preferred bison forage. *Calamagrostis* spp. and *Carex atherodes* cover were substantially greater when non-native plants were absent from the plots than otherwise. Our assumption of potential impacts on nutritional K given further colonization of non-native plants resulted in a large negative change in K. The estimated changes in K assumed that only preferred forage was eaten, and that the non-native species in question do not replace it, though it has been observed that bison will eat *Cirsium arvense* in winter (Fortin et al. 2003). Nevertheless, the PAD remained over 10 times greater than the existing number of bison suggesting that even with substantial invasion of non-native species, and even if the invasive species do not replace preferred forage, bison in the delta would not be limited by food. Furthermore, the potential of the Hay Camp to be food-limited was under the same severe winter conditions as scenarios where non-native species were not considered. In essence, even though non-native plants have a negative impact on nutritional K it is not sufficient at this point in time to limit bison numbers.

The results of this study are best used to compare nutritional K between the Hay Camp and PAD areas of Wood Buffalo National Park rather than to define how many bison the park can support. Because carrying capacity is not a static property of the landscape it would be unwise to assume that K based on my research is an appropriate upper limit for the park in terms of bison numbers. Variation in K can occur from large disturbances (e.g., floods, forest fires, heavy snowfall) to more local effects (e.g., invasion of non-native plants). As such, the strength of this study is that despite these potential changes I have quantified a relationship between the Hay Camp and PAD areas of the park in terms of their respective abilities to support bison. I have further shown through several scenarios that it is improbable that bison in either area are currently limited by food.

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CHAPTER 3

The bison of Wood Buffalo National Park have undergone significant changes in terms of numbers over the past century, rising from around approximately 1500 animals in 1893 to as many as 12 500 in the mid-1900s, then falling to nearly 3000 and rising slightly again to over 4000 today (Carbyn et al. 1993, Bradley 2002). While the period of increase resulted from the introduction of over 6600 bison, the uncertainty behind the more recent decline has given rise to several hypotheses. The two primary hypotheses suggested either a combination of a change in habitat since the 1970s and predation from wolves (Carbyn et al. 1993, Gates et al. 1997) or a combination of exotic diseases and predation (Joly and Messier 2004) was responsible. A less-studied hypothesis was that bison at high numbers modified their own environment and were simply moving towards their habitat's carrying capacity (Nudds 1992). Past efforts to assess carrying capacity (K) in the park include Nudds (1992)'s attempt using allometry, Allison (1973)'s estimate of nutritional K in the Peace-Athabasca Delta (PAD) based on forage availability and bison intake rate, or the assumption that K was equal to the maximum number of bison ever recorded (Campbell and Hinkes 1983).

My research objectives were to determine the nutritional carrying capacity of the Hay Camp and PAD areas of the park based on both forage availability and nutritional requirements and to ascertain whether current population numbers are close to my estimates of K based on forage quality and quantity under a variety of environmental factors including winter severity and the presence of non-native species. The Hanley and Rogers (1989) model allowed me to improve on estimates made by Allison (1973) by simultaneously considering the dry matter digestibility and digestible protein constraints on bison. Such a model based on optimal foraging arguments can yield more realistic results than range-supply/animal-demand models (Focardi et al. 1995). Further, my data on forage biomass and quality were collected directly from the park rather than assumed. Finally, having sampled within the same season from two distinct areas within the park, this study is the first in which estimates of K can be used to compare between two areas of the park where bison numbers have been well-documented for decades.

It is tempting to assume that the greatest numbers of bison observed in the park properly estimate K (e.g., Joly and Messier 2004). Implicit in this, however, is the assumption that the forage base has not changed since the 1930s, yet several changes in the PAD have been speculated. First, Nudds (1992) argued that the bison may have modified their habitat resulting in a decline in bison numbers over the past decades. Second, the building of the Bennett Dam has been hypothesized to have altered vegetation communities in the PAD (PADIC 1987), though Timoney (2002) argues the changes are within the range of normal variation. Regardless of the mechanism, however, that the vegetation in the PAD varies over time is not in question. Third, the presence of non-native species is significant in the PAD and is somehow related to the lower abundance of preferred bison forage. Furthermore, some of these non-native species have reportedly been increasing over the past decade (Timoney 2004), including *Sonchus arvensis*, which I found to be the single most frequent of the four documented species in the PAD, though even widespread increases are unlikely to cause the PAD bison to become food-limited. Nevertheless, these changes may have altered the overall K of bison in the PAD. Whether similar trends have occurred in Hay Camp has not been well studied, but would provide a context for regional changes in vegetation in the Park and may provide a potential link between food availability and bison numbers over time between these two areas.

Non-native species appeared more abundant and widespread in the PAD than the Hay Camp, though my sampling focused mostly on undisturbed sites in the Hay Camp. What can be interpreted from my data, however, is that the majority of meadows bison use in winter in the Hay Camp have few non-native plants. Furthermore, given that Wein et al. (1992) noted many non-native species along roads and in historical communities of the Hay Camp, there seems to be a lack of any mechanism for these species to expand away from disturbed sites. Only one of the twenty-five transects in the Hay Camp had non-natives and was more than a few kilometers from a human-disturbed site. On the other hand, non-native plants were found at many transects in the PAD, all of which were close to either a lake or stream, which reflects the prediction of Wein et al. (1992) that seeds from upstream along the Peace River and changing flood regimes would be the main method of propagation for non-native species in the PAD. If true, one could predict that the influence of non-native plants on available bison forage would be more significant in the PAD in the future, though there seems to be no immediate need for concern with respect to the potential impact on bison.

In all the scenarios I investigated, my estimates of K in the PAD greatly exceeded the current mean number of bison for the same study area from aerial surveys in 2002 (Bradley 2002: 723 $\pm$ 79, Mean, S.E.), but they approached the aerial survey estimate of 1468 $\pm$ 124 bison in the Hay Camp under severe winter conditions and limited forage species availability. Thus, environmental conditions resulting in a reduction in forage availability will more likely affect the bison in the Hay Camp than the PAD. Despite this, winter survey results from 2002 indicate that the PAD currently has fewer bison than Hay Camp. If food is not limiting the animals in the PAD, then, what other mechanisms could be at work? Joly and Messier (2004) reported that populations are limited by a combination of wolf predation and disease, and given the high K of the PAD my research does not disprove their hypothesis for the southern study area. However the lower nutritional K in the Hay Camp indicates that even without predation and disease bison numbers may be constrained by occasional severe winters, which may make the Hay Camp bison even more susceptible to disease during such times. In fact, Joly and Messier (2001) report a higher incidence of disease in the Hay Camp bison than in the PAD, though they suggest this is because of a higher predation rate in the PAD. Nevertheless, because the Peace River is not a clear barrier for bison between the two study areas (Joly and Messier 2004), under severe enough conditions in the Hay Camp bison may simply migrate to the PAD rather than face depleted forages. Such a migration may have occurred in 1976 when around 1000 bison crossed the Peace River from the north in January then returned in April, as documented by Carbyn et al. (1998), though the reasons for this movement are not discussed.

Carbyn et al. (1993) recognized that the PAD had larger, more open meadows than areas north of the Peace River. I found the Hay Camp study area to be more forested than the PAD, with a smaller proportion of area in graminoid or sedge meadow. While forage species and their abundance differed between the two study areas, in both areas the graminoid and sedge meadows had the greatest quantity of forage species. Nevertheless, the PAD meadows had many times more available forage biomass than the

Hay Camp meadows, a higher proportion of which was *Calamagrostis* spp. or *Carex atherodes*, and could support 4 to 12 times the bison. The combination of more meadows and higher quality forage within them not only gives the PAD a higher nutritional K, but also arguably makes it superior bison range. Nevertheless, prior to the introduction of plains bison, there were historically few bison living in the PAD (Carbyn et al. 1993). Since tuberculosis and brucellosis were not present during those years the disease-predation hypothesis could not describe the low numbers. Carbyn et al. (1993) go on to suggest either a history of predation (human and wolf) kept numbers low or that flooding kept the quality of the range, or access to it, in a less attractive state than the meadows north of the Peace River. However it is possible that the bison were few in number in the PAD simply because there was sufficient forage north of the Peace River in areas such as the Hay Camp, and until the introduction of over 6600 bison there was no need for the animals to move into an area where predation rates could be higher. Indeed, it was not until after the introduction of plains bison to the park that the bison moved south of the Peace River, causing the park boundary to be extended (Carbyn et al. 1993).

It has been asked: "How many bison should be in Wood Buffalo National Park?" (Nudds 1992). With the Federal Environmental Assessment and Review Office's 1990 recommendation to eradicate diseased bison from the park and replace them with a disease-free herd (FEARO 1990), knowing what number of animals the park can support would be vital. It may be tempting to use the data I provide to answer the question of how many bison the park can support. However, attempting to extrapolate from my study areas into the rest of the park is not recommended. I found that forage composition and abundance within vegetation types differed between two major regions of the park and this variability is likely to occur in the remaining areas of the park. I also found variation in cover within a study area. For example, a significant difference ($P = 0.02$, this study) in the percent cover of *Calamagrostis* spp. between graminoid meadows near the Slave River on the east boundary of Hay Camp (mean ± SD: 54.2 ± 31.5) and the western portion of Hay Camp (75.2 ± 31.3) was evident (this study). Furthermore, even if additional field studies on forage availabilities and composition were done to first determine spatial variation in biomass prior to estimating bison densities for each section of the park, thus developing estimates for each home range, there is no indication that the nutritional carrying capacity would remain constant once the diseased bison were removed from the ecosystem. The most valuable resource this study provides is not a target number of animals to manage for, but the quantified co-comparison between nutritional K in the Hay Camp and the PAD. Any efforts to estimate K for other bison home ranges in the park should also be taken as values relative to the rest of WBNP.

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Appendix A. Details of the Study Area

Table 1A - Comparison of land cover classes between Jensen (2003) and this study for the 1999 Landsat 7 ETM+ vegetation classification of Wood Buffalo National Park.

Code	Class (Jensen 2003)	Vegetation Type
0	Unclassified	NA
5	Wetland	GRAMINOID MEADOW
6	Mud	NA
7	Sand	NA
8	Rock	NA
9	Cloud	NA
10	Cloud-Shadow	NA
11	Water	NA
12	Urban Residential	NA
13	Urban Commercial	NA
14	Access Major	NA
15	Access Minor	NA
16	Agricultural Cropland	NA
17	Agricultural Pastureland	NA
18	Cut Block	NA
19	Burn (<20 years)	NA
20	Black Spruce Dominated	CONIFEROUS FOREST
21	Jack Pine Dominated	CONIFEROUS FOREST
22	White Spruce Dominated	CONIFEROUS FOREST
23	Deciduous	DECIDUOUS FOREST
24	Deciduous Dominated	DECIDUOUS FOREST
25	Shrubby Poor Fen	SHRUBLAND
26	Shrubby Rich Fen	SHRUBLAND
27	Graminoid Rich Fen	GRAMINOID MEADOW
28	Dwarf Birch, Sedge, Willow	SHRUBLAND
29	Willow, Sedge	SHRUBLAND
30	Willow, Calamagrostis	SHRUBLAND
31	Sedge Fen	SEDGE MEADOW
32	Marsh Reed Grass Fen	GRAMINOID MEADOW
33	True Grassland	GRAMINOID MEADOW
34	Cattail Wetland	GRAMINOID MEADOW
35	Reed Grass Wetland	GRAMINOID MEADOW
36	Bullrush Wetland	GRAMINOID MEADOW
39	Willow/Sedge	SHRUBLAND
55	Treed Rich Fen	CONIFEROUS FOREST
56	Treed Poor Fen	CONIFEROUS FOREST
57	Shrubby Bog	SHRUBLAND
58	Cutline	NA
59	Runway (Airport)	NA
60	Jack Pine - Immature	CONIFEROUS FOREST

Table 2A - Location of transects and the number of plots per transect given by vegetation type. (C = Conifer, D = Deciduous, Sh = Shrubland, G = Graminoid, S = Sedge). All sites with an ID prefix of 'H' were located in the Hay Camp study area, while those with 'P' and 'T' were in the PAD. 'T' transects coincide with permanent vegetation transects established by Timoney (1996).

		Sub-		Start Coordinates			Herbaceous Plots ($0.25m^2$)						Shrub Plots ($10m^2$)					
ID	Area	Region	Access	UTM_E	UTM_N	Length	C	D	Sh	G	S	Tot	C	D	Sh	G	S	Tot
H01	HC	Parson	Road	421726	6647962	240	1	0	2	13	0	16	0	0	1	2	0	3
H02	HC	Parson	Road	409921	6649958	255	6	2	1	4	20	33	1	1	1	1	4	8
H03	HC	Meadows	Heli	463277	6602011	270	0	5	1	33	3	42	0	1	0	6	1	8
H05	HC	Parson	Heli	427841	6644423	220	0	0	0	44	0	44	0	0	0	10	0	10
H06	HC	Parson	Road	416117	6638559	225	5	10	0	0	0	15	2	1	0	0	0	3
H08	HC	Pine	Road	443601	6628641	285	16	0	0	3	0	19	3	0	0	0	0	3
H09	HC	Pine	Road	441254	6632463	630	1	4	2	35	0	42	0	1	1	6	0	8
H10	HC	HC Road	Road	468030	6627092	280	4	0	9	0	17	30	1	0	2	0	4	7
H11	HC	HC Road	Road	469361	6622070	385	4	10	7	3	11	35	1	2	2	0	3	8
H12	HC	HC Road	Road	474237	6611619	250	0	0	10	4	16	30	0	0	2	2	3	7
H13	HC	HC Road	Road	473059	6603245	225	5	2	3	0	15	25	1	0	1	0	3	5
H14	HC	HC Road	Road	474854	6607089	255	2	0	9	4	14	29	0	0	1	1	3	5
H17	HC	Meadows	Heli	456593	6609489	205	0	0	4	25	4	33	0	0	1	5	0	6
H18	HC	Pine	Road	442358	6630512	345	23	0	0	0	0	23	4	0	0	0	0	4
H19	HC	Pine	Road	430465	6610616	30	0	2	0	0	0	2	0	1	0	0	0	1
H20	HC	Pine	Road	425295	6606379	105	0	0	6	0	3	9	0	0	1	0	0	1
H21	HC	Meadows	Heli	454701	6620839	180	0	0	0	11	1	12	0	0	1	1	0	2
H23	HC	Pine	Road	444947	6569623	215	0	0	10	3	10	23	0	0	3	0	2	5
H24	HC	Pine	Road	420543	6585386	225	8	0	7	0	0	15	1	0	2	0	0	3
H25	HC	Pine	Road	414422	6572868	410	5	5	6	13	21	50	1	1	1	3	4	10
H29	HC	Meadows	Heli	458279	6598033	250	0	0	0	42	8	50	0	0	0	8	4	12
H31	HC	Meadows	Heli	463949	6587013	260	0	0	0	50	2	52	0	0	0	13	1	14
H32	HC	Meadows	Heli	442723	6577917	225	0	0	9	11	7	27	0	0	2	3	0	5
H33	HC	Meadows	Heli	440807	6564826	155	2	1	2	16	0	21	1	1	0	3	0	5
H34	HC	Meadows	Heli	454509	6567844	355	12	0	10	0	5	27	3	0	3	0	0	6

Table 2A - cont'd.

ID	Area	Sub-Region	Access	Start Coordinates UTM_E	UTM_N	Length	Herbaceous C	D	Sh	G	S	Tot	Shrub C	D	Sh	G	S	Tot
P02	PAD	Peace	Boat	429286	6553486	320	2	0	5	3	40	50	0	0	2	1	9	12
P12	PAD	Athabasca	Boat	466994	6467794	390	24	1	1	0	0	26	5	1	0	0	0	6
P15	PAD	Peace	Boat	441094	6535142	285	10	9	0	0	0	19	2	2	0	0	0	4
P47	PAD	Mamawi	Boat	472435	6501825	110	0	0	5	6	1	12	0	0	1	1	1	3
P74	PAD	Claire	Boat	452697	6506677	115	0	0	1	11	9	21	0	0	0	2	3	5
T13	PAD	Egg	Boat	475470	6529939	763	0	0	5	1	17	23	0	0	1	0	3	4
T15	PAD	Claire	Boat	455102	6506420	784	0	0	1	19	11	31	0	0	0	4	3	7
T16	PAD	Prairie	Boat	459924	6496217	775	0	0	1	25	5	31	0	0	1	3	2	6
T17	PAD	Sweetgrass	Heli	442875	6521562	459	0	0	0	22	5	27	0	0	0	5	1	6
T21	PAD	Birch	Boat	426750	6484830	585	0	0	7	21	4	32	0	0	1	3	0	4
T22	PAD	Birch	Boat	423816	6478972	173	0	3	5	6	1	15	0	0	2	1	0	3
T25	PAD	Claire	Boat	452170	6482310	685	0	0	15	0	1	16	0	0	3	0	0	3
T31	PAD	Egg	Boat	475700	6529672	850	0	1	4	1	18	24	0	0	1	0	5	6
T32	PAD	Mamawi	Boat	471916	6502742	754	0	0	10	19	1	30	0	0	1	5	1	7

Appendix B. Vegetation Collection Results

Table 1B - Mean ± SD % cover (not proportional) of plots in Hay Camp per species.

Vegetation Type (n)	Conifer (72)		Deciduous (41)		Shrub (98)		Graminoid (98)		Sedge (44)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
GRAMINOID										
Agropyron trachycaulum	0.03	0.24	0.00	0.00	0.04	0.32	0.37	2.16	0.00	0.00
Agrostis scabra	0.03	0.24	0.10	0.62	0.00	0.00	0.20	1.54	0.11	0.75
Calamagrostis canadensis	0.00	0.00	0.32	1.19	0.16	0.92	2.87	6.68	0.57	1.78
Calamagrostis inexpansa	0.03	0.24	0.00	0.00	0.22	1.21	0.77	3.58	0.41	1.15
Calamagrostis stricta	0.13	0.50	0.00	0.00	0.85	2.62	1.17	3.58	0.41	1.15
Distichlis stricta	0.00	0.00	0.00	0.00	0.06	0.51	0.06	0.51	0.00	0.00
Elymus innovatus	0.43	1.29	1.20	2.91	0.06	0.43	0.43	2.37	0.00	0.00
Festuca saximontana	0.11	0.64	0.00	0.00	0.00	0.00	0.11	0.62	0.00	0.00
Hierochloe odorata	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.59	0.00	0.00
Hordeum jubatum	0.00	0.00	0.00	0.00	0.00	0.00	0.81	2.32	0.00	0.00
Poa palustris	0.00	0.00	0.13	0.56	0.04	0.28	0.04	0.32	0.00	0.00
Puccinellia nuttalliana	0.03	0.24	0.00	0.00	0.02	0.14	0.84	2.47	0.00	0.00
Scolochloa festucacea	0.00	0.01	0.41	2.65	0.00	0.00	0.42	2.42	0.00	0.00
Spartina gracilis	0.00	0.00	0.00	0.00	0.05	0.51	0.04	0.32	0.00	0.00
Unknown Grass	0.60	1.15	0.00	0.00	0.39	1.16	2.03	8.70	0.32	1.41
SEDGE										
Carex aenea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.60
Carex aquatilis	0.06	0.47	0.00	0.00	1.58	3.89	0.11	0.66	4.80	9.58
Carex atherodes	0.00	0.00	0.00	0.00	0.62	2.25	0.48	2.29	3.55	6.65
Carex aurea	0.00	0.00	0.00	0.00	0.04	0.40	0.00	0.00	0.00	0.00
Carex concinna	0.07	0.39	0.37	1.35	0.00	0.01	0.00	0.00	0.00	0.00
Carex disperma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.45
Carex norvegica	0.00	0.00	0.00	0.00	0.24	0.97	0.00	0.00	0.48	1.76
Carex rostrata	0.00	0.00	0.00	0.00	0.19	0.97	0.05	0.51	1.18	3.80
Carex siccata	0.22	0.97	0.27	1.00	0.55	2.15	0.32	1.15	0.00	0.00
Carex vaginata	0.08	0.37	0.00	0.00	1.14	5.59	0.00	0.00	0.11	0.75
Unknown Sedge	1.67	5.35	0.83	2.54	1.35	2.82	0.42	1.24	3.02	7.85

Table 1B – cont'd.

Vegetation Type (n)	Conifer (72)		Deciduous (41)		Shrub (98)		Graminoid (98)		Sedge (44)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
FORB										
Achillea millifolium	0.05	0.20	0.56	1.40	0.16	0.71	0.06	0.32	0.00	0.00
Antennaria parvifolia	0.00	0.00	0.00	0.00	1.07	8.80	0.00	0.00	0.00	0.00
Arenaria lateriflora	0.00	0.00	0.00	0.00	0.15	0.84	0.00	0.00	0.02	0.15
Aster spp.	0.07	0.35	0.00	0.00	0.16	1.05	0.39	1.51	0.03	0.15
Astragalus americanus	0.00	0.01	0.00	0.00	0.02	0.20	0.00	0.00	0.00	0.00
Castilleja raupii	0.00	0.00	0.00	0.00	0.04	0.40	0.00	0.00	0.00	0.00
Cornus Canadensis	1.65	5.44	0.71	1.85	0.00	0.00	0.00	0.00	0.00	0.00
Delphinium glauca	0.00	0.00	0.15	0.94	0.00	0.00	0.00	0.00	0.00	0.00
Dodecatheon pauciflorum	0.00	0.00	0.00	0.00	0.42	2.81	0.35	2.60	0.00	0.00
Eleocharis palustris	0.00	0.00	0.00	0.00	0.00	0.00	0.23	1.71	0.23	1.51
Epilobium angustifolium	0.75	2.77	2.98	5.52	0.24	0.87	0.02	0.14	0.00	0.00
Equisetum spp.	3.68	10.20	2.90	6.06	1.19	4.05	0.24	0.96	0.49	1.72
Erigeron spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.42	0.00	0.00
Fragaria virginiana	0.18	1.42	0.69	1.86	0.22	1.29	0.00	0.00	0.00	0.00
Galium boreale	0.05	0.20	0.22	0.76	0.15	0.77	0.10	0.55	0.00	0.00
Galium spp.	0.00	0.00	0.00	0.00	0.10	0.32	0.00	0.00	0.14	0.63
Heracleum lanata	0.00	0.00	0.00	0.00	0.00	0.00	1.73	8.58	0.00	0.00
Juncus balticus	0.29	2.36	0.00	0.00	0.22	0.86	0.64	1.92	0.00	0.00
Liliacea spp.	0.00	0.02	0.12	0.78	0.15	1.14	0.01	0.10	0.00	0.00
Linnea borealis	0.03	0.24	0.00	0.00	0.01	0.10	0.03	0.30	0.00	0.00
Maianthemum canadense	0.85	2.36	1.63	5.31	0.05	0.36	0.00	0.00	0.00	0.00
Mentha arvense	0.07	0.59	0.17	0.67	0.00	0.00	0.00	0.00	0.00	0.00
Mentha spp.	0.00	0.00	0.00	0.00	0.03	0.22	0.00	0.00	0.00	0.00
Petasites sagittatus	0.76	3.91	0.12	0.78	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.28	2.36	0.49	3.12	0.30	1.26	0.14	1.08	1.39	5.71
Polygonum spp.	0.04	0.35	0.00	0.00	0.29	2.07	0.02	0.14	0.00	0.00
Potentilla norvegica	0.03	0.24	0.00	0.00	0.02	0.20	0.00	0.00	0.00	0.00
Pyrola spp.	0.14	0.68	0.90	1.96	0.08	0.55	0.02	0.20	0.00	0.00

Table 1B – cont'd.

Vegetation Type (n)	Conifer (72)		Deciduous (41)		Shrub (98)		Graminoid (98)		Sedge (44)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rubus acaulis	0.90	3.66	0.22	0.79	0.62	2.62	0.01	0.10	0.00	0.00
Scirpus pungens	0.00	0.00	0.00	0.00	0.01	0.10	0.03	0.30	0.59	2.69
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.95	0.00	0.00
Scutellaria galericulata	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.20	0.00	0.00
Smilacina stellata	0.00	0.00	0.05	0.31	0.02	0.20	0.01	0.10	0.00	0.00
Solidago canadensis	0.03	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sonchus arvense	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.40	0.00	0.00
Stachys palustris	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.20	0.00	0.02
Thalictrum venulosum	0.00	0.00	0.22	0.99	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin maritime	0.00	0.00	0.00	0.00	0.14	0.64	7.57	14.11	0.75	2.01
Vivia americana	0.07	0.48	0.12	0.64	0.02	0.20	0.00	0.00	0.00	0.00
Aquatic vegetation	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.90
Unknown Forb	0.27	1.30	0.12	0.56	0.13	0.63	1.57	10.01	0.01	0.03
SHRUB < 25 cm										
Arctostaphylos rubra	0.56	2.87	0.49	3.12	0.00	0.00	0.00	0.00	0.00	0.00
Arctostaphylos uva-ursi	0.57	2.68	1.88	5.30	0.00	0.00	0.00	0.00	0.00	0.00
Betula glandulosa	0.04	0.35	0.00	0.00	0.23	1.02	0.03	0.30	0.05	0.30
Juniperus spp.	0.72	3.30	0.73	4.69	0.26	2.53	0.54	4.61	0.00	0.00
Ledum groenlandicum	3.53	12.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Picea spp..	0.60	2.32	0.20	0.98	0.04	0.40	0.00	0.00	0.00	0.00
Pinus spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.20	0.00	0.00
Populus balticus	0.00	0.00	0.07	0.47	0.00	0.00	0.00	0.00	0.00	0.00
Populus tremuloides	0.00	0.00	0.07	0.47	0.00	0.00	0.00	0.00	0.00	0.00
Ribes hudsonianum	0.00	0.00	0.00	0.00	0.03	0.30	0.00	0.00	0.00	0.00
Ribes spp.	0.00	0.00	0.24	1.56	0.00	0.00	0.00	0.00	0.00	0.00
Rosa acicularis	0.81	2.92	1.98	3.66	0.34	1.46	0.02	0.20	0.00	0.00
Rubus ideaus	0.03	0.24	0.00	0.00	0.15	1.52	0.00	0.00	0.00	0.00
Salix spp.	2.44	7.94	2.46	9.10	2.77	7.40	0.04	0.32	0.20	0.85
Shepherdia canadensis	0.03	0.24	0.12	0.78	0.47	2.99	0.02	0.20	0.00	0.00
Symphoricarpos occidentalis	0.04	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 1B – cont'd.

Vegetation Type (n)	Conifer (72)		Deciduous (41)		Shrub (98)		Graminoid (98)		Sedge (44)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Vaccinium myrtilloides	0.14	1.18	0.00	0.00	0.00	0.00	0.19	1.44	0.00	0.00
Vaccinium vitis-idaea	1.89	5.22	0.00	0.00	0.05	0.51	0.02	0.20	0.00	0.00
Vaccinium spp.	0.74	2.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Viburnum edule	0.13	0.67	0.56	2.53	0.00	0.00	0.00	0.00	0.00	0.00
Unknown Shrub	0.56	2.97	0.12	0.78	0.35	3.05	0.00	0.00	0.00	0.00
OTHER										
Bare Ground	6.69	18.33	0.98	4.18	0.44	4.05	13.50	26.96	0.50	1.69
Grassy Litter	4.08	11.53	4.42	10.37	36.81	31.65	63.54	39.37	52.39	35.55
Other Litter	37.36	34.40	74.32	29.28	30.32	35.84	6.23	18.41	2.80	14.37
Woody Material	6.06	11.23	7.29	15.14	2.37	6.38	0.23	1.06	0.00	0.00
Moss	34.52	39.58	2.83	6.47	28.89	27.72	3.56	12.45	11.23	17.51
Lichen	7.88	17.85	5.55	18.47	0.86	1.95	0.04	0.32	0.11	0.75
Water	0.00	0.00	1.00	5.50	1.32	7.91	5.30	16.75	35.62	41.42

Table 2B - Mean ± SD % cover (not proportional) of plots in PAD per species.

Vegetation Type (n)	Conifer (36)		Deciduous (13)		Shrub (57)		Graminoid (47)		Sedge (32)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
GRAMINOID										
Agropyron trachycaulum	0.03	0.17	0.15	0.55	0.00	0.00	0.02	0.15	0.00	0.00
Agrostis scabra	0.00	0.00	0.00	0.00	1.67	9.00	0.66	2.53	0.16	0.88
Beckmannia syzigachne	0.00	0.00	0.00	0.00	1.67	9.00	0.66	2.97	0.00	0.00
Calamagrostis canadensis	0.00	0.00	0.00	0.00	5.95	13.51	15.64	25.10	2.53	7.13
Calamagrostis inexpansa	0.00	0.00	0.00	0.00	0.00	0.00	0.53	1.41	0.00	0.00
Calamagrostis stricta	0.00	0.00	0.00	0.00	0.00	0.00	0.70	2.35	0.22	1.24
Cinna latifolia	0.01	0.02	1.15	4.16	0.11	0.67	0.02	0.15	0.00	0.00
Deschampsia caespitose	0.00	0.00	0.00	0.00	0.14	1.06	0.00	0.00	0.00	0.00
Hordeum jubatum	0.00	0.00	0.00	0.00	0.00	0.00	0.83	1.77	0.09	0.30
Phalaris arundinacea	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.46	0.00	0.00
Poa palustris	0.00	0.00	0.00	0.00	0.67	1.68	0.32	1.14	0.47	2.65
Poa pratensis	0.00	0.00	0.00	0.00	0.00	0.00	1.26	2.69	0.00	0.00
Puccinellia nuttalliana	0.00	0.00	0.00	0.00	0.44	3.31	0.38	2.20	0.00	0.00
Scolochloa festucacea	0.00	0.00	0.00	0.00	0.21	1.35	6.98	19.48	0.19	0.78
Unknown Grass	0.00	0.00	0.00	0.00	0.00	0.00	0.74	2.05	0.00	0.00
SEDGE										
Carex aquatilis	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.15	1.31	4.92
Carex atherodes	0.00	0.00	0.00	0.00	1.39	4.72	3.89	6.88	24.22	26.04
Carex concinna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.56	21.19
Carex sychnocephala	0.00	0.00	0.00	0.00	0.18	1.32	1.02	4.70	2.13	10.66
Unknown Sedge	0.06	0.33	0.00	0.00	0.00	0.00	0.04	0.29	1.31	7.07
FORB										
Aralia nudicaulis	0.56	2.32	2.69	7.25	0.00	0.00	0.00	0.00	0.00	0.00
Aster puniceus	0.00	0.00	0.00	0.00	0.12	0.80	0.53	3.65	0.25	1.41
Aster spp.	0.00	0.00	0.00	0.00	0.25	1.35	0.00	0.00	0.00	0.00
Cirsium arvense	0.00	0.00	0.00	0.00	0.19	1.03	3.74	8.55	2.75	7.38
Cornus canadensis	4.89	6.53	1.92	4.79	0.00	0.00	0.00	0.00	0.00	0.00

Table 2B - cont'd.

Vegetation Type (n)	Conifer (36)		Deciduous (13)		Shrub (57)		Graminoid (47)		Sedge (32)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Epilobium angustifolium	0.31	1.41	0.00	0.00	0.09	0.66	0.00	0.00	0.00	0.00
Equisetum spp.	5.50	12.50	21.77	23.94	16.77	23.96	0.00	0.00	0.09	0.39
Fragaria vesca	5.83	10.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fragaria virginiana	0.22	1.33	0.23	0.83	0.00	0.00	0.00	0.00	0.00	0.00
Galium boreale	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Galium spp.	0.00	0.00	0.00	0.00	0.25	1.00	1.64	5.65	0.51	1.46
Glaux maritime	0.00	0.00	0.00	0.00	0.88	4.21	0.43	2.29	0.00	0.00
Hedysarum boreale	0.00	0.00	0.00	0.00	0.70	4.06	0.00	0.00	0.00	0.00
Juncus balticus	0.00	0.00	0.00	0.00	0.00	0.00	1.81	10.40	0.00	0.00
Lathyrus ochryleucus	0.00	0.00	0.38	1.39	0.44	3.31	0.00	0.00	0.00	0.00
Linnaea borealis	0.06	0.33	0.00	0.00	0.09	0.66	0.00	0.00	0.00	0.00
Maianthemum canadense	4.06	14.25	1.15	3.00	0.00	0.00	0.00	0.00	0.00	0.00
Mentha arvensis	0.17	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mentha spp.	0.00	0.00	0.00	0.00	0.05	0.40	0.00	0.00	0.00	0.00
Petatsites palmatus	0.00	0.00	0.08	0.28	0.56	1.70	0.45	2.34	0.00	0.00
Plantago major	0.08	0.50	0.00	0.00	0.05	0.40	0.00	0.00	4.69	13.13
Polygonum spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.21	1.46	0.00	0.00
Potentilla anserine	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.00	0.00
Potentilla fruticosa	0.00	0.00	0.00	0.00	0.19	0.88	0.62	1.58	0.41	1.83
Pyrola spp.	6.33	5.85	2.15	3.67	0.05	0.40	0.00	0.00	0.00	0.00
Rubus acaulis	1.03	2.40	5.15	10.74	0.00	0.00	0.00	0.00	0.00	0.00
Rumex spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.92	0.00	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.29	0.09	0.53
Scutellaria galericulata	0.00	0.00	0.00	0.00	0.37	2.65	0.11	0.73	0.22	1.07
Sium suave	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.44	0.00	0.00
Sonchus arvensis	0.00	0.00	0.00	0.00	0.55	2.34	14.91	23.42	3.72	9.63
Sparganium angustifolium	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.29	0.88	4.43
Stachys palustris	0.00	0.00	0.00	0.00	0.00	0.00	2.23	7.83	0.31	1.45
Utrica dioca	0.00	0.00	0.00	0.00	0.18	0.68	1.60	5.81	0.09	0.53

Table 2B – cont'd.

Vegetation Type (n)	Conifer (36)		Deciduous (13)		Shrub (57)		Graminoid (47)		Sedge (32)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Vicia americana	0.00	0.00	0.00	0.00	0.58	3.38	0.00	0.00	0.00	0.00
Unknown Forb	0.89	2.54	1.08	2.40	0.60	2.46	0.17	0.67	0.19	0.74
SHRUB < 25 cm										
Cornus stolonifera	0.00	0.00	0.62	2.22	0.05	0.40	0.00	0.00	0.00	0.00
Corylus cornuta	0.14	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Picea spp.	0.00	0.00	0.00	0.00	0.12	0.71	0.00	0.00	0.00	0.00
Populus balticus	0.08	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ribes hudsonianum	0.28	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ribes triste	0.06	0.33	2.00	4.42	0.00	0.00	0.00	0.00	0.00	0.00
Ribes spp.	0.06	0.33	1.15	3.60	0.00	0.00	0.00	0.00	0.00	0.00
Rosa acicularis	1.81	5.97	0.77	2.77	0.09	0.66	0.00	0.00	0.00	0.00
Rubus idaeus	0.00	0.00	0.54	1.94	1.44	4.14	0.00	0.00	0.00	0.00
Salix spp.	0.17	0.74	0.00	0.00	0.18	0.80	0.00	0.00	0.00	0.00
Vaccinium spp.	0.14	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Viburnum edule	0.44	1.87	0.77	1.88	0.09	0.66	0.00	0.00	0.00	0.00
OTHER										
Bare Ground	0.14	0.83	0.00	0.00	1.82	10.75	3.26	10.01	0.31	1.77
Grassy Litter	1.00	5.83	0.08	0.28	24.20	36.02	69.79	32.69	50.44	43.92
Other Litter	55.6`	34.12	85.54	20.23	56.18	41.33	10.00	15.07	4.32	14.53
Woody Material	3.25	8.54	3.62	5.08	9.00	15.77	0.21	1.46	0.13	0.71
Moss	24.89	29.38	0.08	0.28	6.42	17.61	3.77	13.44	7.38	19.33
Lichen	0.56	1.23	0.00	0.00	0.35	2.08	0.00	0.00	0.00	0.00
Water	0.14	0.83	0.00	0.00	0.18	1.32	5.74	21.94	38.59	45.07

Table 3B - Stem counts and frequency of occurrence of shrub species > 25 cm in Hay Camp.

Vegetation Type (n)	Conifer (19)		Deciduous (9)		Shrub (25)		Graminoid (64)		Sedge (32)	
Species	Stems	Freq.	Stems	Freq.	Stems	Freq.	Stems	Freq.	Stems	Freq.
Amelanchier alnifolia	0	0	2	1	0	0	0	0	0	0
Betula glandulosa	6	2	47	1	273	9	0	0	0	0
Cornus stolonifera	0	0	0	0	2	1	0	0	0	0
Picea spp.	2	1	1	1	9	1	0	0	0	0
Populus balticus	0	0	6	1	2	1	0	0	0	0
Populus tremuloides	27	1	14	4	10	1	0	0	0	0
Rosa acicularis	0	0	2	1	0	0	0	0	0	0
Salix spp.	10	1	31	4	378	13	58	4	102	4
Shepherdia canadensis	0	0	5	2	0	0	0	0	0	0

Table 4B - Stem counts and frequency of occurrence of shrub species > 25 cm in PAD.

Vegetation Type (n)	Conifer (7)		Deciduous (3)		Shrub (13)		Graminoid (25)		Sedge (30)	
Species	Stems	Freq.	Stems	Freq.	Stems	Freq.	Stems	Freq.	Stems	Freq.
Alnus rugosa	2	1	0	0	1	1	0	0	0	0
Betula occidentalis	1	1	1	1	0	0	0	0	0	0
Betula papyrifera	1	1	0	0	0	0	0	0	3	1
Cornus stolonifera	4	2	1	1	7	2	0	0	0	0
Corylus cornuta	1	1	0	0	0	0	0	0	0	0
Picea spp.	2	2	0	0	0	0	0	0	0	0
Populus balticus	0	0	7	2	0	0	0	0	0	0
Rosa acicularis	68	4	24	2	0	0	0	0	0	0
Rubus ideaus	0	0	0	0	3	1	0	0	0	0
Salix spp.	0	0	0	0	178	9	1	1	36	2
Viburnum edule	0	0	9	3	0	0	0	0	0	0

Table 5B - Mean biomass and percent of forage cover of the major sources of herbaceous and woody forage for bison collected in summer 2003 in Wood Buffalo National Park. Values have been broken down by study area (Hay Camp and Peace-Athabasca Delta), and by five vegetation types.

	Hay Camp					PAD				
		Biomass (kg/ha)		Cover (%)			Biomass (kg/ha)		Cover (%)	
	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD
Coniferous Forest	72					36				
Calamagrostis spp.		1.03	11.53	4.18	15.64		0.00	0.00	0.00	0.00
Carex aquatilis		0.31	2.61	1.28	9.25		0.00	0.00	0.00	0.00
Carex atherodes		0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Scolochloa festucacea		0.47	3.94	1.92	13.87		0.00	0.00	0.00	0.00
Other Grass		13.76	51.57	56.08	45.02		0.07	0.55	75.00	50.00
Other Sedge		8.96	15.91	36.53	42.98		0.02	2.10	25.00	50.00
Salix spp.	19	3.26	14.2	NA	NA	7	0.00	0.00	NA	NA
TOTAL		*27.79*	*57.18*	*NA*	*NA*		*0.09*	*2.17*	*NA*	*NA*
Deciduous Forest	41					13				
Calamagrostis spp.		4.21	41.24	8.57	26.90		0.00	0.00	0.00	0.00
Carex aquatilis		0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Carex atherodes		0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Scolochloa festucacea		1.74	11.09	3.55	18.79		0.00	0.00	0.00	0.00
Other Grass		23.70	100.28	48.24	48.14		8.33	28.03	100.00	0.00
Other Sedge		19.48	35.47	39.64	46.02		0.00	0.00	0.00	0.00
Salix spp.	9	21.12	29.75	NA	NA	3	0.00	0.00	NA	NA
TOTAL HERBACEOUS		*70.25*	*111.01*	*NA*	*NA*		*1.67*	*10.57*	*NA*	*NA*
Shrubland	98					57				
Calamagrostis spp.		50.36	274.62	17.40	32.36		55.41	216.27	53.31	42.70
Carex aquatilis		51.24	113.56	17.70	33.68		0.00	0.00	0.00	0.00
Carex atherodes		20.94	67.98	7.24	21.62		16.67	42.38	16.01	29.68
Scolochloa festucacea		0.00	0.00	0.00	0.00		2.62	14.07	2.51	10.96
Other Grass		48.65	277.82	16.81	33.15		55.41	147.50	27.93	37.45
Other Sedge		118.24	175.80	40.85	42.30		0.35	2.59	16.01	29.68
Salix spp.	25	80.20	133.06	NA	NA	13	68.91	115.78	NA	NA
TOTAL HERBACEOUS		*369.64*	*378.56*	*NA*	*NA*		*199.37*	*192.77*	*NA*	*NA*

Table 5B – cont'd

	Hay Camp					PAD				
		Biomass (kg/ha)		Cover (%)			Biomass (kg/ha)		Cover (%)	
	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD
Graminoid Meadow	98					47				
Calamagrostis spp.		230.61	912.48	36.50	43.48		1153.96	4269.93	38.07	40.33
Carex aquatilis		4.32	25.59	0.68	3.94		3.21	21.92	0.11	0.71
Carex atherodes		24.51	104.16	3.88	15.78		531.25	879.94	17.53	22.62
Scolochloa festucacea		21.57	109.10	3.41	16.67		427.39	1052.74	14.10	31.28
Other Grass		288.12	1008.39	45.61	43.02		795.01	3136.74	26.23	31.21
Other Sedge		62.61	158.07	9.91	22.57		120.46	513.38	3.97	16.27
Salix spp.	64	6.34	40.50	NA	NA	25	0.17	0.87	NA	NA
TOTAL HERBACEOUS		*638.07*	*1032.90*	*NA*	*NA*		*3031.44*	*3462.04*	*NA*	*NA*
Sedge Meadows	44					32				
Calamagrostis spp.		72.96	449.63	9.64	20.76		160.84	924.11	7.65	14.16
Carex aquatilis		192.46	359.29	25.42	37.95		79.51	352.38	3.78	14.92
Carex atherodes		201.00	383.35	26.55	40.87		1404.36	1764.97	66.81	36.30
Scolochloa festucacea		0.00	0.00	0.00	0.00		39.27	159.38	1.87	6.71
Other Grass		43.48	308.12	5.77	19.54		1.68	4.53	2.07	4.96
Other Sedge		247.07	419.58	32.63	42.13		374.54	933.24	17.82	36.55
Salix spp.	32	22.40	115.34	NA	NA	28	13.93	55.85	NA	NA
TOTAL HERBACEOUS		*779,55*	*790.72*	*NA*	*NA*		*2115.93*	*2057.59*	*NA*	*NA*

Appendix C. Carrying Capacity Estimates

Table 1C - Area weighted mean number of bison ± SE (bison/km^2 ± SE) that can be supported over winter (180 days) in the Hay Camp (6565 km^2) and PAD (8614 km^2) areas of Wood Buffalo National Park assuming minimum DMD = 48.0%, minimum DP = 5.5%, and minimum daily intake = 10.4 kg/day. n = 1000 for each case.

Location	Scenario	Conifer	Deciduous	Shrubland	Graminoid Meadow	Sedge	All
Hay Camp	S1	1911 ± 77	2136 ± 74	17 764 ± 447	3712 ± 123	5361 ± 138	30 887 ± 497
		(0.62 ± 0.02)	*(1.63 ± 0.06)*	*(12.40 ± 0.31)*	*(11.96 ± 0.40)*	*(31.90 ± 0.82)*	*(4.88 ± 0.08)*
	S2	643 ± 30	804 ± 30	6350 ± 173	1270 ± 42	1922 ± 51	10 991 ± 185
		(0.21 ± 0.01)	*(0.61 ± 0.02)*	*(4.43 ± 0.12)*	*(4.09 ± 0.14)*	*(11.44 ± 0.30)*	*(1.74 ± 0.03)*
	S3	0 ± 0	0 ± 0	1694 ± 99	772 ± 48	615 ± 36	3082 ± 115
		(0.00 ± 0.00)	*(0.00 ± 0.00)*	*(1.18 ± 0.07)*	*(2.49 ± 0.15)*	*(3.66 ± 0.21)*	*(0.49 ± 0.02)*
	S4	0 ± 0	0 ± 0	580 ± 34	257 ± 16	209 ± 12	1046 ± 40
		(0.00 ± 0.00)	*(0.00 ± 0.00)*	*(0.41 ± 0.02)*	*(0.83 ± 0.05)*	*(1.24 ± 0.07)*	*(0.17 ± 0.01)*
PAD	S1	0 ± 0	0 ± 0	3770 ± 139	86 880 ± 2494	41 699 ± 1266	132 350 ± 2819
		(0.00 ± 0.00)	*(0.00 ± 0.00)*	*(3.11 ± 0.11)*	*(69.75 ± 2.00)*	*(73.40 ± 2.23)*	*(20.07 ± 0.43)*
	S2	0 ± 0	0 ± 0	1400 ± 51	27 615 ± 837	14 816 ± 425	43,830 ± 951
		(0.00 ± 0.00)	*(0.00 ± 0.00)*	*(1.15 ± 0.04)*	*(22.17 ± 0.67)*	*(26.08 ± 0.75)*	*(6.65 ± 0.14)*
	S3	0 ± 0	0 ± 0	1223 ± 66	31 610 ± 1528	6029 ± 291	38 863 ± 1556
		(0.00 ± 0.00)	*(0.00 ± 0.00)*	*(1.01 ± 0.05)*	*(25.38 ± 1.23)*	*(10.61 ± 0.51)*	*(5.89 ± 7.46)*
	S4	0 ± 0	0 ± 0	366 ± 21	10 547 ± 515	1881 ± 96	12 795 ± 519
		(0.00 ± 0.00)	*(0.00 ± 0.00)*	*(0.30 ± 0.02)*	*(8.47 ± 0.41)*	*(3.31 ± 0.17)*	*(1.94 ± 0.08)*

Appendix D. Non-Native Plant Locations

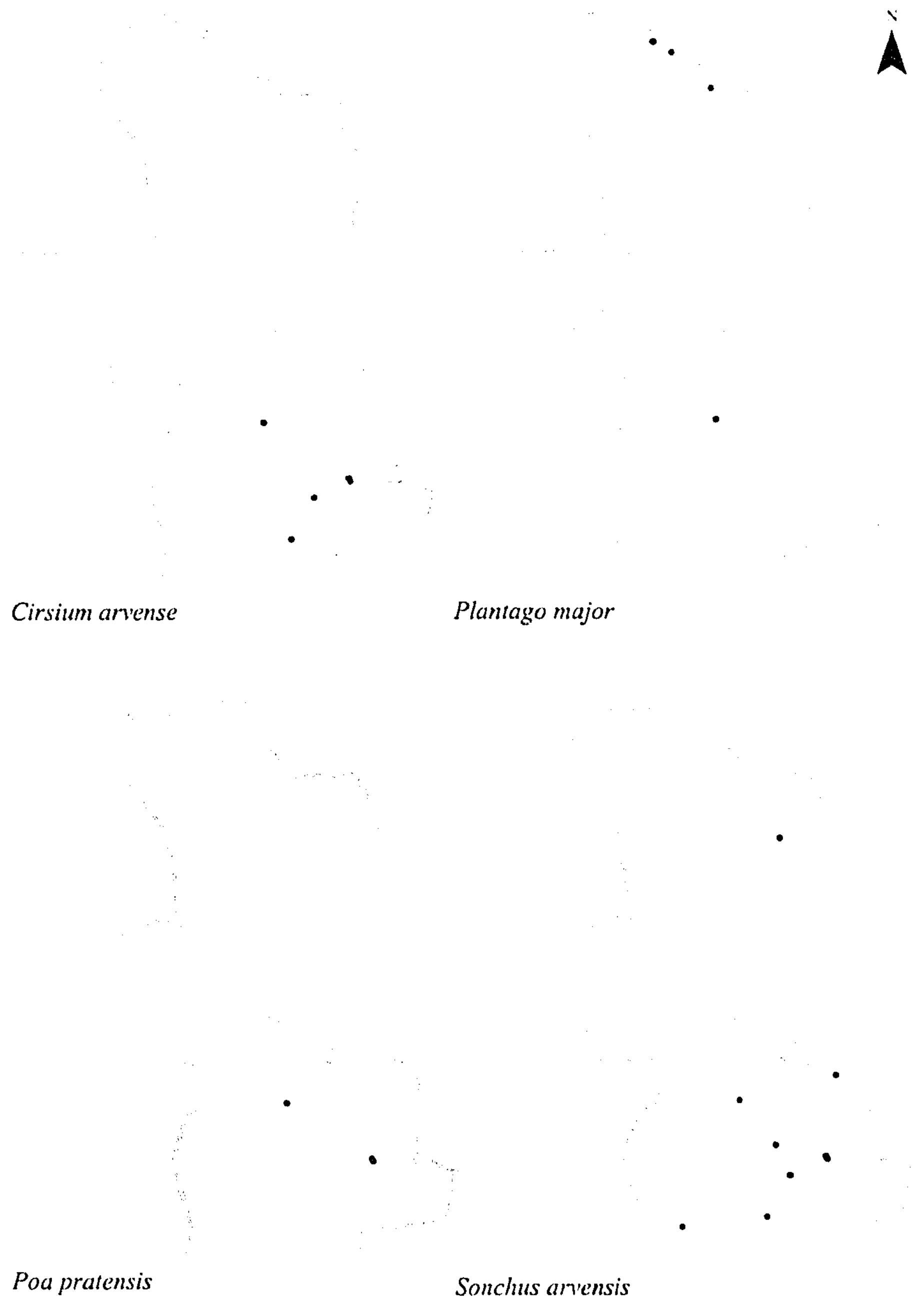

Figure 1D - Distribution of non-native plant species in the Hay Camp (north) and PAD (south) areas of Wood Buffalo National Park. Points on the map represent transects where at least one of the species of interest is present.