DIET AND HABITAT SELECTION OF AN ERUPTING WOOD BISON POPULATION

By

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ABSTRACT

In this study I examine diet and habitat selection of wood bison (Bison bison athabascae) in the Mackenzie Bison Sanctuary, Northwest Territories. This reintroduced population has increased exponentially since 1963 (r=0.21), and represents the only free-ranging population in existence. A 1987 total count showed at least 1718 animals. The aims of the study were to: 1) determine changes in forage quality and forage quantity amongst the different habitats, 2) determine dietary components on a seasonal basis, 3) determine what biotic and abiotic factors affected habitat selection, and 4) determine home ranges and describe seasonal movement patterns as they relate to the changing distribution of forage.

All forages except lichen demonstrated a linear decrease in percent nitrogen concentration and a linear increase in percent indigestible fiber concentration over the growing season. Lichen had consistentent low nitrogen and indigestible fiber concentrations. The ratio of percent nitrogen concentration to percent indigestible fiber concentration (N/ADF) was used as a measure of forage quality. Phalaris arundinacea and willow were better quality forages during summer, while lichen was a better quality forage in fall. The presence of alkaloids and silicates is proposed as the reason P. arundinacea is avoided by bison. Green biomass increased until mid-July, remained high until mid-August and decreased rapidly into September. Wet sedge meadows provided three times more green biomass than willow savannas, however wet sedge meadow forage was of inferior quality and was inaccessible. Forages from willow savannas and willow-aspen habitats were of consistently superior quality until fall when forested habitats provided superior quality forage, the most important of which was lichen. Willow savannas provided the highest available crude protein of all habitats during summer and fall.

Wood bison were catholic feeders, and showed pronounced seasonal changes in diet. Sedges, especially Carex atherodes, constituted 96.1-98.8% of the winter diet. During the summer growing season the diet became a more diverse mix of sedge, grass, and willow (Salix spp.). During fall lichen (Cladina mitis) became a major dietary component representing as much as 52.1% of the diet in October. The diet was more diverse at this time of year. There was a pronounced difference between summers in the amount of sedge in the diet. During 1987 the sedge proportion dropped to 30-40% from its 1986 value of 70-90%, while the grass and willow proportions rose. Willow represented as much as 38.7% of the diet during 1987, indicating browse as a viable alternative to monocotyledonous sedges and grasses. A decreased standing crop of sedge in 1987 is proposed as a factor causing the changes in summer forage proportions. Dietary crude was higher in 1986 than 1987. Dietary crude protein levels were intermediate to the levels found in the different forages.

Forage availability was the major factor determining habitat selection. Wet sedge meadows were preferred in winter, while willow savannas were preferred in summer. The lack of habitat preference in fall corresponded with the dispersion of animals into forested habitats and the increased use of lichen for forage. Group size and weather conditions had little effect on

habitat selection. Snow characteristics affected forage availability. The deeper and denser snow of the 1987-88 winter caused a shift from almost exclusive use of wet sedge meadows to use of both wet sedge meadows and willow savannas.

Home ranges were calculated using the minimum convex polygon method. Wood bison home ranges were larger than those of other North American ungulates, ranging in size from 178.5km^2 to 1441.9km^2, and far exceeded those predicted by home range-body size relationships. Females had larger home ranges than males. Median daily travel (km/day) was generally greater for females than males. Females travelled more in summer than in fall or winter. Males travelled more during pre-rut and the rut than during post-rut. Forage distribution and availability are proposed as the main determinants of large home range size. Interspecific competition for forage is proposed as a reason for larger home ranges and greater daily travel in females than males. Competition for copulations is proposed as a reason for greater daily travel by males in the pre-rut and rut.

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ACKNOWLEDGEMENTS

CHAPTER 1. GENERAL INTRODUCTION

The transplant of wood bison (<u>Bison bison athabascae</u>) to the Mackenzie Bison Sanctuary (61° 30' N, 117° 00' W) in 1963, remains the only truly successful re-establishment of wood bison to the wild. The 16 animals known to have survived the transplant have increased at an exponential rate of r=0.21, and at last count the population numbered 1718 (pers. obs. April, 1987). This increase in population has been matched by a similar increase in the area occupied by the bison (Gates and Larter, in prep.). Currently the area occupied by wood bison exceeds 9000 km^2, and extends well beyond the western border of the Sanctuary. Wolves are the major predators. A few moose (<u>Alces alces</u>) and woodland caribou (<u>Rangifer tarandus</u>) inhabit the Sanctuary, but there is probably little interspecific competition for forage. Although 40 animals (mostly cows and calves) were taken for research purposes during 1986-1988, and limited hunting (initiated in the spring of 1988) resulted in four bulls being taken, this situation offers an opportunity to study the ecology of an unexploited, erupting population of free-ranging wood bison.

Although the population continues to expand exponentially, one could predict some density-dependent factor, or combination of factors, to negatively affect population growth in future years. Three main factors are generally considered to regulate large herbivore populations: resource availability, predation, and disease. Evidence of food limitation has been documented by Bobek (1977), Sinclair (1977), and Sinclair <u>et al</u>. (1985). Gasaway <u>et al</u>. (1983), Mech and Karns (1977), and Messier and Crete (1985) present evidence that populations are limited by predators. Christian <u>et al</u>.

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(1960), and Sinclair and Norton-Griffiths (1979) present evidence that disease is a population limiting factor. In the absence of epidemic diseases or heavy predation, one would expect a population of large ungulates to increase until food resource shortages prevent further growth. In the three documented cases of erupting natural populations (African buffalo, wildebeest, and red deer), numbers increased until food was limiting (Sinclair, 1977; Sinclair and Norton-Griffiths 1979; Clutton-Brock et al., 1982).

Wood bison in the Mackenzie population are not infected with brucellosis or tuberculosis. These two diseases are prevalent in bison found in Wood Buffalo National Park and vicinity, and they have been suggested as an important factor in recent population declines in the Park (Tessaro, 1988). Currently, wolf predation on the Mackenzie population does not appear to be heavy. The proposed hypothesis for this study is that the availability of nutritious forage will limit population growth, thus implying that food availability will determine many aspects of the ecology of wood bison. If food limitation is beginning to take effect then one can predict: 1) a decrease in diet selectivity with the progression of the growing season because of the decrease in high quality forage, 2) a switch from a summer diet consisting almost exclusively of the best quality forage to a summer diet including more poorer quality forages, if summer food availability declines 3) heavy use of habitats that provide the most available nutritious forage, and 4) summer travel between habitat patches to be greater and more uniform than winter travel because bison will abandon and move to adjacent patches sooner in summer than in winter. In winter, travel will not lead to superior forage, so bison will remain in patches until forage depletion forces them to move.

In chapter two, I test the first two predictions by determining changes in nutritional quality for the different forages found in each habitat. I compare changes in the levels of percent nitrogen, percent indigestible fiber, crude protein (CP), and the ratio of percent nitrogen to percent indigestible fiber (N/ADF) between forages with the progression of the growing season. I compare dietary CP with forage CP levels and compare available CP between habitats.

In chapter three, I describe the seasonal changes in the diet of wood bison in comparison to those predicted by four morphological characteristics: body size, digestive system, rumino-reticular to body weight ratio, and mouth size (following Hanley 1982). I determine if changes in the diversity of the diet meet the food limitation hypothesis prediction of decreased selectivity as forage quality declines. Having shown differences in diet composition between males and female dominated mixed herds, and between years, I discuss these differences in relation to changes in resource availability between the sexes, and between years.

In chapter four I determine if there are seasonal shifts in habitat selection, and test the prediction that habitats providing the most available nutritious forage are used more frequently. Having shown seasonal shifts in habitat selection, I examine changing weather conditions, snow conditions, forage availabilities, and group sizes to determine which factors most affect habitat choice.

I describe home range sizes and movement patterns of adult female and male bison in chapter five. Home range sizes are compared with those predicted by current home range-body weight relationships (McNab, 1963; Harestad and Bunnell, 1979). The differences in daily movements between

seasons are compared to the prediction of greater summer than winter movements. Seasonal movement patterns are discussed in relation to different female and male strategies for reproductive success and in relation to competition for forage. In chapter six I present a general discussion and summarize my conclusions.

The term "northern bison" used throughout this thesis represents the bison found in Wood Buffalo National Park and adjacent areas. These bison are neither pure plains nor pure wood, but hybrids of the two subspecies.

STUDY AREA

The Mackenzie Bison Sanctuary covers an area exceeding 6,200km^2 on the western side of Great Slave Lake (61° 30' N, 117° 00' W) in the Northwest Territories (Figure 1.1). It is located in the Upper Section of the Boreal Forest Region (Rowe, 1972), in the emerged bed of a once vast glacial lake. Glacial action is evident from the occurrence of oriented lakes, drumlins, and eskers. Post glacial isostatic lift has lowered the water table and dried the shallow lakebeds in the area. The lakes are gradually filling in with sedges and grasses, while woody plants are invading the lake margins. Three main open habitat types are associated with these shallow lakebeds: (i) wet sedge meadow, (ii) willow savanna, and (iii) sparsely vegetated marls.

Wet sedge meadows are found where there is year round standing water. This habitat contains a high biomass of sedges dominated by Carex atherodes and C. aquatilis. The willow savanna habitat is found in more mesic areas often bordering wet sedge meadows. Grass-sedge associations comprised of
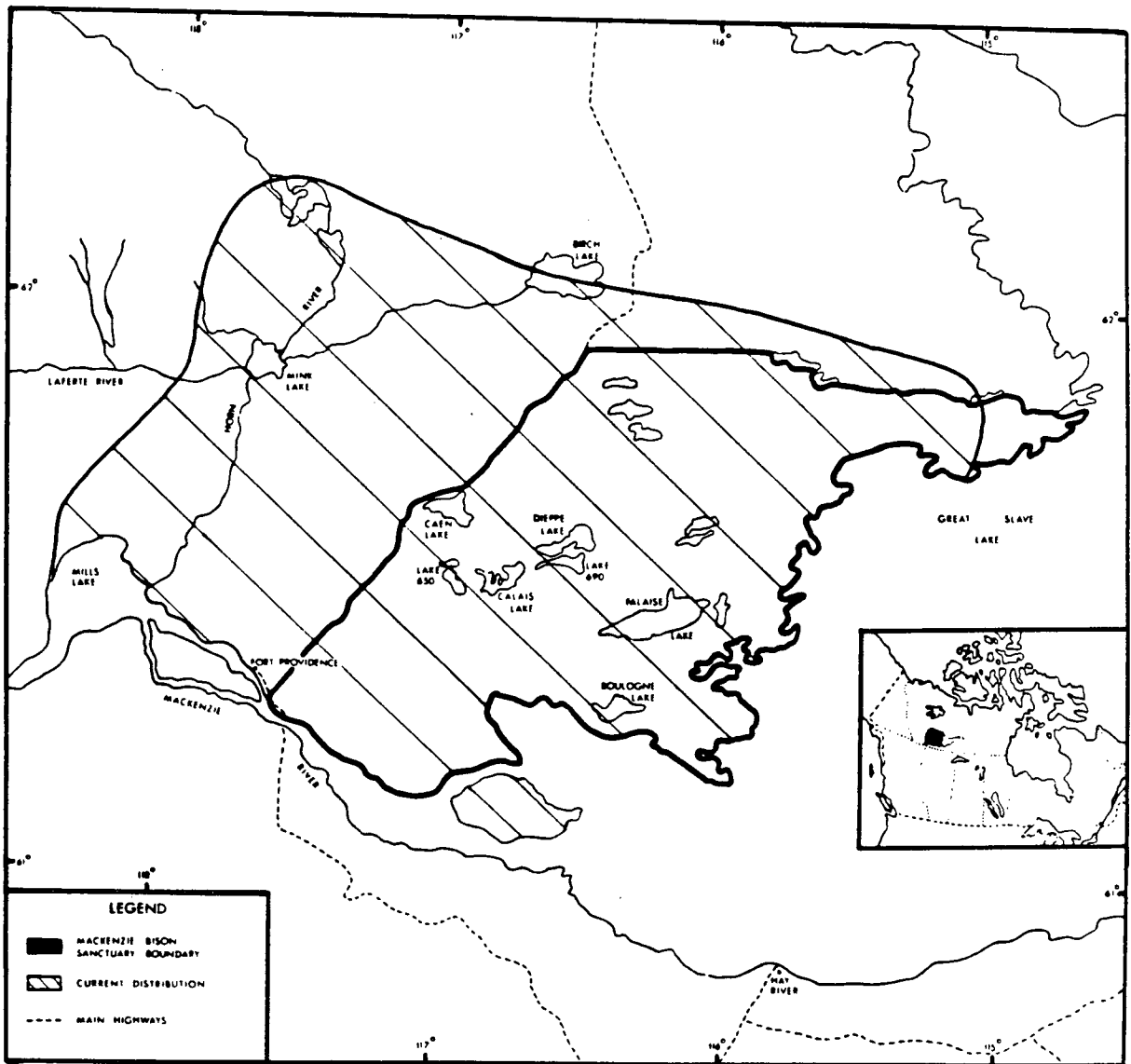
Figure 1.1. The study area, Mackenzie Bison Sanctuary, Northwest Territories.

Calamagrostis spp., Agropyron trachycaulum, and C. atherodes dominate the willow savanna plant community, with Hordeum jubatum, Phalaris arundinacea, Agrostis scabra, and C. aquatilis also present. Willow (Salix spp.) represents only a minor portion of the ground cover. The sparsely vegetated marl habitat is typified by a rocky substrate supporting low plant densities. Grasses, sedges, forbs, and shrubs are scattered throughout this habitat. A minor fourth habitat is found at the transition zone between the forest and the willow savanna: this is the willow-aspen habitat. Willows and trembling aspen poplar (Populus tremuloides) dominate this habitat. The understory plant associations resemble those found in the willow savanna.

The main forest habitats are: (v) coniferous forest, dominated by black spruce (Picea mariana), white spruce (P. glauca), jack pine (Pinus banksiana), and larch (Larix laricina); (vi) mixed deciduous-coniferous forest, dominated by white spruce, aspen, and balsam poplar (P. balsamifera). Birch bog (vii), dominated by shrub birch (Betula glandulosa) and low heath forming shrubs (Arctostaphylos uva-ursi, Potentilla fruticosa) are found in open poorly drained areas of the forest.

A fire in 1980 burnt a large area to the south and east of Mink Lake. This area has become the main population expansion zone. The regenerating vegetation has become dominated by lush graminoid meadows which are not separated by large expanses of forest unlike the major meadows found in the Sanctuary.

CHAPTER 2. SEASONAL CHANGES IN FORAGE QUALITY AND QUANTITY

INTRODUCTION

Optimal foraging theory predicts that animals, when faced with an abundant supply of food types varying in nutritional value, will select only the better quality foods, ignoring the others, even if these are abundant (Pyke, et al., 1977; Krebs, 1978). Conversely, with the scarcity of better foods, the diet will include more lower quality food types. Sinclair (1975; 1977) found large mammal grazers, such as wildebeest and African buffalo, showed strong selectivity for high protein grass leaves when they were abundant, but ate low-quality stems as leaf biomass declined, thus demonstrating a decline in selectivity.

During the start of the summer growing season, wood bison choose from an abundance of nutritious forage types. As the growing season progresses, changes in both forage quantity and quality occur. Tissues mature, causing an increase in lignin and cellulose content, and consequently a decrease in digestibility. Protein levels vary greatly with these changes in plant phenological stages. Sullivan (1962) found that crude protein was significantly positively correlated with digestible protein and that crude protein levels provided reasonably reliable indicators of forage value. Crude protein is calculated by the standard conversion: Percent Nitrogen x 6.25 = Percent Crude Protein. Hence, forages high in nitrogen should be more protein rich and be more valuable than forages low in nitrogen. However, forages with high fiber content may negatively affect nitrogen accessibility (Bell, 1971;

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Janis, 1976). Therefore, using only nitrogen concentration to rank forages by may be inappropriate. A ratio of nitrogen concentration to percent fiber may provide a more realistic measure of forage quality, because it takes fiber levels into account. I use this ratio to define forage quality.

If wood bison forage in an optimal fashion then one can predict that they should only consume that forage with the highest ratio of percent nitrogen to percent fiber until it becomes scarce. In this chapter I: 1) document changes in quantity and quality of the different forage types, found in six different habitats, with the progression of the growing season, 2) determine if changes in diet composition are related to changing plant qualities, associated with phenological change, as predicted by food limitation, and 3) compare the observed bison diet with that predicted by optimal foraging theory.

METHODS

Plant sampling was conducted in six of the seven major habitats between 1 June and 15 October, 1987. The birch bog habitat type was not sampled because of logistical problems. The coniferous habitat was split into dry and wet areas: dry areas dominated by jackpine and white spruce and wet areas dominated by larch and black spruce. Samples were gathered on a two week rotation from June to mid August, and on a monthly rotation from mid August to October, resulting in nine sample dates. I was unable to collect data on forage quantity during the final sample date (15 October). Forages sampled included <u>Carex atherodes</u>, <u>C. aquatilis</u>, <u>Carex</u> spp., <u>Cladina mitis</u>, <u>Phalaris</u>

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arundinacea, Salix spp., and grass (Calamagrostis spp., Agropyron trachycaulum, Hordeum jubatum, Agrostis scabra, and Elymus innovatus). Because reed canarygrass (P. arundinacea) appeared to be actively avoided by foraging bison, it was sampled separately from the other grasses in an attempt to determine the cause of this apparent avoidance.

Forage Quality

To determine seasonal nutrient quality changes in individual forage types, samples of each forage were analyzed for percent nitrogen concentration and percent acid-detergent fiber. Forage samples were collected from fixed patches in each habitat. The current year's growth of grasses and sedges was clipped to 3cm above ground level. Current annual growth, with accompanying leaves, was clipped from willows. Lichen was harvested with accompanying attached evergreen needles and dead twigs. Samples were dried at approximately 60° C in a propane oven for 12 hours, ground in a cyclone mill through a 0.1mm screen, and submitted to the Animal Science Department at the University of British Columbia for analyses.

The micro-Kjeldahl technique (Nelson and Sommers, 1973) was used to determine percent nitrogen concentrations. Forage fiber analyses follows the chemical technique developed by Van Soest (1967). The acid-detergent analysis was used to determine fiber content. This analysis provides a measure of the indigstible cell wall contents (lignocellulose). All samples were ranked by the (i) percent nitrogen concentration, (ii) percent acid-detergent fiber, and (iii) the ratio of percent nitrogen concentration/percent

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acid-detergent fiber (N/ADF) for each time period. This resulted in rankings, for both forage classes and habitats, by the highest percent nitrogen, the lowest acid-detergent fiber, and the highest ratio of N/ADF.

Percent dietary crude protein for each month was estimated by summing forage crude protein multiplied by percent forage in the diet (see chapter 3). C. atherodes represented the sedge crude protein values. Monthly forage crude protein values represent the mean value, over all habitats, from samples collected on 15 June, 15 July, 12 August, 24 September, and 15 October. Crude protein in the diet was estimated for both summers based upon the assumption that forage crude protein levels were similar between years.

T-tests were used to compare lichen quality measures between habitats.

Forage Quantity

Data on forage biomass were gathered by two different methods: one destructive and one non-destructive. The destructive method consisted of fixed transects being chosen within each habitat. At each sample date, ten $0.25m^2$ plots were selected on these transects. All transect placement and sample plots were determined on a random systematic basis. At each plot all current year's grass and sedge growth, falling within the three dimensional plot boundaries, was clipped in the same method as mentioned above. Grass species were determined when possible and grazed forage types were noted. The clipped forage was separated into current year's live and current year's dead before being dried in a propane oven at approximately 60° C for 12 hours. Both live and dead dry matter were weighed on an electronic

balance. Estimates of green biomass were calculated for each habitat type from each sampling date. The percent forage composition of total green biomass was also calculated for each date. Because of negligible lichen growth over the sampling period, a single estimate of biomass was made for each habitat from data gathered over the entire sampling period. Estimates of standing crop present at the start of winter were calculated from data collected during the final sampling date (24 September). Standing crop was defined as the sum of current year's green, dead, and lichen (where occurring) biomass. Estimates of available graminoid crude protein (g/m^2 dry weight) for each habitat were calculated by multplying the standing crop of each forage by its percent crude protein. P. arundinacea was excluded from the estimates because of its absence in the diet. Wet sedge meadow was excluded from this analysis because forage was not deemed available. Estimates were calculated for each sampling date.

A one meter wide swath, the length of each transect, was checked for the presence of individual willow plants greater than 25cm tall. All willows with at least half of the plant falling within this 1.0m swath were included in the sample. These willows were individually marked so that repetitive observations on known individuals could be made. Decadent willows with only crown growth were discarded because they did not provide available browse. The following data were gathered from each willow: 1) browsing occurrence, 2) maximum width at 75cm height or at maximum height, and 3) height if under 75cm tall.

Non-destructive green biomass estimates were determined for open habitats by using a digital photometer. The photometer consisted of two probes with filters which allowed light at 800nm (infra red) and 675nm (red)

wavelengths to pass through. Red light is absorbed by chlorophyll in green vegetation, while it is reflected by non-green matter. Infrared light is reflected by both green and non-green material. Thus, the ratio between the reflectance values is correlated with the amount of green biomass (Tucker et al., 1973; McNaughton, 1979). Photometer readings were calibrated against measurements of the dry weight of green material obtained from $0.25m^2$ clip plots. Calibrations were conducted for each of the marl and wet sedge meadow habitat. One calibration was conducted for both the willow savanna and willow-aspen habitats. The resulting regression lines were used to estimate green biomass from digital photometer readings (Figures 2.1-2.3).

Photometer readings were taken from parallel transects 2m to the right of those used for plant clipping to avoid confounding the methods. Fifty readings were taken from random systematically chosen plots. Readings were conducted in the shade for consistency. Wet sedge meadow readings were conducted one hour before sunset in order to avoid problems with water reflection. An ocular estimate of percent forb cover was recorded for each plot in the willow-aspen and willow savanna habitat types, as forbs represented green matter not being sampled from the clip plots. Both methods gave similar estimates of green biomass (Table 2.1). Correlation coefficients of the two estimates were highly significant (0.95 to 0.97) for all habitats except marl (0.48). Green biomass estimates for all open habitats are based upon the combined results of both methods.

MARL HABITAT

$y = 36.61x - 36.08$
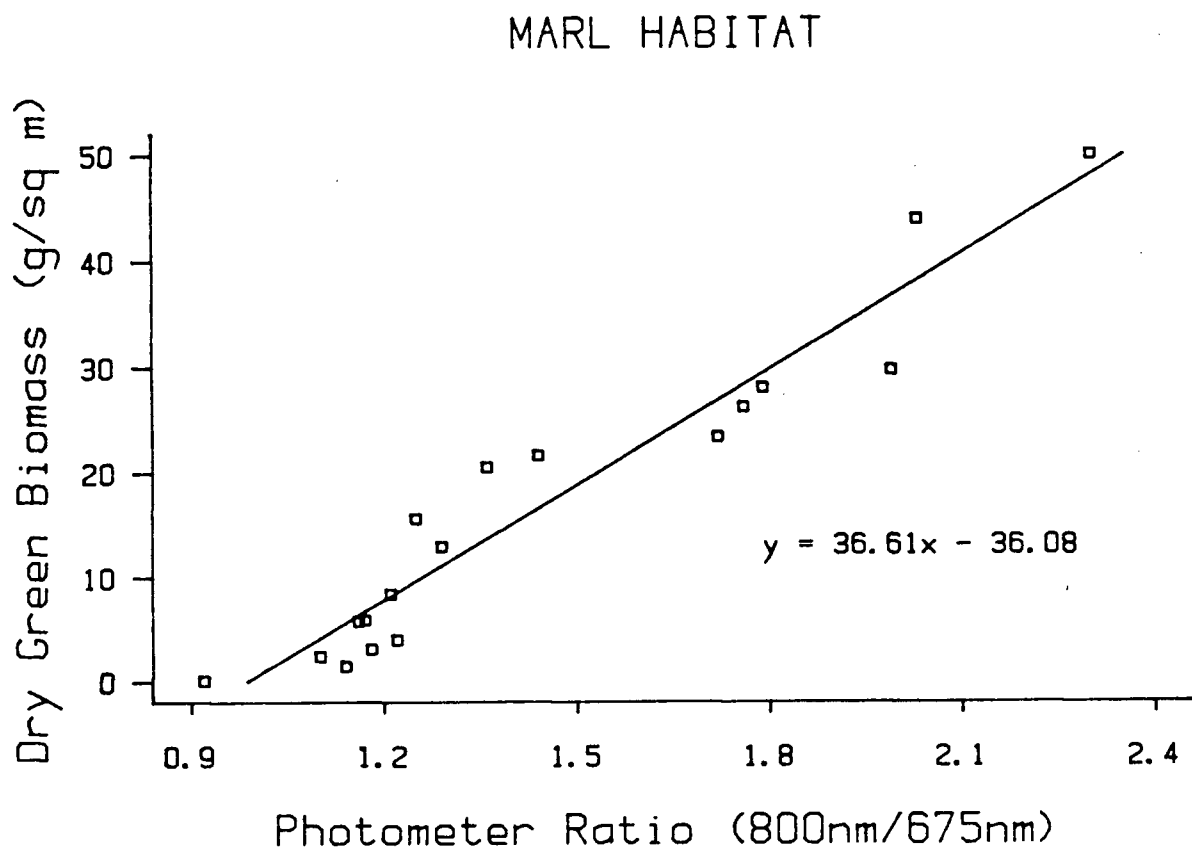
Figure 2.1. Calibration of photometer readings for marl habitat. The ratio of reflectance values recorded by the 800nm and 675nm probes was positively related to green biomass dry weight (R^2=0.924; p<0.01).

WET SEDGE MEADOW HABITAT

$y = 103.13x - 155.62$
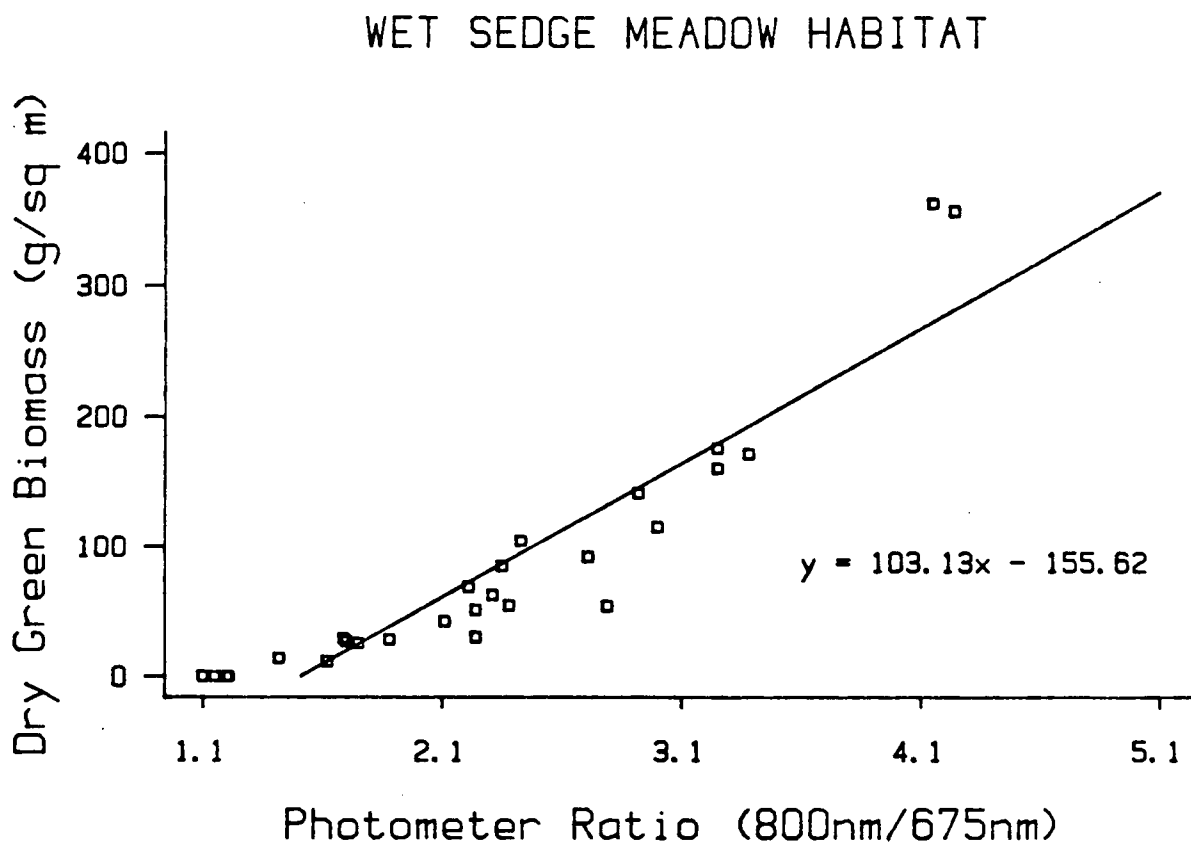
Figure 2.2. Calibration of photometer readings for wet sedge meadow habitat. The ratio of reflectance values recorded by the 800nm and 675nm probes was positively related to green biomass dry weight (R^2=0.858; p<0.01).

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WILLOW SAVANNA AND WILLOW-ASPEN HABITATS
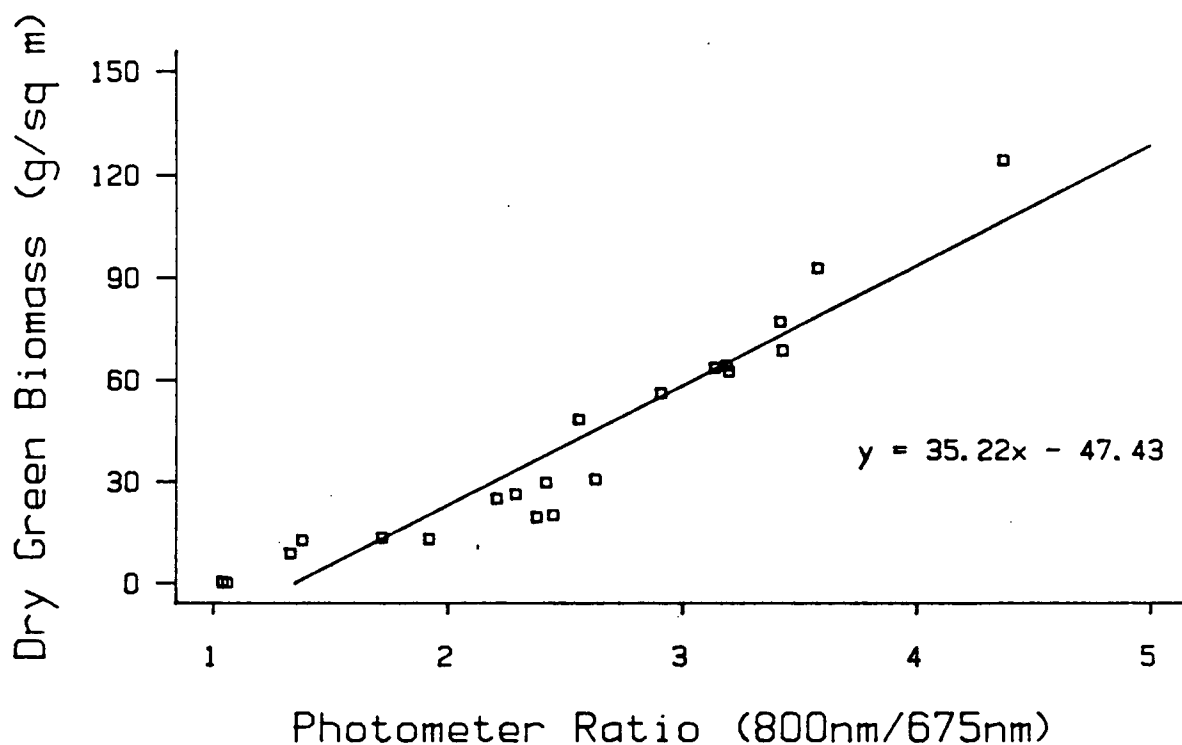
Figure 2.3. Calibration of photometer readings for both willow savanna and willow-aspen habitat. The ratio of reflectance values recorded by the 800nm and 675nm probes was positively related to green biomass dry weight (R^2=0.904; p<0.01).

Table 2.1. Estimates of green biomass production (g/m^2 dry weight) in open habitats, using both non-destructive (ND) and destructive (DS) methods, for eight dates during the 1987 sampling period.

Habitat		1 JN	16 JN	1 JL	15 JL	30 JL	12 AG	25 AG	24 SE
Wet Sedge	ND	42.9	119.8	162.3	207.1	187.9	174.4	138.0	20.6
	DS	28.2	73.5	104.4	138.8	130.2	136.5	110.3	32.8
Willow Sav.	ND	21.1	31.4	46.2	60.1	47.2	38.9	n/a	7.2
	DS	13.8	21.7	27.3	46.0	31.6	33.6	38.0	3.2
Willow-Asp.	ND	16.5	26.0	32.6	36.4	36.8	30.8	n/a	5.8
	DS	6.9	7.6	14.5	16.3	15.1	11.6	8.3	2.9
Marl	ND	7.9	11.0	9.7	10.3	10.9	13.4	n/a	5.5
	DS	3.1	3.0	2.0	7.2	3.0	3.3	4.4	0.2

RESULTS

Forage Quality

Percent Nitrogen

All forages, except lichen, in all habitats had the highest nitrogen percentages during early June, then declined at a constant rate (p<0.001) over time (Figure 2.4). Percent nitrogen in lichen was consistently low, ranking last throughout all sampling periods except the final one. Lichen in the mixed forest had a significantly higher mean nitrogen percentage (0.59, s.e. 0.016) than lichen in either wet or dry coniferous habitats (0.49, s.e. 0.010; 0.47, s.e. 0.015 respectively).

P. arundinacea consistently ranked highest in percent nitrogen until mid-August when willows ranked highest, remaining so until the end of the sampling period (Figure 2.5). Grasses, willows, and sedges had intermediate rankings until August when grass rankings dropped and willow and sedge ranked highest. C. atherodes generally had higher nitrogen percentages than C. aquatilis.

Willow savanna and willow-aspen habitats consistently provided forages containing the highest percent nitrogen until the final sampling period. Forages in marl habitat contained less nitrogen than forages in willow savanna or willow-aspen habitats, but more than forages located in forested habitats. Generally forages in the forested habitats contained more nitrogen than forages in wet sedge meadows until mid-August (Figure 2.6).

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LICHEN – WET CONIFEROUS

CAREX ATHERODES – WILLOW SAVANNA
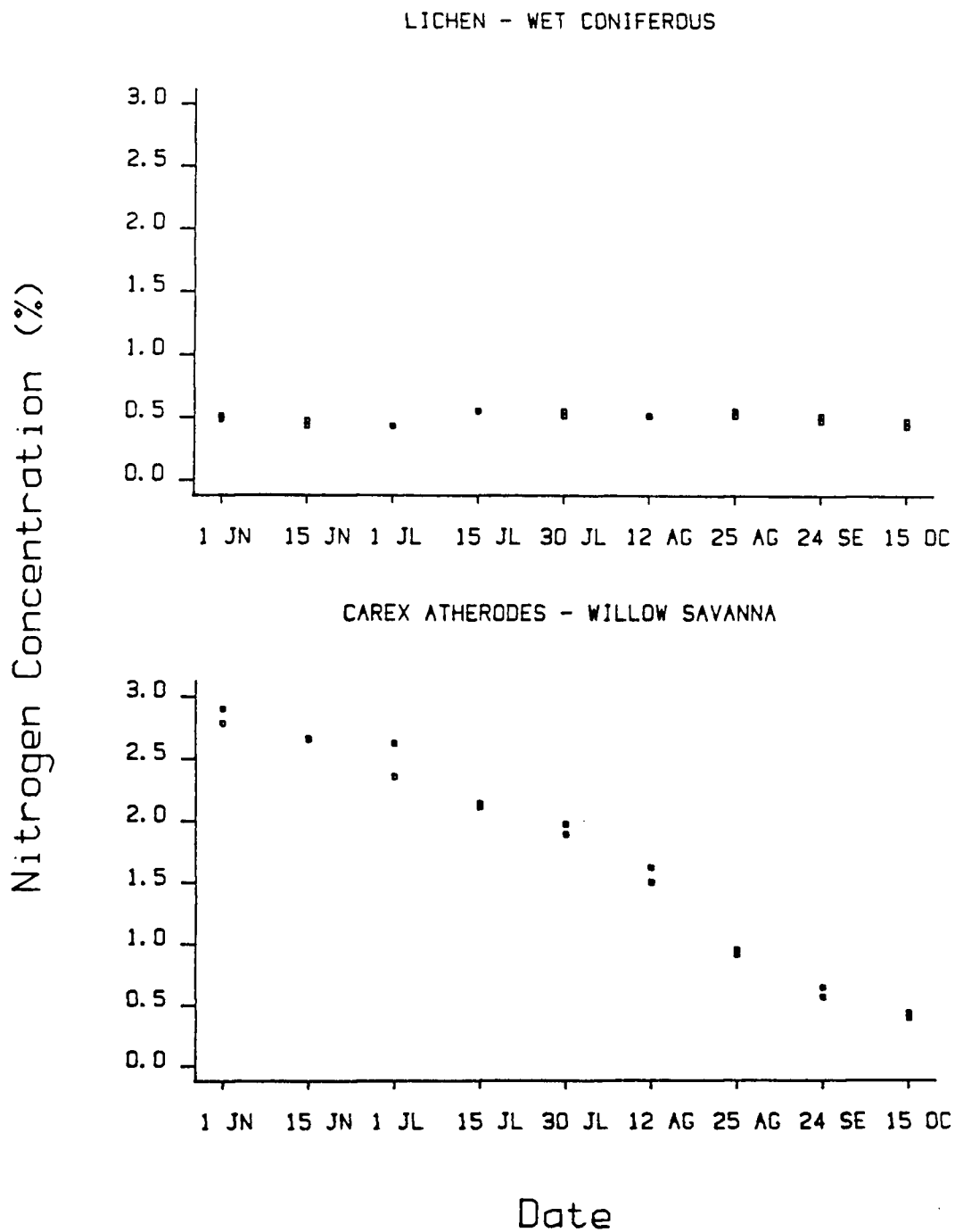
Figure 2.4. Typical examples of the changes in nitrogen concentration (%) over time for lichen and for other forages.

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Figure 2.5. Changes in forage class rankings during the sampling period with changes in ranking criteria. CX = <u>Carex</u> spp, CT = <u>C</u>. <u>atherodes</u>, CQ = <u>C</u>. <u>aquatilis</u>, GR = grass, LI = lichen, PA = <u>P</u>. <u>arundinacea</u>, and SX = <u>Salix</u> spp. Time represents sampling dates (see text and Figure 2.4 for actual dates).
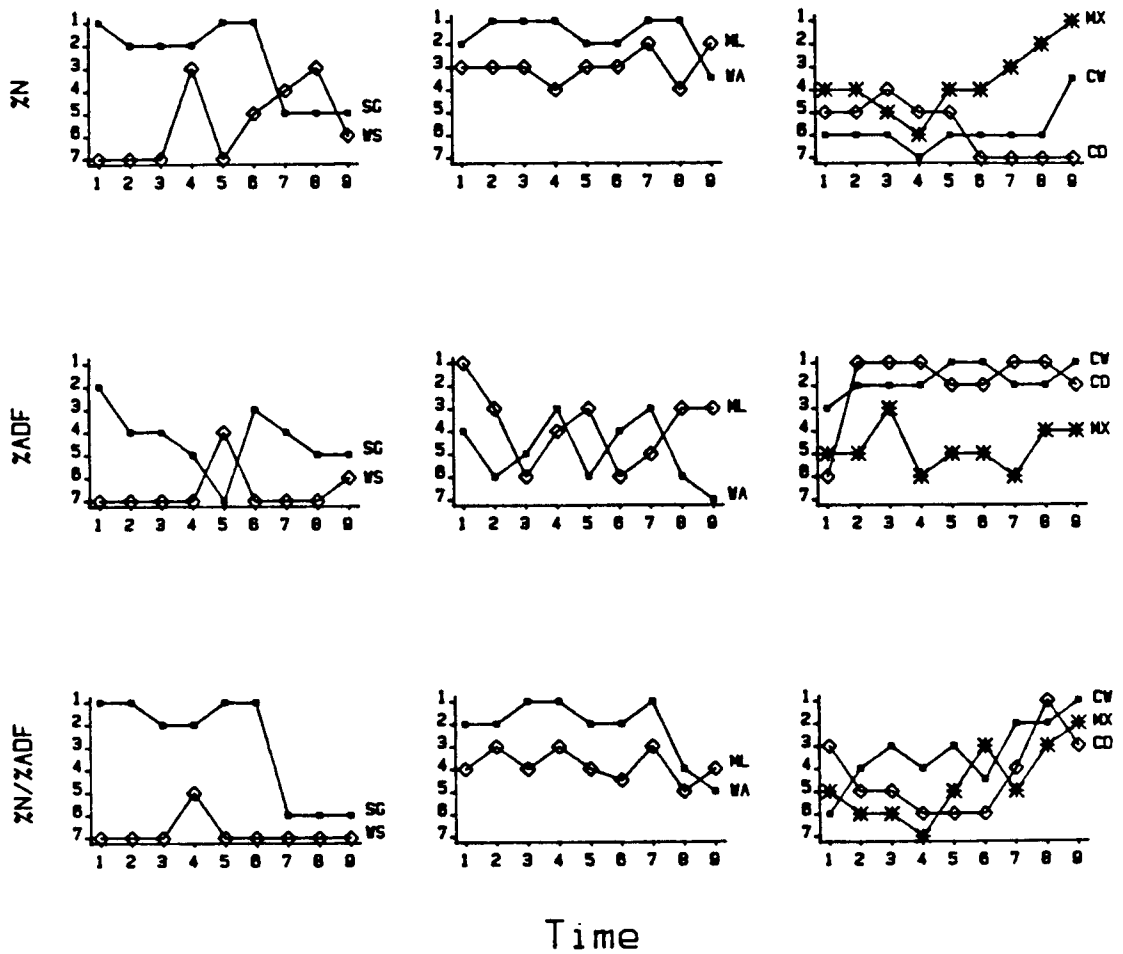
Figure 2.6. Changes in habitat rankings during the sampling period with changes in ranking criteria. CD = dry coniferous, CW = wet coniferous, ML = marl, MX = mixed forest, SG = willow savanna, WA = willow-aspen, WS = wet sedge meadow. Time represents sampling dates (see text and Figure 2.4 for actual dates).

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Acid-Detergent Fiber

The proportion of indigestible fiber generally increased in all samples, except lichen, over the sampling period. The relationships were not as linear as those for percent nitrogen (Figure 2.7). Lichen had the lowest amounts of indigestible fiber throughout the entire sampling period. Mean percentages were 16.87 (s.e. 1.30), 15.51 (s.e. 1.54), and 13.92 (s.e. 1.37) for mixed forest, dry coniferous, and wet coniferous habitats respectively. These values were not significantly (p>0.05) different.

P. arundinacea, and willow ranked highest, i.e. had the lowest amounts of indigestible fiber, after lichen until late-September when P. arundinacea showed an abrupt increase in indigestible fiber (Figure 2.5). C. atherodes and Carex spp. had intermediate amounts of indigestible fiber, and grasses and C. aquatilis had high amounts of indigestible fiber throughout the sampling period. E. innovatus, the dominant grass in dry coniferous habitats, consistently had lower amounts of indigestible fiber than grasses in other habitats which are dominated by Calamagrostis spp.

The forested habitats consistently provided forages with low indigestible fiber content (Figure 2.6), while forages from wet sedge meadows had consistently higher indigestible fiber content. Willow savanna, willow-aspen, and marl habitats provided forages with intermediate indigestible fiber contents.

LICHEN - DRY CONIFEROUS

GRASS - MARL

GRASS - DRY CONIFEROUS

Date
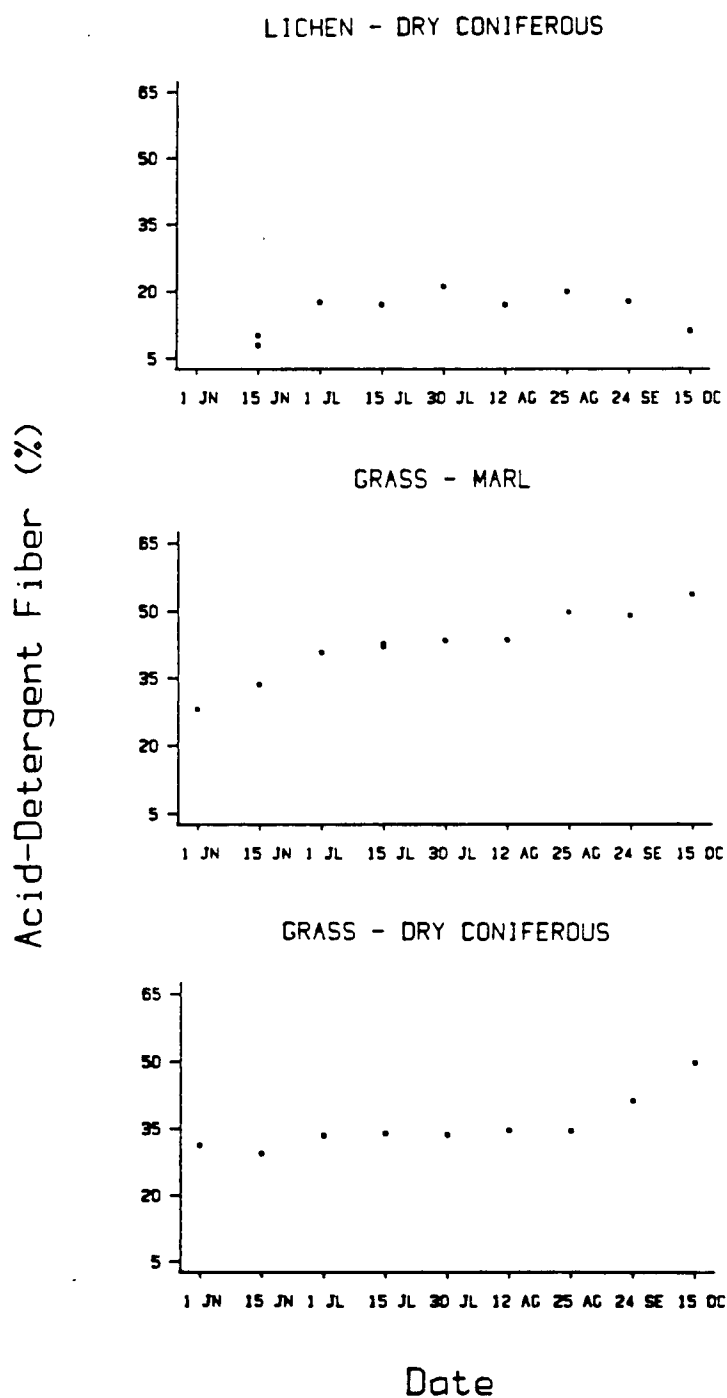
Figure 2.7. Typical examples of the changes in acid-detergent fiber (%) over time for: (i) lichens, (ii) most forage-habitat combinations, and (iii) an extreme example of the few exponential relationships.

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Percent Nitrogen/Percent Acid-Detergent Fiber Ratio

All forages, except lichen, had their highest N/ADF values, and hence were of their highest nutrient quality, at the start of the growing season. These values generally decreased in a linear fashion ($p<0.003$) (Figure 2.8). Lichen quality remained relatively constant throughout the sampling period. Mean values were 3.63 (s.e. 0.27), 3.12 (s.e. 0.32), and 3.82 (s.e. 0.62) for mixed forest, dry coniferous, and wet coniferous habitats respectively. These values were not significantly ($p>0.05$) different.

P. arundinacea and willow consistently ranked highest in quality until late August when lichen abruptly switched from ranking lowest to highest and replaced P. arundinacea (Figure 2.5). Sedges and grasses were of intermediate quality throughout the sampling period. C. atherodes generally was a better quality forage than C. aquatilis.

Willow savanna and willow-aspen habitats provided forages of better quality until late August when forested habitats provided better quality forage (Figure 2.6). Wet sedge meadows consistently provided forages of inferior quality, while marl forages were of intermediate quality.

Crude Protein

Dietary crude protein (CP) decreased from June until September when it leveled off at about 3% (Figure 2.9). June to August dietary CP was slightly higher in 1986 than in 1987. C. atherodes CP values were always higher than dietary CP. Grass CP levels were higher than dietary CP levels only during

LICHEN - DRY CONIFEROUS

CAREX ATHERODES - WILLOW SAVANNA

GRASS - WILLOW SAVANNA

Nitrogen (%)/Acid-Detergent Fiber (%)

Date
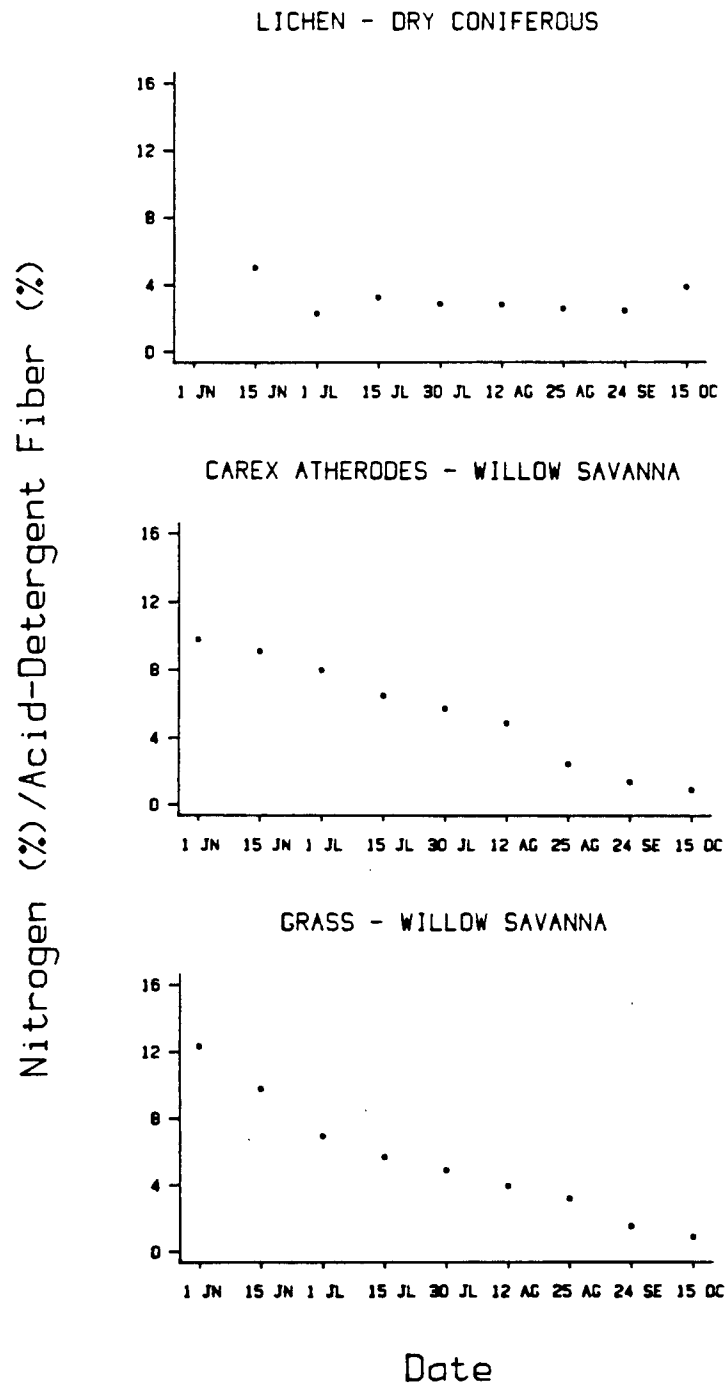
Figure 2.8. Typical examples of the changes in the N/ADF values over time for: (i) lichen, (ii) most forage-habitat combinations, and (iii) grasses.

1986

1987
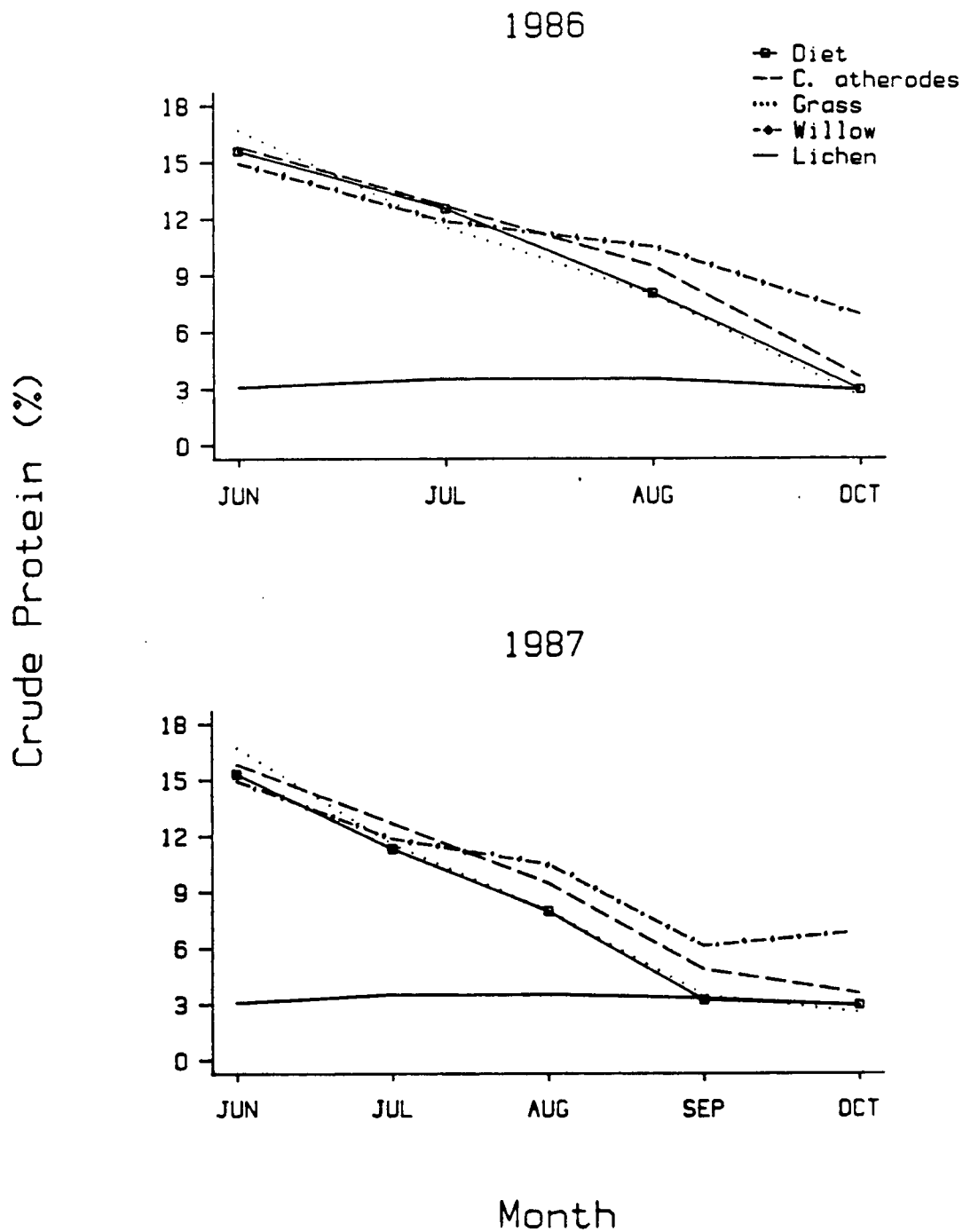
Figure 2.9. Comparison of percent crude protein levels available from different forages with crude protein levels found in the diet.

early summer being lower from August on. Willow showed a reversal of this trend having higher CP levels during late summer and fall.

Forage Quantity

Green Biomass Estimates

Generally, green biomass increased until mid-July, stayed consistently high until mid-August, and decreased rapidly into September. Green biomass peaked in mid-July. Dead current year's growth first appeared during the July 30 sampling period. This trend was seen amongst all habitats (Figure 2.10). Wet sedge meadows produced the most green biomass throughout the growing season, some five times more than willow savanna or willow-aspen habitats. Willow savannas produced more green biomass than willow-aspen habitats. Marl and all forested habitats produced little green biomass, generally three time less than the willow-aspen habitat.

Whenever grass was present it was the dominant green biomass component (Figure 2.11). $\underline{C}$. atherodes was the second most dominant green biomass component. Forb growth was very similar in both willow savanna and willow-aspen habitats, with mean cover (per $0.25m^2$ plot) of 14.2% and 13.3% respectively.

As winter approached, wet sedge meadows provided the largest standing crop of forage. At $186.6g/m^2$ (dry weight), the standing crop in wet sedge meadows was three times that of willow savannas, and eight times that of
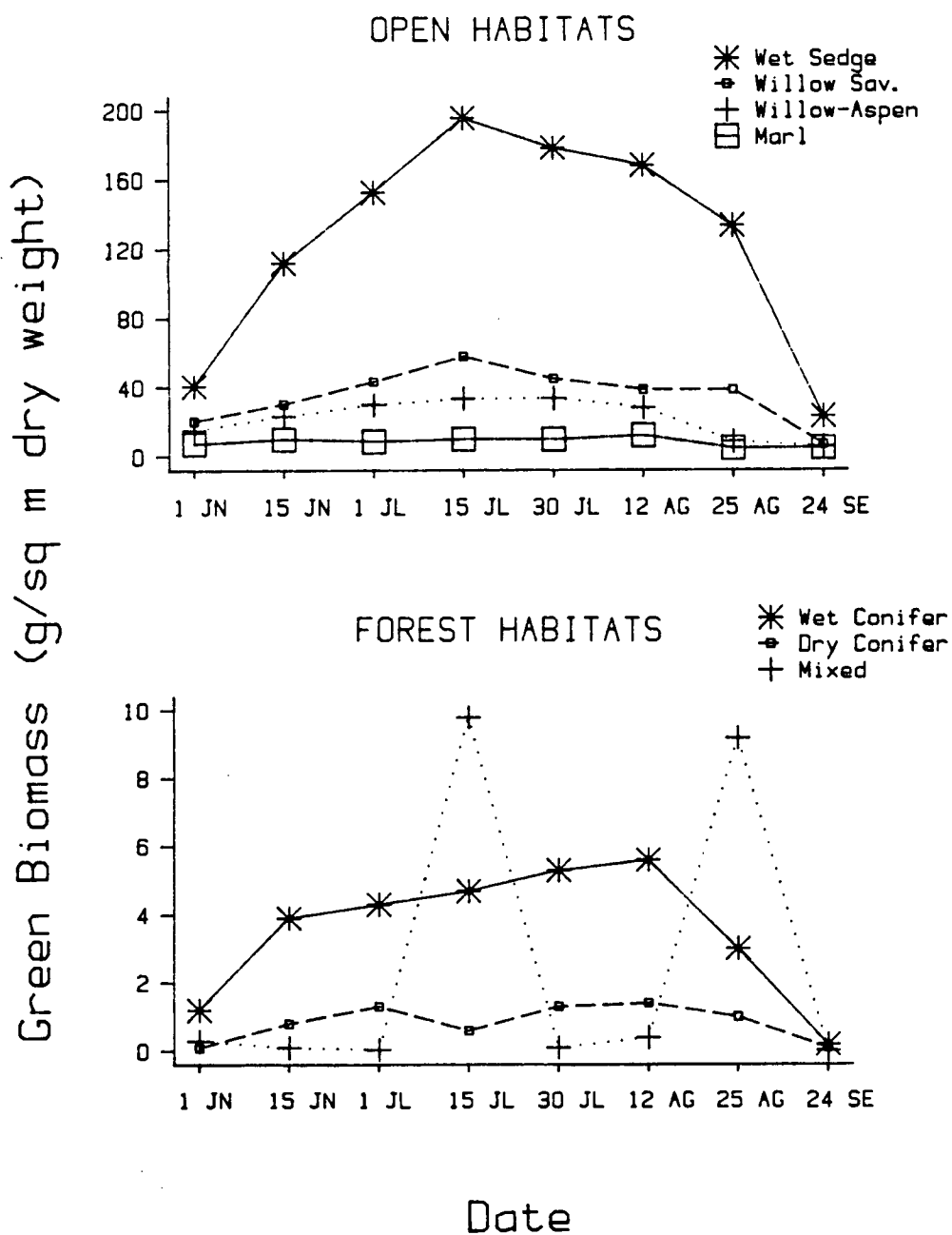
Figure 2.10. Green biomass estimates (g/m^2 dry weight) for all habitats.
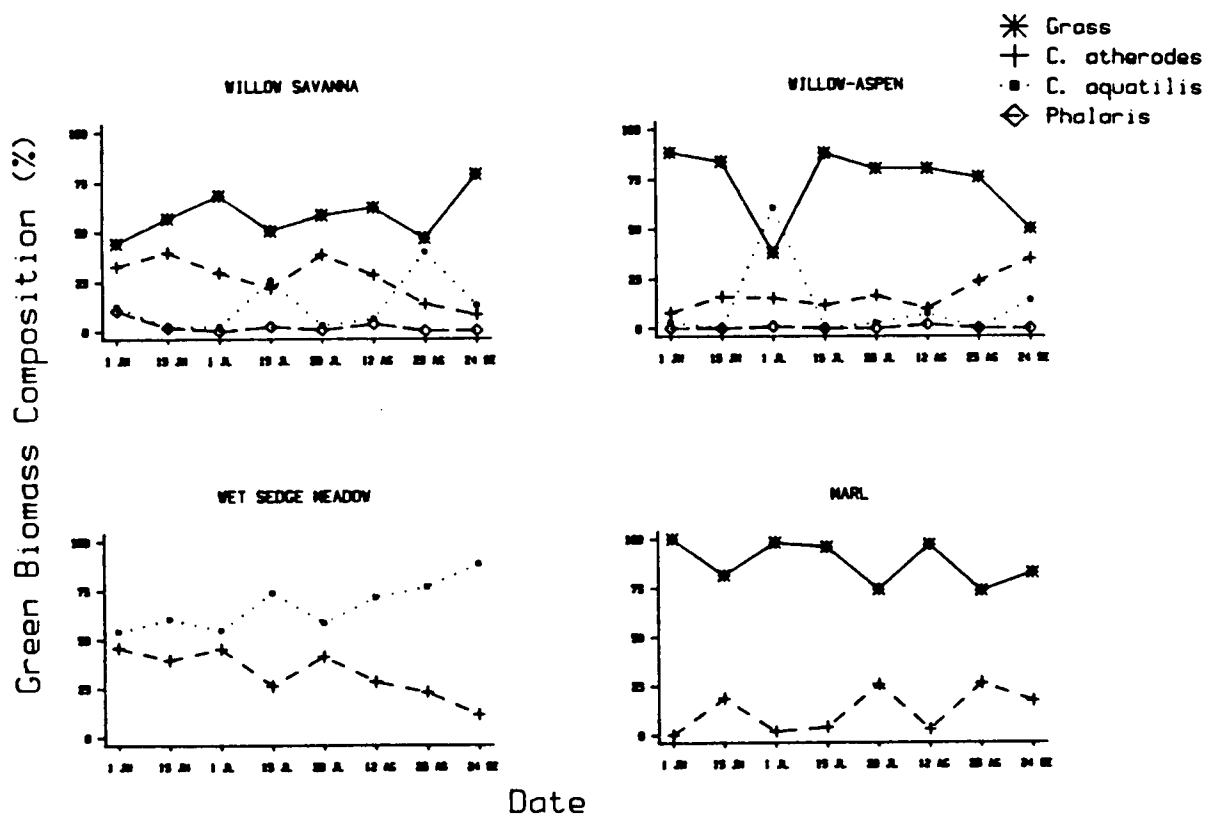
Figure 2.11. Forage composition (%) of the green biomass found in all habitats.

willow-aspen habitats. All the other habitats provided standing crops of less than $8g/m^2$.

Willows

Willow density was highest in willow-aspen habitats and lowest in willow savannas. Willows in willow-aspen habitats were much taller and wider than those found in other habitats (N. Larter, unpubl. data) and presumably provided greater biomass of current annual growth than any other habitat. However, the percent of browsed willow plants in willow savannas was at least three times that of willow-aspen or mixed forest habitats (Table 2.2).

Lichen

Wet coniferous areas provided three times more lichen biomass than either dry coniferous or mixed forests, $5.2g/m^2$ (dry weight) versus $1.5g/m^2$ and $1.4g/m^2$ respectively. Thus coniferous forests, wet and dry areas lumped, would be expected to provide more lichen biomass than mixed forests.

Crude Protein

Willow savanna and willow-aspen habitats provided the most available crude protein (g/m^2 dry weight) (Figure 2.12). As summer progressed the difference in available crude protein between habitats was reduced, but was still higher in willow savannas.

Table 2.2. Willow density (plants/km^2) and the observed percent of willow plants browsed between 1 June and 25 September, 1987. n represents the number of marked willows used for the calculations.

Habitat	Density	Browsed	n
Willow Savanna	17.9	58.8	17
Willow-Aspen	138.0	15.9	69
Marl	92.0	10.5	57
Mixed Forest	46.0	17.4	23
Coniferous (Wet)	88.8	0.0	16
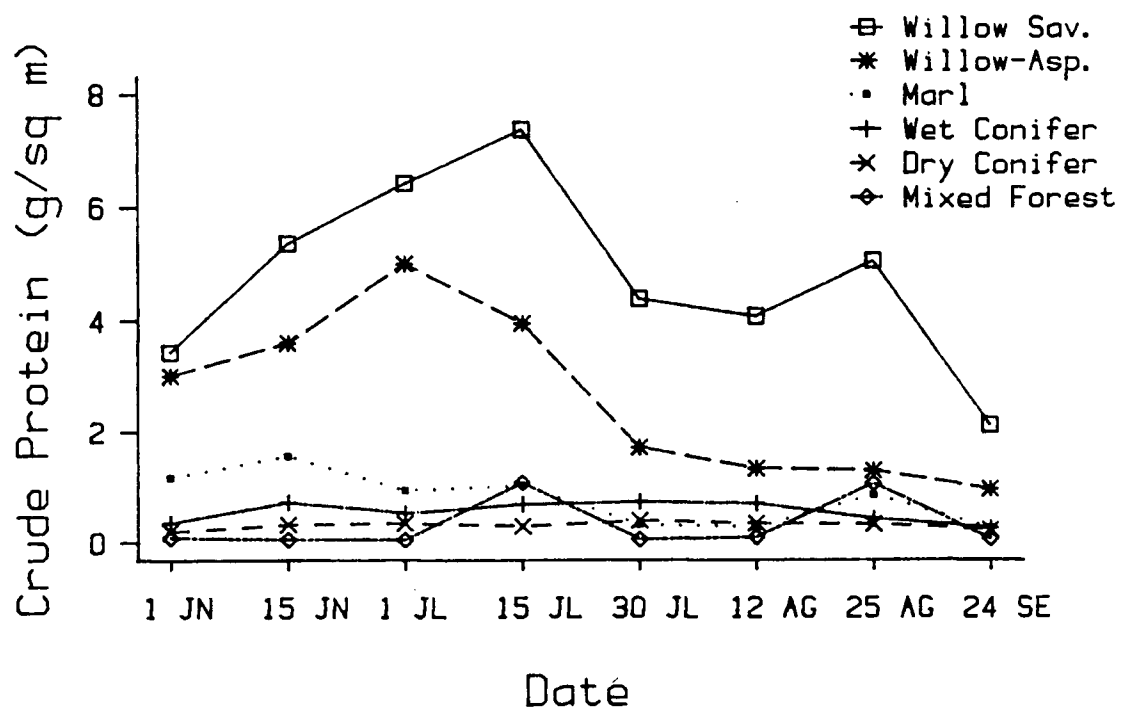
Figure 2.12. Changes in available crude protein (g/m^2 dry weight) for all habitats with the progression of the growing season. P. arundinacea and willow were excluded from the calculations.

DISCUSSION

Forage Quality

Forage quality rankings changed with the factors used to determine forage quality (Figure 2.5). Using N/ADF values to rank forage quality, optimal foraging theory would predict P. arundinacea to be the major dietary component throughout the summer, with willow and lichen dominating the fall diet. Bison diets did not meet these predictions; P. arundinacea was not consumed at any time. Willows formed a large proportion of the diet in early summer, but had dropped out of the diet by September. Lichen however, was a major dietary component during the fall which did agree with the predictions.

Other factors beyond the nitrogen and fiber content I investigated may influence forage quality. P. arundinacea has a substantial alkaloid content (Audette et al., 1970; Hagman et al., 1975). This alkaloid content increases with foliage removal (Woods and Clark, 1971). Alkaloids exert strong action on the central nervous system and affect muscle contraction, cardiac activity, and brain function (Gallagher et al., 1964). Arnold et al. (1980) showed that forage intake by sheep was drastically reduced (50%) by the presence of 1% of the alkaloid gramine in the diet. Gramine is one of the alkaloids that has been isolated in P. arundinacea (Audette et al., 1970; Woods and Clark, 1971). Alkaloid concentrations were negatively correlated with palatability of this grass when offered to sheep and cattle (Marten, et al., 1976). Additionally, P. arundinacea has been shown to be high in silicates (Van Soest, 1967)

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especially after stems have matured. The combination of these antiherbivory components may explain why P. arundinacea is avoided by bison.

Data on the lignin component of the indigestible fiber fraction of my forage samples were unavailable. Schwartz and Hobbs (1985) indicated that shrubs and forbs have a larger lignin fraction within the cell wall than do grasses. As the growing season progresses lignin may represent an increasing proportion of the indigestible fiber in willows. Accordingly, willows should be eaten when lignin is low but rejected when lignin is high. Lignin is essentially indigestible (Van Soest, 1963). This would explain the decrease in willow use during August and its low incidence in the September and October diet.

C. atherodes is a better quality forage than grass except during early June. Sedge is a major component of the summer diet. However, the grass component of the diet generally increases from June into July and August, while its quality in relation to sedge quality decreases. Possibly this difference is because new grass growth is associated with clumps of previous year's dead material. Because the bison's large mouth does not permit selectivity of individual stems, both current growth and dead material is ingested, causing a lower quality of food than if only live material were ingested. New sedge growth is not associated with clumps of dead material. Visual observations indicating a preference for foraging on C. atherodes over C. aquatilis (see chapter 3) agree with the hypothesis that diet compositon is based upon choosing forages of superior quality, because not only does C. atherodes have consistently higher N/ADF values than C. aquatilis, but the presence of potentially toxic calcium oxalates in C. aquatilis may additionally reduce its forage quality (Abaza et al., 1967; Baltzi and Jung, 1980).

Crude protein levels of forage below 5.9% are inadequate for the maintenance requirements of dry, pregnant mature beef cows (National Academy of Sciences - National Research Council, 1976) and crude protein levels below 7% appear to depress rumen cellulolysis (Hawley et al., 1981). By the 25 August sampling period crude protein content of some forages was below these levels. All forages had crude protein levels below 5.9% by 24 September (Figure 2.9). The diet during this time period had become more diverse with lichen, representing the best quality forage, becoming dominant. Rochelle (1980) demonstrated that the arboreal lichen Alectoria sarmentosa enhanced the digestibility of other forages found in the diet of black-tailed deer. Possibly terrestrial lichens, like Cladina mitis, have the same effect on other forages in the diet of bison and permit easier access to what little crude protein is available, thus allowing maintenance requirements to be met.

Reynolds and Hawley (1987) found that forages in wet meadows had higher crude protein and lower crude fiber content than forages in dry meadows except in early June. When comparing species between the two meadow types I found dry meadow forages had lower indigestible fiber content throughout the June to October sampling period. Crude protein was highest in dry meadow forages from June until mid-August when it was higher in wet meadow forages. However, the N/ADF ratio remained higher in dry meadow forages until late September. These opposing results indicate that the nutritional quality of forages cannot be generalized from general features of the habitat they occupy. For example, unmeasured differences in soil nutrient regimes may play a major role in determining forage quality. Wet sedge meadow substrates in the Slave River Lowlands may be more nutrient rich than those found in the Mackenzie Bison Sanctuary.

Forage Quantity

With sedge, most notably C. atherodes, being an important part of the summer diet, bison would be expected to concentrate foraging efforts in willow savannas where the greatest biomass of high quality C. atherodes is found (Figure 2.12). Wet sedge meadows provide more biomass, but it is of much inferior quality (Figure 2.6). Willow savanna habitats are preferred by bison in summer (see chapter 4.). If bison actively searched for the greatest biomass of high quality willow they should concentrate their efforts in willow-aspen habitats. However, most browsing occurred in willow savannas (Table 2.2), and willow-aspen habitats were rarely utilized in summer (see chapter 4). This indicates that bison will browse willows in an opportunistic manner, but will not abandon habitats with higher sedge and grass biomass in order to do so.

During the fall lichen provides the best forage quality and becomes a major component of the diet. Because lichen is only found in forested habitats, bison would be expected to use the forests more. Bison move into forested habitats during the fall (Larter and Gates, 1987). Wet coniferous areas provide more lichen biomass than mixed forest areas. The majority of relocations of radio-collared bison during fall were in wet coniferous areas (N. Larter, unpubl. data).

SUMMARY

1) The percent nitrogen concentration of all forages, except lichen, decreased linearly over the sampling period.

2) By 24 Spetember the crude protein levels of all forages were below 5.9%, the minimum required by cattle to meet maintenance requirements.

3) The indigestible fiber content of all forages, except lichen, increased over the sampling period.

4) Lichen had consistently low nitrogen and indigestible fiber content.

5) When only the ratio of percent nitrogen to percent indigestible fiber was used to determine forage quality, optimal foraging theory could not predict the wood bison diet. The presence of alkaloids and silicates probably explained the absence of P. arundinacea from the diet. Lignin probably negatively affected willow forage quality.

6) During the growing season willow savannas provided more high quality green biomass than any other habitats. Wet sedge meadows provided the greatest standing crop of green biomass of all habitats, but the forage was only available during winter when the water was frozen and provided access to this forage. During winter all forage was of low quality and wet sedge meadows supplied the greatest forage biomass. Wet coniferous areas provided the greatest lichen biomass.

7) The changes in dietary components demonstrated by wood bison appeared to follow changes in forage quality.

8) Bison switched from foraging on high quality forage in early summer to foraging on a diversity of low quality forages at end of summer.

CHAPTER 3. DIET COMPOSITION

INTRODUCTION

Although the analysis of bison dietary components has been of interest to wildlife ecologists, for example Peden (1976), Reynolds et al. (1978), and Waggoner and Hinkes (1986), mere tabulations of diet composition data cannot explain differences between animal species. Hanley (1982) suggested that ungulate diets can be predicted by four morphological parameters: body size, type of digestive system (cecal or ruminant), rumino-reticular volume to body weight ratio, and mouth size.

The wood bison is the largest North American ungulate. It inhabits the northern boreal forest, and is exposed to extreme seasonal shifts in forage quality and availability. General theory predicts that where forage quality is a limiting factor for the population, large body size is advantageous (Bell, 1969, 1971; Case, 1979). Large body size permits an animal to consume a lower quality diet because of a lower specific metabolic rate. Amongst ruminants, this is associated with slower passage of food through the gut (Westoby, 1974), and longer retention time permits more thorough digestion of a diet high in cellulose. This implies that the main strategy of the ruminant digestive system structure and function is to maximize the rate of nutrient assimilation and efficient use of protein (Bell, 1971).

The wood bison has a mean rumino-reticular volume to body weight ratio of 0.188 (n=31 four year or older adult bison, s=0.035, C. Gates unpubl. data). This is an intermediate value for those ungulates Hanley and Hanley (1982)

studied, where values ranged from about 0.10 for pronghorn (<u>Antilocapra</u> <u>americana</u>) and mule deer (<u>Odocoileus</u> <u>hemionus</u>) to 0.25 for domestic cow (<u>Bos</u> spp.) and domestic sheep (<u>Ovis</u> <u>aries</u>). Bison also have a large mouth. According to Hanley's (1982) criteria, the diet of wood bison diet should be intermediate between strictly monocotyledonous (grasses, sedges etc.) and dicotyledenous (shrubs, herbs etc.). Such a diet would permit wood bison to use a wide range of forages and habitats, while avoiding plant parts high in lignin. In this chapter I shall: 1) compare the diet predicted by these morphological parameters to the actual wood bison diet, 2) determine seasonal changes in diet composition and diversity and compare the results with the food limitation prediction of increasing diet diversity with the decrease in forage quality caused by changing plant phenologies, and 3) compare the diet composition of bulls with animals from mixed herds.

METHODS

Fecal samples were collected monthly during the summer and fall (June to October) and approximately bimonthly during winter and spring. Samples were collected during both 1986 and 1987 for months June, July, August, and October. Approximately 30ml (wet weight) samples were collected from fresh fecal pats, and combined into single samples for both mixed herd fecal material and bulls only fecal material. Samples were kept frozen until they could be oven dried at 60° C for 48 hours.

Diet composition was determined by analysis of fecal plant fragments (Sparkes and Malechek, 1968). Samples were ground in a Wiley Mill through

a 1mm mesh screen, and washed with Hertwig's clearing solution before being mounted on microscope slides for identification of cellular plant fragments (Hansen, et al., 1976). The analysis was performed by the Composition Analysis Laboratory, Fort Collins, Colorado, and by C. Melton. Because the majority of dietary components could only be identified to genus, they were placed into five major forage groups: grasses, sedges, shrubs, forbs, and lichens. Shrub material was represented almost exclusively by willow, and other species were found in very small proportions -- three occurrences of less than 1.5%, of buffaloberry (Shepherdia canadensis). Trace quantities of Equisetum spp., moss, pine, and spruce needles were discarded from the analyses. Samples were lumped by month. Diet breadth was calculated as the inverse of the sum of squared proportions of dietary components (Levins, 1968).

Microhistological examinations of fecal material for predicting animal diets is a controversial method. Hansen et al. (1973), Todd and Hansen (1973), Holechek et al. (1982), and Johnson et al. (1983) found the technique gave favorable results by being able to accurately estimate a known diet. Conversely, Voth and Black (1973), Smith and Shandruk (1979), Leslie et al. (1983), Putman (1984), and Barker (1986) found the technique to be badly flawed. The major problems with the technique result from variabilities in fragmentation, digestibility, and the proportion of identifiable plant fragments. Because I was not interested in specific species components of the diet, but in following trends of forage classes, I considered this technique to provide a suitable index for different dietary components.

Opportunistic observations of foraging were gathered between June 1986 and March 1988. These observations, although qualitative in nature, provided

a cross-reference for fecal analyses.

Water table height was measured by a stake placed on the Calais Lake shoreline, and the distance the shoreline retreated was measured during two summer periods, 1986 and 1987. The water depth in the wet sedge meadows was noted.

Because of the lack of independence between forage class proportions, parametric tests could be conducted only on one forage class. Sedge was determined the most important bison forage (Table 3.1.). Single and multifactor analyses of variance were used to determine differences in the dietary sedge component between years, and between mixed herds and bulls (Sokal and Rohlf, 1969).

RESULTS

Differences in Diet Between Years

Wood bison diets vary seasonally (Table 3.1.). During winter (December to April) sedges constitute from 96.1% to 98.8% of the diet. During summer (June to August) the diet becomes a more diverse mix of sedges, grasses, and shrubs. In the fall (September to October), the diet is most diverse and lichen becomes a prominent component.

There were significant ($p < 0.05$) yearly differences in the amount of sedge in the summer diet for all animals (Figure 3.1.); sedge made up a much

Table 3.1   Composition (%) of wood bison diets, based on fecal plant fragment analysis of pooled male and mixed herd samples. June, July, August, and October values represent data from more than one year. Diet breadth (Levins, 1968) is a measure of diet diversity.

Month	Sedge	Grass	Shrub	Forb	Lichen	Breadth
December	98.8	1.2	0.0	0.0	0.0	1.02
March	96.1	1.4	2.4	0.1	0.0	1.08
April	97.4	1.1	0.4	0.4	0.7	1.05
May	36.2	15.9	47.0	0.9	0.0	2.65
June	61.3	11.7	25.3	1.5	0.2	2.20
July	71.0	8.5	18.8	1.4	0.3	1.83
August	37.8	18.0	24.2	4.0	16.0	3.83
September	7.1	42.2	10.3	6.1	34.3	3.17
October	29.1	22.9	6.5	0.9	40.6	3.27
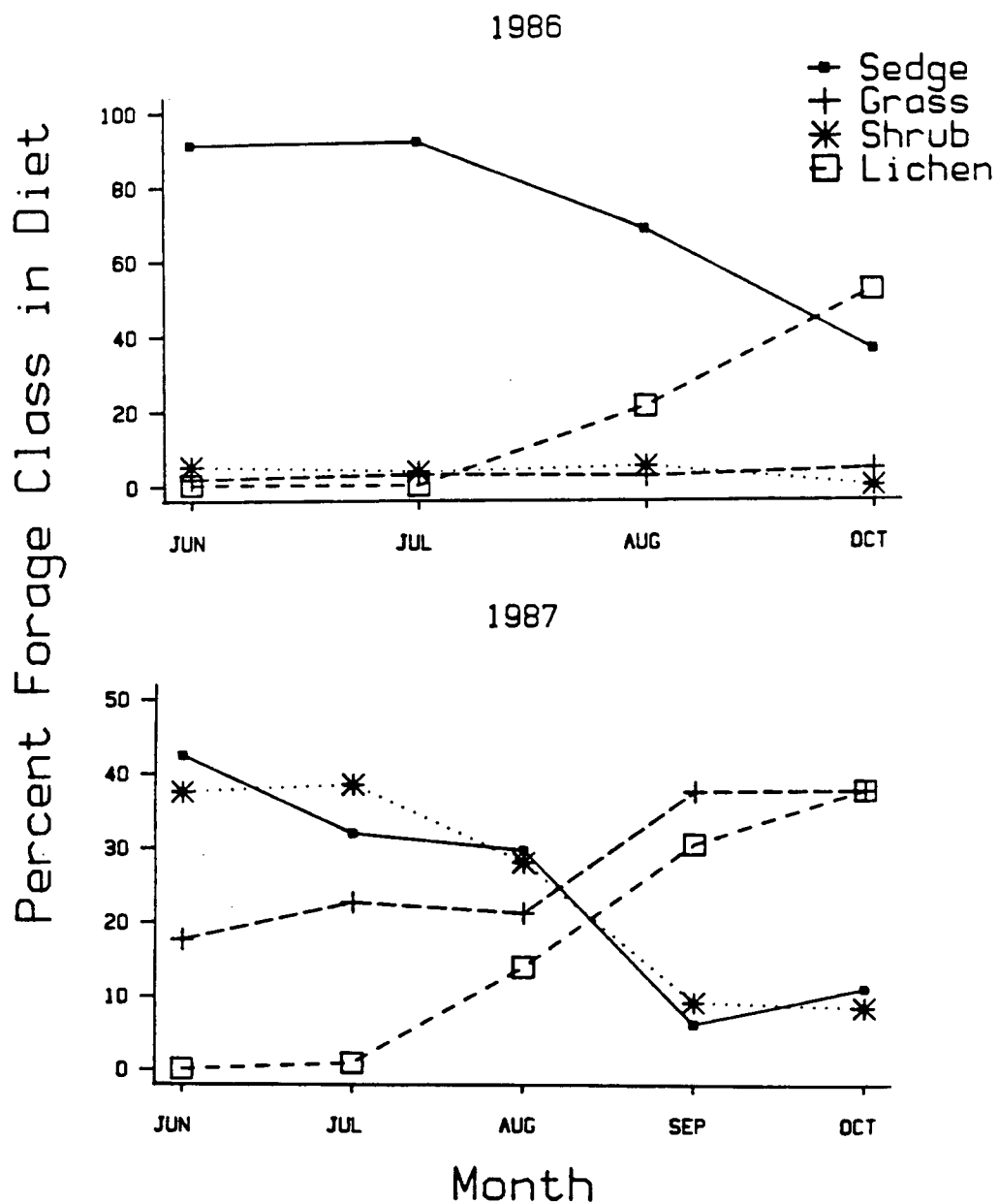
Figure 3.1. Diet composition (% of four major forage classes) of wood bison during 1986 and 1987, based upon analysis of fecal plant fragments.

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smaller proportion of the diet in 1987 while the amount of grass, shrub, and forb increased.

The October diet of mixed herds showed significantly lower amounts of sedge in 1987 when compared to 1986. There was no information on bull diets during this time period.

The summer of 1987 was much drier than the summer of 1986. From 6 June to 24 August, 1986 the Calais Lake shoreline receded 9.1m. From 1 June to 22 September, 1987 the Calais Lake shoreline receded 81.3m. The initial shoreline on 1 June, 1987 was 2.2m lower than the 24 August, 1986 measurement. The water level in the wet sedge meadows along Calais Lake dropped at least 35cm from summer 1986 to summer 1987.

Differences in Diet Between Bulls and Mixed Herds

There were significant differences between bulls and mixed herds, regardless of year, in the amount of dietary sedge during both July ($p<0.0001$) and August ($p=0.0808$) (Figure 3.2.). During both months bulls consumed more sedge than did animals in mixed herds. Bulls also consumed significantly ($p=0.014$) more sedge than mixed herd animals during June, 1986.

Foraging Observations

During the summer of 1986, bison were consistently observed grazing sedges, C. atherodes in particular. C. atherodes-dominated patches were often
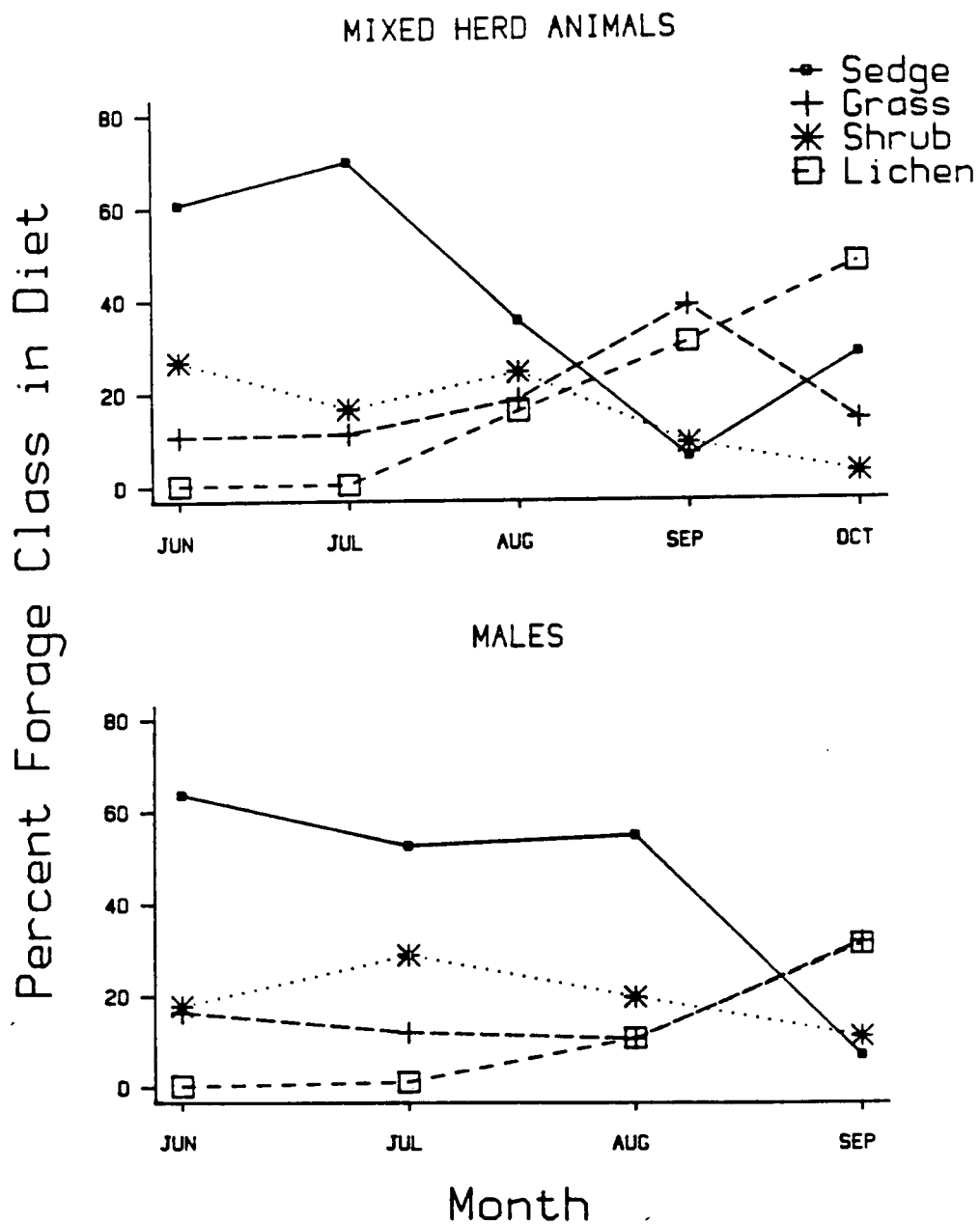
Figure 3.2. Diet composition (% of four major forage classes) of female and male wood bison, based upon analysis of fecal plant fragments.

grazed right up to the border of grass-dominated patches. Grazing on grasses, C. aquatilis or browsing on willows was rarely witnessed. During the summer of 1987, bison were again observed grazing on sedges. However, grazing on grasses and willow browsing was also a common occurrence. Grazing on P. arundinacea was never observed in either summer.

During the 1986-87 winter, bison were consistently observed grazing only on sedge, C. atherodes in particular. However, in the 1987-88 winter, bison were observed grazing grass in addition to sedge. Fall foraging observations were lacking owing to the difficulty of observing bison in forest habitats.

DISCUSSION

Differing digestibilities could affect interpretation of the summer and fall results. In particular forbs, being highly digestible, may be underestimated (Vavra, et al., 1978; Vavra and Holechek, 1980; McInnis et al., 1983), and lichen, although fragmenting more than most forages, may be underestimated because it is highly digestible (Person, 1975). Forb underestimation may be of little significance: bison were rarely seen actively foraging on forbs which are generally clumped throughout the open habitats. No evidence of grazing on forbs was found in the plots used to estimate green biomass (see chapter 2). Underestimation of lichen may affect estimates of actual percent in the diet, but it does not alter the conclusion that lichen use increased during late summer and became a major dietary component in the fall.

Most recent studies of bison diet rely solely on a limited collection of fecal material (Reynolds et al., 1979; Campbell and Hinkes, 1983; Waggoner

and Hinkes, 1986). In one instance results are based on three samples. I attempted to supplement the fecal analyses with direct feeding observations. The feeding observations gave results consistent with those from the fecal fragment analysis, thus providing additional confidence in the results.

The results of dietary composition indicate that the wood bison diet is more varied than the diets of plains or northern bison who forage almost exclusively on grass, or grass and sedge (Soper, 1941; Peden, 1976; Reynolds et al., 1978; Cairns and Telfer, 1980). The less diverse diet of plains bison inhabiting short grass plains way be a factor of forage availability. With mostly grasses present one would expect a diet high in grass. Plains bison inhabiting areas dominated by riparian willow communities do utilize browse (Waggoner and Hinkes, 1986). However, northern bison inhabiting Wood Buffalo National Park, an area with similar vegetation characteristics to the Mackenzie Bison Sanctuary, utilize little browse and no lichen (Reynolds et al., 1978). Summer browsing by wood bison is similar to that of European bison (B. bonasus), which includes up to 33% browse in its summer diet (Borowski and Kossak, 1972). The wood bison's versatile feeding habits and diverse diet, including browse and lichen, meet Hanley's (1982) predictions based on morphological characteristics.

Only Soper (1941) mentions lichen as a potential bison forage. He noted that lichen was eaten during winter, contrary to my findings of use in late-summer and fall. I found that increased lichen use corresponded with the time bison moved from open habitats into forested habitats where lichens are found (Larter and Gates, 1987). The increasing occurence of lichen in the diet in fall may be of nutritional significance: lichen has a low fiber content and is readily digested (Person, 1975), making it a suitable food when animals

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need to put on fat rather than growing lean tissue (Adamczewski et al., 1987).

The diet was more diverse in both summer and fall than in winter. This agrees with the food limitation hypothesis predictions of: 1) a more diverse summer diet caused by switching from less abundant superior forage to more abundant inferior forage, and 2) a further increase in diet diversity with the progression of the growing season as high quality forage becomes increasingly scarce. Diet was most diverse in early summer and in fall when available green biomass and crude protein (g/m^2 dry weight) was lowest for all habitats (see chapter 2).

A diet high in sedge, especially during the winter, has also been noted for plains bison in Yellowstone National Park (Meagher, 1973), in Elk Island National Park in central Alberta (Van Camp, 1975) and northern bison in the Slave River Lowlands (Reynolds et al., 1978). Bison, being large bulk feeders, can process large amounts of low quality forage (Hanley, 1982; Hudson and Frank, 1987). They would be expected to have a diet high in sedge during winter because frozen wet sedge meadows provide access to extensive stands of previously ungrazed sedge. These areas are heavily utilized by bison in the Sanctuary (Larter and Gates, 1987), with the majority of radio-collared animals being located in these areas. It is not unusual to see up to 1000 animals in the sedge meadows associated with Falaise Lake during winter. During the summer, bison forage primarily in the willow savanna habitat, choosing grass-sedge patches dominated by Calamagrostis spp. and C. atherodes. C. atherodes plants rarely go ungrazed in this habitat and appear to be an important forage for the Mackenzie bison, as was found for the Slave River Lowland bison (Reynolds et al., 1978; Hawley et al., 1981).

As expected, the browse component of the diet was highest during the

growing season, dropping off during August when stem lignification and leaf fall occurs, and being absent in the winter.

The marked difference in diet between years appears to be a result of a lower water table in 1987 caused by a dry winter. There was no shift in habitat preference between years. The decreased surface water in 1987 reduced the standing crop of all forages, especially sedges, in the willow savanna, the preferred summer foraging habitat (D. Smith pers. comm.; pers. obs.). The lower amount of sedge eaten in 1987 with the higher use of the other foods (except lichens) indicates that wood bison can switch from a diet high in sedge when it is scarce. The consistent use of lichen during late-summer and fall indicates that bison actively forage on lichen during this time of the year.

Data on bull diets are hampered by small sample sizes; however there were statistically significant differences between the diets of bulls and mixed herd animals. The general trend of a higher sedge component in bull diets indicates that bulls are capable of using sedge material that mixed herds cannot use. Because bull groups rarely number more than six individuals while mixed herds may contain over 250 individuals, there may be more individual competition for forage in mixed herds than in bull groups. The amount of sedge available per individual may be lower for animals in mixed herds and hence the lower sedge component in the mixed herd diet. It has been sugested that mixed groups require larger food patches than males (Coppock and Detling, 1986; Melton et al., in prep. a). This may allow bulls access to more sedge.

SUMMARY

1) Wood bison showed a versitile diet. They were capable of utilizing large proportions of browse during summer and utilizing lichen during fall, as well as the more standard grazing on grasses and sedges. Their versatile diet agreed with Hanley's (1982) prediction based upon morphological characteristics.

2) The diet was more diverse in the summer and fall than in winter as predicted by the food limitation hypothesis.

3) The winter diet was almost exclusively sedge and when available it was sought after during summer. C. atherodes appeared to be a very important forage item.

4) The higher diversity in the 1987 summer diet in comparison to the 1986 summer diet appeared to be a result of a reduced standing crop of all forages. The food limitation hypothesis predicts a more diverse diet in response to decreased forage availability.

5) The differences in diet between bulls and mixed herd animals may have been a result of differences in available forage on a per animal basis. Males, were in smaller groups than bison in mixed groups.

6) Analysis of fecal plant fragments and direct observations gave similar results when forages were lumped into forage classes.

CHAPTER 4. HABITAT SELECTION

INTRODUCTION

Selection of habitat by large mammals is influenced by a combination of factors such as forage requirements, predator avoidance, social behaviour, season (for example rut, calving, winter, summer), forage availability and dispersion within habitats, insect harassment, and microclimate. One popular hypothesis is that habitat selection is a consequence of resource exploitation (MacArthur and Levins, 1964; MacArthur and Pianka, 1966; Schoener, 1974; Pyke et al., 1977; Krebs, 1978). Rosenzweig (1974) maintained that different concentrations of food caused habitat selection.

Studies on habitat selection of plains bison, B. b. bison, (Meagher, 1973; Van Camp, 1975; Campbell and Hinkes, 1983) and northern bison (Soper, 1941; Reynolds et al., 1978) in montane areas and northern latitudes have been mostly descriptive, and indicate that bison prefer sedge-dominated habitats during the winter. Plains bison in Elk Island National Park, Alberta preferred upland grasslands during both winter and summer (Cairns and Telfer, 1980). Upland prairie and pure poplar habitats were important for northern bison in Wood Buffalo National Park (Soper, 1941).

Wood bison females do not use habitat randomly; they use certain habitats during different seasons (Larter and Gates, 1987). If habitat utilization is related to differing forage availabilitites, then the following predictions can be made: 1) bison should prefer willow savannas during summer because they provide the most available quality forage during this season, 2) bison should

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disperse throughout habitats during fall because all forages are of low quality and available crude protein is similar among habitats, and 3) bison should prefer wet sedge meadows in winter, because they provide the greatest available crude protein of all habitats. In this chapter I present seasonal habitat preferences for both female and male wood bison, compare my results with those from other bison populations, and finally examine biotic and abiotic factors to determine which factors influence habitat choice.

METHODS

Habitat Availability

The area of each habitat in the Mackenzie Bison Sanctuary was determined from digital satellite images. Different satellite images were checked by ground truthing at training sites (Mychaisw, 1987). I reduced Mychasiw's 11 habitat types to six: wet sedge meadow, willow savanna, willow-aspen, mixed deciduous-coniferous forest, marl, and coniferous forest. Unclassified and open water habitats were discarded from the calculations of percentage of available habitat. Radio locations of animals outside the Sanctuary boundaries were excluded from this analysis because available habitat had not been calculated for these areas.

Habitat Utilization

Aerial Radio Relocations

Twelve adult female and eight adult male wood bison were radio-collared during three collaring operations between February 1986 and July 1987. The females were radio-collared in February 1986 and March 1987; the males were radio-collared in July 1987. Carfentanil, Naltrexone, R51163, and Rompun were the drugs used for the immobilization procedure. Two females died of natural causes during the study period. One male lost his collar in a fight, and one male was possibly poached near the end of the study period.

Aerial relocations of radio-collared bison were conducted between February 1986 to April 1988. Flights were conducted on an approximate monthly rotation, except during the summer and fall of 1987, when they were conducted on an approximate bimonthly schedule. During aerial reconnaissance flights, the habitat type occupied by each radio-collared animal was noted and the animal's position was plotted on 1:250,000 maps.

Ground Observations of Bison

Ground observations of habitat use by bison were gathered between June 1986 and March 1988. In order to eliminate sightability bias in open habitat, all travel routes used were mapped. The amount of each habitat traversed by observers (in km^2) was calculated so the available area of each habitat could be determined. The number and composition of bison groups observed, habitat occupied, time and distance of travel, and travel route taken by the observer

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were recorded during each day that ground observations were conducted. In order to eliminate mode of travel effects (for example 3-wheeled trikes, snowmobiles), encounter rates of bison were calculated as the number of observations of bison groups per 10km traversed, instead of groups per time spent travelling. Because observer travel routes covered more open than forest habitat, encounter rates represent a relative measure of open habitat use.

All data were divided into three seasonal periods: winter (November to April), summer (May to 7 August), and fall (8 August to October). The division between summer and fall was determined on the basis of changing plant phenology.

Weather Recordings

Weather parameters were recorded with each bison group observation. Cloud cover categories were designated by quartiles (i.e. 0-25% etc.). Wind speed categories were: 0-5km/hr, 6-25km/hr, and greater than 25km/hr. Precipitation (rain or snow) was recorded as present or absent. Temperatures were recorded continually on thermo-hygrographs placed in both open and forest habitats. The temperature at the time of observation was recorded from the appropriate thermo-hygrograph.

Snow Measurements

Measurements of snow characteristics were gathered concurrently with winter ground observations of bison. Early winter (November to December) and late winter (March to April) snow characteristics were collected for both the 1986-87 and the 1987-88 winter. Mid-winter snow characteristics were gathered for the 1987-88 winter only. Three to eight snow stations were set up in each of the six habitat types. The height (cm) and density (g/cm^3) of the snow pack were measured at each station. Density was determined by weighing the snow column of known height from a tube with known diameter. During early winter in 1986-87, the snow pack was so shallow that its weight did not register on the measuring scale. In order to obtain an estimate of the mean snow density, other density measurements gathered elsewhere in the Sanctuary by members of the Department of Renewable Resources, N.W.T. were used. A mean of eight measurements was $0.034g/cm^3$ (std. dev. 0.0036). I used this value for early winter 1986-87.

Statistical Analyses

Analysis of data on habitat use and availabilty followed the statistical technique of Neu et al. (1974), and Byers et al. (1984). A chi-squared test using a Bonferroni confidence interval was calculated to determine which habitat types were used more or less frequently than expected on the basis of availability. This analysis was conducted on both aerial relocations and ground observations lumped over the study period.

Multifactor analyses of variance were used to analyse the effects of weather variables on group size and the proportion of observations in various habitats. Snow height and density were tested for habitat and year effects. Multiple regression analysis was used to determine which factors could predict the proportion of animal observations in various habitats during winter. All proportional data were transformed using the arcsine square root transformation. Because ground observations of bison cannot be assumed to represent independent events, the results of the statistical analyses must be viewed with this potentially violated assumption in mind.

RESULTS

Habitat Utilization

Aerial Radio Relocations

Aerial relocation data showed that male bison preferred willow savannas during summer (p<0.05), and wet sedge meadows during winter (p<0.05) (Table 4.1). Coniferous forests were avoided during these seasons. Female bison preferred willow savannas during summer (p<0.05), and both wet sedge meadows and willow savannas during winter (p<0.05) (Table 4.2). Coniferous forests were avoided during these seasons, with mixed forests avoided during winter. Statistically, no habitat preferences were shown by either sex during fall. However, coniferous habitat was used much more at this time.

Table 4.1. The proportion of male bison sightings in six habitat types during different seasons, in relation to an expectation based upon random distribution amongst all available habitat. Values based upon aerial locations of radio-collared animals. n= the number of relocations.

	Habitat	Expected	Observed	Bonferroni
SUMMER n=23	Savanna	0.024	0.478	0.203-0.753*
	Wet Sedge	0.029	0.000	- - - - - -
	Marl	0.099	0.087	0.000-0.242
	Mixed Forest	0.170	0.217	0.000-0.444
	Willow-Aspen	0.059	0.130	0.000-0.315
	Coniferous	0.619	0.087	0.000-0.242*
FALL n=24	Savanna	0.024	0.125	0.000-0.303
	Wet Sedge	0.029	0.042	0.000-0.150
	Marl	0.099	0.083	0.000-0.232
	Mixed Forest	0.170	0.083	0.000-0.232
	Willow-Aspen	0.059	0.125	0.000-0.303
	Coniferous	0.619	0.542	0.724-0.810
WINTER n=16	Savanna	0.024	0.188	0.000-0.446
	Wet Sedge	0.029	0.375	0.056-0.694*
	Marl	0.099	0.000	- - - - - -
	Mixed Forest	0.170	0.188	0.000-0.446
	Willow-Aspen	0.059	0.063	0.000-0.223
	Coniferous	0.619	0.188	0.000-0.446*

* Indicates a difference at the 0.05 level of significance

Table 4.2. The proportion of female bison sightings in six habitat types during different seasons, in relation to an expectation based upon random distribution amongst all available habitat. Values based upon aerial locations of radio-collared animals. n= the number of relocations.

	Habitat	Expected	Observed	Bonferroni
	Savanna	0.024	0.771	0.548-0.958*
	Wet Sedge	0.029	0.000	- - - - - -
SUMMER	Marl	0.099	0.000	- - - - - -
n=35	Mixed Forest	0.170	0.200	0.022-0.378
	Willow-Aspen	0.059	0.000	- - - - - -
	Coniferous	0.619	0.029	0.000-0.104*
	Savanna	0.024	0.079	0.000-0.194
	Wet Sedge	0.029	0.105	0.000-0.236
FALL	Marl	0.099	0.000	- - - - - -
n=38	Mixed Forest	0.170	0.132	0.000-0.277
	Willow-Aspen	0.059	0.026	0.000-0.094
	Coniferous	0.619	0.658	0.455-0.861
	Savanna	0.024	0.154	0.046-0.262*
	Wet Sedge	0.029	0.551	0.402-0.700*
WINTER	Marl	0.099	0.000	- - - - - -
n=78	Mixed Forest	0.170	0.064	0.000-0.137*
	Willow-Aspen	0.059	0.064	0.000-0.137
	Coniferous	0.619	0.167	0.056-0.278*

* Indicates a difference at the 0.05 level of significance

Ground Observations

Ground observations showed trends similar to aerial relocations, with males preferring willow savanna during summer and wet sedge meadow during winter (p<0.05) (Table 4.3), however there were noticeable differences. Marl was preferred and wet sedge meadow avoided during summer (p<0.05). During winter, willow savanna was avoided (p<0.05). Both willow savanna and mixed forest were preferred in fall, with wet sedge meadow being avoided (p<0.05).

For females, ground observations showed trends similar to aerial relocations during summer, with willow savanna preferred (p<0.05) (Table 4.4.). The differences from aerial locations were: preference for willow savanna during fall, avoidance of wet sedge meadow during both summer and fall, and the lack of habitat prefernces during winter (p<0.05), however wet sedge meadows were heavily used.

Encounter Rates

The rate at which bison were encountered during ground travel (groups/10km) indicates that bison leave open habitats with the onset of fall (Figure 4.1). This departure was accompanied by a significant decrease in group size (Table 4.5).

Table 4.3. The proportion of male bison sightings in six habitat types during different seasons, in relation to an expectation based upon random distribution amongst all available habitat. Values based upon ground observations of bulls and bull groups. n= the number of relocations.

	Habitat	Expected	Observed	Bonferroni
	Savanna	0.230	0.585	0.499-0.681*
	Wet Sedge	0.573	0.066	0.023-0.109*
SUMMER	Marl	0.110	0.210	0.139-0.281*
n=229	Mixed Forest	0.033	0.061	0.019-0.103
	Willow-Aspen	0.034	0.066	0.023-0.109
	Coniferous	0.020	0.013	0.000-0.033
	Savanna	0.244	0.511	0.375-0.647*
	Wet Sedge	0.564	0.021	0.000-0.060*
FALL	Marl	0.076	0.170	0.068-0.272
n=94	Mixed Forest	0.049	0.181	0.076-0.286*
	Willow-Aspen	0.041	0.096	0.016-0.176
	Coniferous	0.026	0.022	0.000-0.062
	Savanna	0.237	0.114	0.025-0.213*
	Wet Sedge	0.645	0.852	0.752-0.952*
WINTER	Marl	0.038	0.034	0.000-0.085
n=88	Mixed Forest	0.025	0.000	- - - - - -
	Willow-Aspen	0.025	0.000	- - - - - -
	Coniferous	0.030	0.000	- - - - - -

* Indicates a difference at the 0.05 level of significance

Table 4.4. The proportion of female bison sightings in six habitat types during different seasons, in relation to an expectation based upon random distribution amongst all available habitat. Values based upon ground observations of mixed herds. n= the number of relocations.

	Habitat	Expected	Observed	Bonferroni
SUMMER n=139	Savanna	0.230	0.734	0.657-0.811*
	Wet Sedge	0.573	0.101	0.034-0.168*
	Marl	0.110	0.101	0.034-0.168
	Mixed Forest	0.033	0.022	0.000-0.055
	Willow-Aspen	0.034	0.036	0.000-0.078
	Coniferous	0.020	0.007	0.000-0.051
FALL n=57	Savanna	0.244	0.596	0.425-0.767*
	Wet Sedge	0.564	0.053	0.000-0.131*
	Marl	0.076	0.140	0.019-0.261
	Mixed Forest	0.049	0.123	0.008-0.238
	Willow-Aspen	0.041	0.035	0.000-0.099
	Coniferous	0.026	0.053	0.000-0.131
WINTER n=59	Savanna	0.237	0.220	0.078-0.362
	Wet Sedge	0.645	0.763	0.589-0.937
	Marl	0.038	0.000	- - - - - -
	Mixed Forest	0.025	0.000	- - - - - -
	Willow-Aspen	0.025	0.000	- - - - - -
	Coniferous	0.030	0.017	0.000-0.061

* Indicates a difference at the 0.05 level of significance.
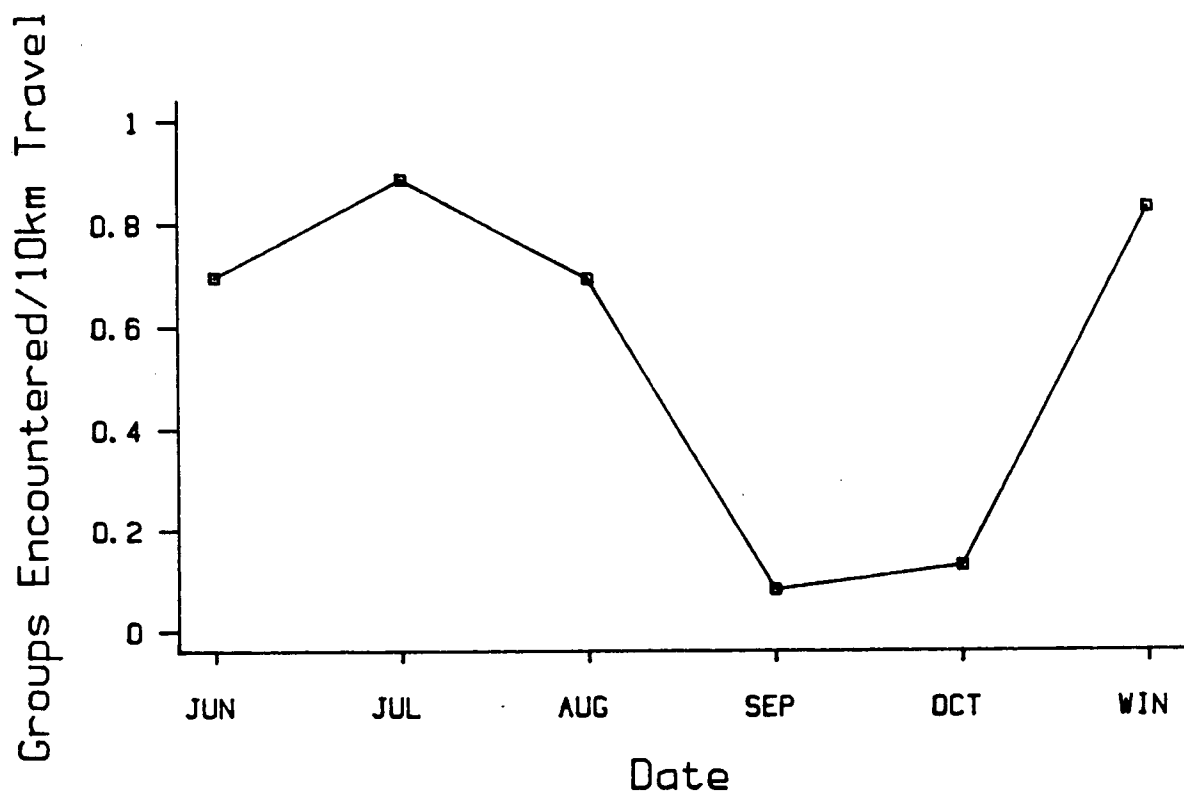
Figure 4.1. The rates at which bison groups were encountered each month. Observations made during daily travel through mostly open habitat.

Table 4.5. Mean group sizes for male only and mixed groups, during different seasons and different years. Values in parentheses are standard errors of the mean, n= number of groups.

MALE GROUPS

	Summer	n	Fall	n	Winter	n
1986	1.86 (0.14)	84	1.04 (0.03)	48	3.76 (0.37)	66
1987	1.44 (0.10)	163	1.04 (0.03)	48	2.67 (0.30)	21

MIXED GROUPS

	Summer	n	Fall	n	Winter	n
1986	58.42 (7.58)	50	13.96 (1.49)	27	62.41 (13.8)	29
1987	41.63 (3.79)	84	16.26 (1.36)	32	24.38 (4.00)	32

Group Size

Group size was affected by sex, season, year, and temperature. Habitat occupied did not influence group size, even when the analysis was conducted with the six habitats lumped into two classes: open and forested. However, there was a tendency towards smaller groups in forested habitats. Male groups were always smaller than mixed groups. Both male and mixed groups were smaller during fall than in other seasons, and were smaller in 1987-88 than in 1986-87.

Effects of Weather on Habitat Choice

Precipitation, wind speed, and cloud cover had little affect on the proportion of observations in different habitats. However, temperature did affect both the proportion of observations and group size. At intermediate temperatures (-10° C to $+10^o$ C) groups were smaller than when temperatures were either high ($+10^o$ C to $+30^o$ C) or low (-40 C to -10° C). At high temperatures a greater proportion of observations were in willow savannas, while at low temperatures there was a greater proportion of observations in wet sedge meadows. With temperature being highly correlated with season ($r=0.70$), these effects may not be only temperature related.

Snow Effects

Snow depth and snow density differed between years (p<0.0001). The snow was deeper and denser in all habitats during the 1987-88 winter than during the 1986-87 winter (Table 4.6.). Snow density and snow height measurements were highly positively correlated (p<0.001, r=0.927). Forage biomass per habitat, estimated in late fall (see chapter 2), and snow depth were the best predictors of bison presence in habitats (R^2 = 0.871), when including only habitats where bison were observed. Forage biomass was the best predictor when all habitats were included in the analyses.

DISCUSSION

Habitat Selection

Studies on plains and northern bison have demonstrated habitat preferences (Soper, 1941; Fuller, 1961; Meagher, 1973; Van Camp, 1975; Reynolds, et al., 1978; Cairns and Telfer, 1980; Campbell and Hinkes, 1983) just as this study on wood bison has. While most of these authors described the favoured habitat, they seldom noted that all the preferred habitats probably possessed a superior quality or quantity of forage when compared to less preferred habitats.

Table 4.6. Mean snow depths and snow densities for each habitat type in the winters of 1986-87 and 1987-88.

| Habitat Type | 1986-87 | | 1987-88 | |
	Snow Depth (cm)	Snow Density (g/cm^3)	Snow Depth (cm)	Snow Density (g/cm^3)
Savanna	18.3	0.068	56.8	0.196
Wet Sedge	19.0	0.084	59.6	0.181
Marl	20.9	0.077	56.8	0.201
Mixed Forest	19.1	0.080	59.1	0.188
Willow-Aspen	20.4	0.077	52.8	0.189
Coniferous	19.7	0.073	61.7	0.193

Seasonal habitat preferences of wood bison followed the pattern predicted from changing forage availabilities. In summer, wet sedge meadows provided the greatest quantity of green biomass and crude protein (see chapter 2), but the muddy substrate, combined with bison's high foot loading, makes movement in this habitat difficult. Willow savannas provided the next highest quantity of green biomass and crude protein, and bison preferred this habitat. As both forage quantity and quality declined in willow savannas and became more homogeneous throughout all habitats, bison dispersed equally amongst all habitats (Figure 4.2.). In winter, freezing provided access to the virtually ungrazed wet sedge meadows, and bison switched to this habitat. Although both sexes showed similar patterns of habitat preference, mixed groups were more often observed than male groups in preferred habitats.

The major trends in habitat preference were similar for both aerial relocations and ground observations. Differences in significantly preferred or avoided habitats between the two methods may have been caused by a combination of: i) large variations in sample size between methods, ii) lack of independence between ground observations, and iii) ground observations being limited to mostly open habitats. When only the proportional use of habitats were compared there was little difference in results between the two methods. Larger sample sizes did not show different trends in proportional use of habitats, but did show more significant differences could be detected.

Aerial relocation of individually radio-collared animals provided the best data set for determining habitat selection because it: i) provided independent events, ii) covered the entire area, and iii) provided data totally unaffected by differing sightabilities between habitats. Unfortunately, this method was limited by small sample size. The ground observation method used in this

SUMMER

Observations
Cr. Protein

FALL

Frequency Occurrence (%)

Crude Protein (g/sq m dry wt.)

WINTER
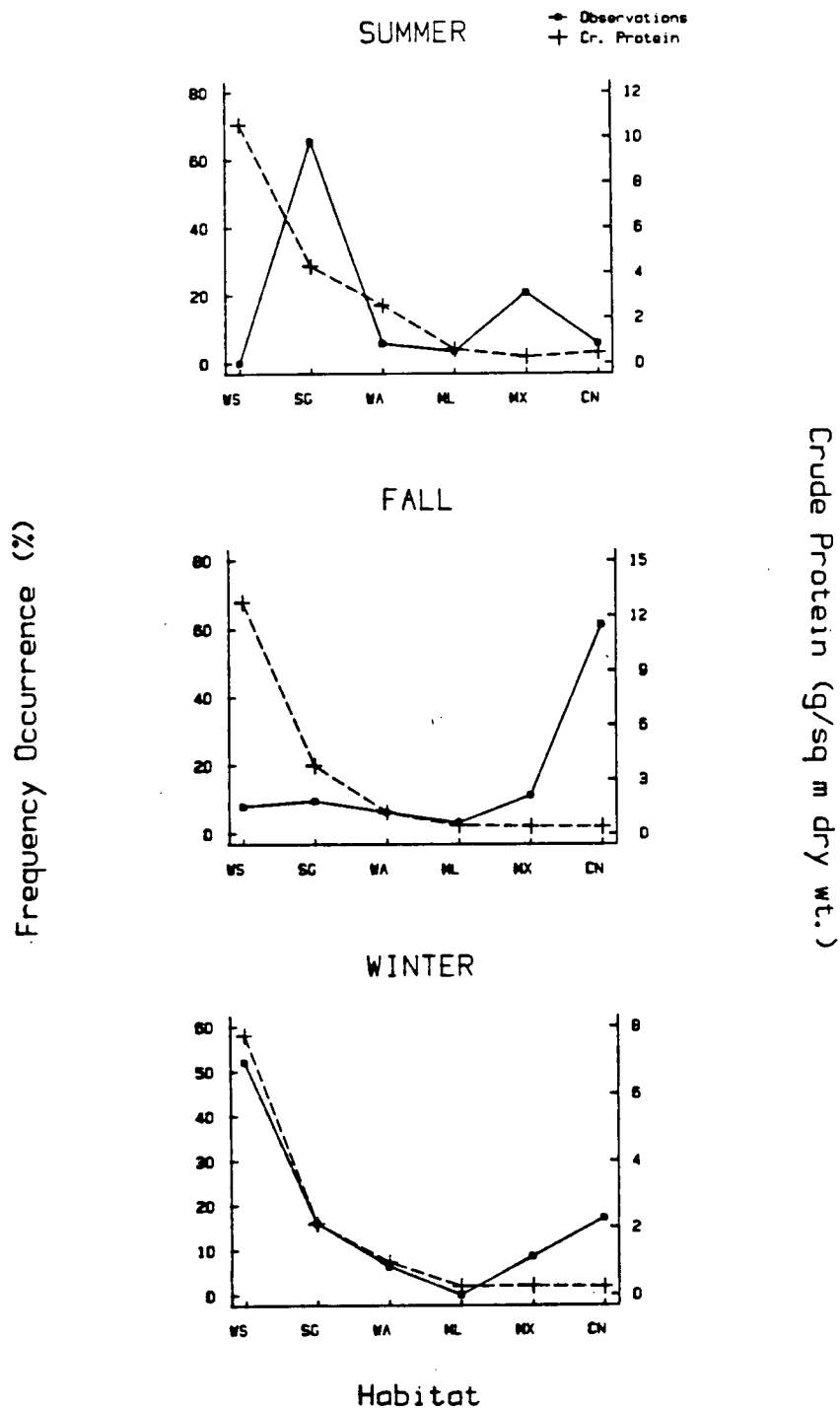
Habitat

Figure 4.2. Changes in available crude protein (g/m^2 dry weight) and percent frequency occurrence of bison in different habitats with changes in season. Crude protein values do not include P. arundinacea or willow, and the 15 October value was used to represent winter levels. WS = wet sedge meadow, SG = willow savanna, WA = willow-aspen, ML -= Marl, MX = mixed forest, and CN = coniferous forest (lumped wet and dry).

study gave similar results and with its increased sample size provided more power to the analysis.

Factors Affecting Habitat Selection

Weather

Weather conditions generally appeared to have little effect on habitat choice. Soper (1941) and Fuller (1961; 1966) implied this, while Herrig and Haugen (1969) and Van Den Brink (1980) demonstrated that changing weather conditions had little effect on activity budgets. With extreme weather conditions, most notably harsh storms in winter combining extremes of wind, snow, and temperature, short-term shifts in habitat use are expected. Soper (1941) and Fuller (1966) both mention use of forested habitats for protection during adverse weather conditions.

Snow Conditions

Bergerud (1974) suggested that the distribution of caribou in Newfoundland depended on the effects of snow conditions on the availability of forage. Bison can withstand deeper, denser snow while foraging than other North American ungulates. However, historical accounts reviewed in Van Camp (1975) suggest deep, crusted snow has been responsible for major bison die-offs. More recent accounts suggest that winter weather can limit populations (Meagher, 1971; 1976), and that snow hardness is the principal

factor influencing choice of feeding sites (Reynolds and Peden, 1987).

My data indicate that snow depth was associated with increased use of willow savannas at the expense of wet sedge meadows during the harsher 1987-88 winter. Habitat biomass was still the major determinant of habitat use during winter. Fuller (1966) observed bison in Wood Buffalo National Park foraging through 120cm snow depths. Normally snow depth and snow density are not highly correlated, and it is a combination of these factors rather than depth or density alone that limits forage availability. Meagher (1971) indicated snow depth as a major influence on bison distribution in Yellowstone. Van Camp (1975) found that the combination of snow depths in excess of 60cm, snow density between 0.18 and $0.20g/cm^3$, and water content of the snow column in excess of 12cm caused calves in Elk Island National Park to abandon head swinging. These values are quite similar to the ones I found during the 1987-88 winter.

Group Size

Trends in seasonal group size paralleled trends in seasonal forage availability. The smallest female and male groups occurred in fall when available forage was low in all habitats. This was the only time when bison frequented forested habitats. Similar trends in group size were found by Calef and Van Camp (1987) for northern bison in the Slave River Lowlands. Shackleton (1968) found habitat influenced group size of plains bison: larger groups were found in open habitats. These larger groups were found in June and July when food was apparently at its best. Rutberg (1984) also found

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habitat influenced group size in plains bison. He suggested that larger groups in open habitats were in response to predation. I found habitat occupied was not closely related to group size. However, the habitat type occupied may affect social organization.

All types of groups were smaller during 1987-88 than during 1986-87. The summer growing season of 1986 produced greater sedge and grass biomass in willow savannas than the summer of 1987 (D. Smith, pers. comm.; pers. obs.). Snow conditions were harsher during the 1987-88 winter, causing decreased forage availabilities. Available forage appeared to be a major influence on group size.

Insect Harassment

Insect harassment of caribou (Rangifer tarandus), causes changes in activity and habitat choice (Skoog, 1968; Bergerud, 1971; Boertje, 1981; Downes et al., 1986). Blackflies (Simuliidae), mosquitos (Culicidae), and horseflies (Tabanidae) are prolific throughout northern bison range, but their influence on habitat choice and activity of bison has been almost ignored. Soper (1941) noted that severe harassment caused bison to wallow more. Calef and Van Camp (1987) dismissed insect harassment as a factor influencing large group sizes during the post-calving season. Melton et al. (in prep. b) found flies, especially blackflies, could be severe from June to September and did reduce feeding. They also found flies were more severe in open than closed habitats, but bison remained in open habitats well into fly

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season (June to September), and used forest habitats long after fly season ended.

SUMMARY

1) Seasonal forage biomass, quality, and availability within habitats were the main factors affecting habitat choice by bison.

2) Snow conditions, especially depth and density, can affect forage availability and caused bison to shift to habitats providing less biomass.

3) Various weather factors in combination may have caused short-term changes in habitat use. However, changing weather conditions have little effect on long-term habitat selection.

4) Although insect harassment can affect the activity budgets within habitats (Melton et al., in prep. b), it did not displace bison from preferred habitats.

5) Forage availability but not habitat occupancy affected group size. However, there was a relation between group size and habitat type.

CHAPTER 5. HOME RANGES AND SEASONAL MOVEMENT PATTERNS

INTRODUCTION

Different life histories of female and male wood bison, with regard to divergent parental investment on offspring, suggest that each sex adopts different strategies to maximize reproductive success. Female reproductive success should be determined by survival of offspring, while male reproductive success should be determined by competition for copulations (Maher and Byers, 1987). Because the distribution of resources in time and space affects life histories (Clutton-Brock and Harvey, 1978; Guiness and Gibson, 1980), female bison should always maximize food intake and food quality to maximize reproductive success. Males should maximize food intake and food quality during pre-rut, as reproductive success will depend upon their energy reservesduring the rut. During the rut, males should select habitats with the highest density of females in order to maximize their mating opportunities.

Home range size is affected by the way in which a species exploits its food resources (McNab, 1963; Clutton-Brock and Harvey, 1978; Damuth, 1981), and depends on body size. In this chapter I report home ranges and seasonal movements of mature male and female wood bison, compare home ranges with those predicted by the body size-home range relationships proposed by McNab (1963) and Harestad and Bunnell (1979), and compare seasonal movements with those predicted by the food limitation hypothesis, and those predicted by maximizing reproductive success. I expected: 1) bison to have

larger home ranges than other North American ungulates, 2) males, being larger and thus requiring more forage, to have larger home ranges than females, 3) males to be most mobile during the rut, 4) females to be more mobile than males, except during the rut, as they endeavor to exploit superior forage throughout the year, and 5) bison to move less during winter because of metabolic constraints associated with thermal regulation.

METHODS

Locations of Radio-Collared Bison

Adult wood bison were radio-collared as described in chapter 4. During aerial reconnaissance flights, locations of radio collared animals were plotted on 1:250,000 maps. Universal Transverse Mercator (UTM grid coordinates were determined for each location so that the distance travelled between locations could be calculated.

Ground locations, and observations of radio-collared bison were gathered between June 1986 and March 1988. Locations were plotted on 1:50,000 maps and UTM coordinates were determined.

Estimation of Home Range

Analysis of home ranges was performed using the McPAAL (Micro-computer Programs for the Analysis of Animal Locations, version 1.21, Smithsonian Institution) software package (Stuwe and Blohowick, 1985). The minimum convex polygon method was used to determine home range size with the accuracy of locations being set at $0.04km^2$.

Home ranges were calculated for those individuals who were located throughout an entire yearly cycle. Locations for bulls were lacking in early summer, but home ranges were calculated regardless. One female moved from the Sanctuary to the Mink Lake expansion area (see chapter 1) and never returned. Her home range was calculated from both the entire set of locations, and the subset of points from the expansion area only. The number of relocations used to determine female and male home range and the home range size were tested for correlations, to check whether factors other than the number of loctaions influenced home range size.

Calculation of Distance Travelled

Analysis of movements was performed with a computer program "Track" designed by J.G. Woods (Environment Canada-Parks). Distances travelled were calculated from locations separated by a maximum of 21 days, and were normalized to kilometres travelled/24 hours. Only locations within the Sanctuary boundaries were used. The calculated distances are linear distances between locations, so certainly underestimate actual distances

travelled.

Travel distances were divided into six periods: pre-rut (1 June to 15 July), rut (16 July to 31 August), post-rut (1 September to 31 October), summer (1 May to 7 August), fall (8 August to 31 October), and winter (1 Novemer to 30 April). The dates associated with the rut follow Melton et al. (in prep. b).

Statistical Analyses

T-tests were used to compare male and female home range sizes. Because mean daily travel distances followed a geometric distribution, the Mann-Whitney U test was used to compare travel distances between the sexes and between time periods. Travel distances were grouped into classes of 0-2km/day, 2-4km/day etc. for each of the time periods. If significant differences were found between male and female travel distances, a chi-squared contingency analysis was performed to determine where the major differences in travel distance were. A regression of the natural logarithm of daily travel distance and the natural logarithm of days between relocations was performed in order to check for positive correlations between lower daily travel distances with locations separated by greater time intervals.

RESULTS

Home Ramge

Home range size and the number of locations used to determine home range size were not significantly correlated (females r=0.529, p=0.094; males r=0.386, p=0.45), but were positively related. Female home ranges were significantly (p<0.02) larger than male home ranges (mean female home range 897.0km^2, s.e. 118.0; mean male home range 432.5km^2, s.e. 128.4) (Table 5.1). The smallest female home ranges were found outside the Sanctuary boundaries in the Mink Lake expansion zone. These home ranges were significantly smaller (p=0.02) than those of females inhabiting the sanctuary. A recent fire near Mink Lake resulted in lush forage patches over a widespread area.

Travel Distance

Because the daily travel distance was neagatively correlated with the time between locations (Figure 5.1), travel distances are only considered as indicies of travel. They are not regarded as absolute mesures of distances travelled. These data do provide comparative information for male and female movements during different seasons.

Table 5.1. Home ranges of adult bison in the Mackenzie Bison Sanctuary. n = number of locations.

Females		Males	
Size (km^2)	n	Size (km^2)	n
1441.9	25	1033.4	23
1371.0	38	441.5	8
1222.7	18	434.5	10
1022.1	35	301.1	15
974.5	21	205.7	11
773.5 *	27	178.5	22
680.3	19		
659.1	28		
501.0	21		
387.3 **	19		
323.4 *	16		

* = animals living in the expansion zone.

** = home range calculated only from locations in the expansion zone.
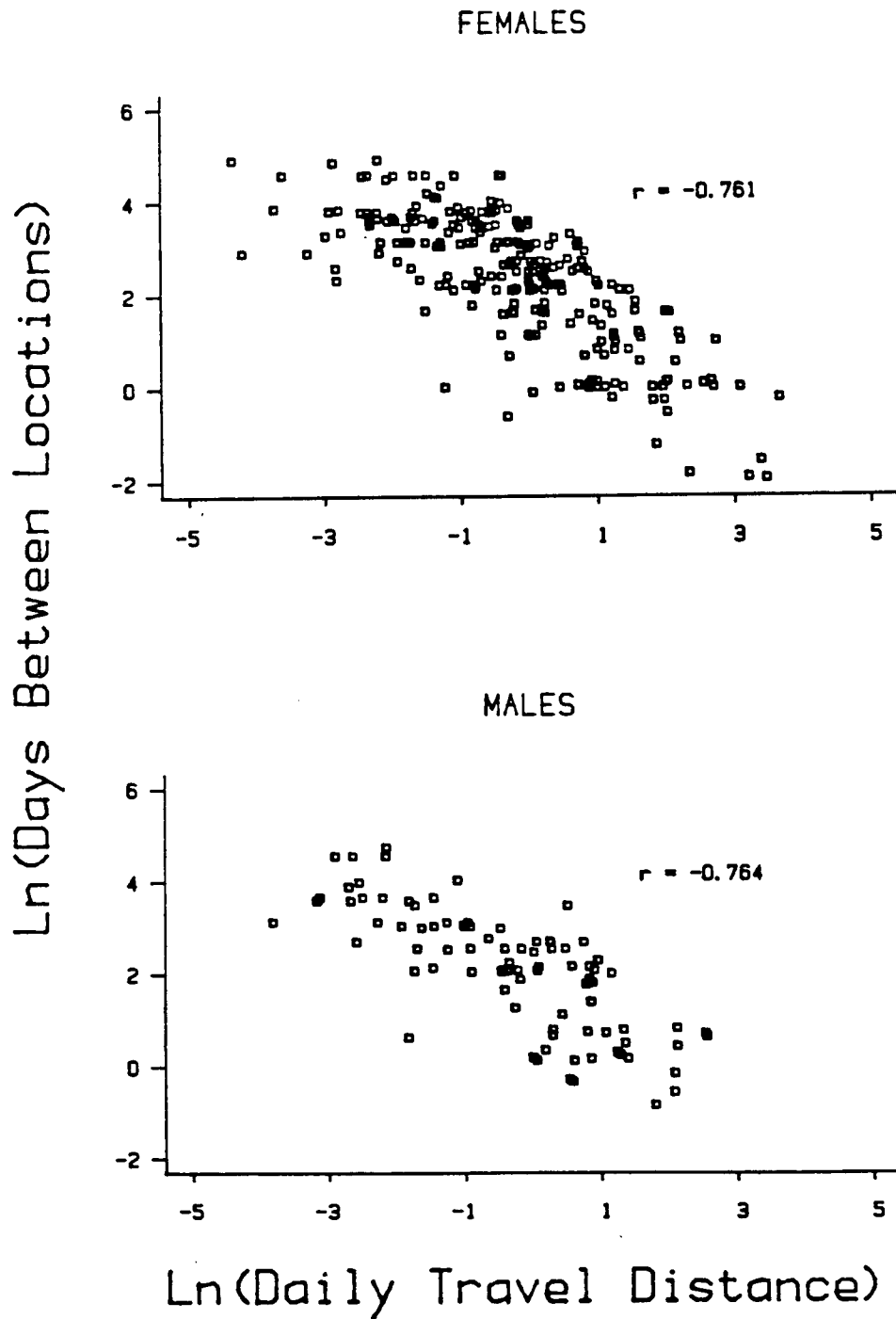
Figure 5.1. The relationship between daily travel distance and days between locations for both female and male bison.

Differences Between the Sexes

Bulls generally travelled less than females, but only during fall were these differences significant (Table 5.2). During this period, bulls rarely travelled more than 2km/day (Figures 5.2 and 5.3), whereas females often travelled more than 2km/day.

Differences Between Season

Both males and females moved significantly less during post-rut than during either the rut or pre-rut (Table 5.2.). Males made fewer daily movements exceeding 2km, while females made fewer daily movements greater than 4km during post-rut in comparison to either the rut or pre-rut (Figure 5.2.).

Both males and females moved less during fall than in summer. For females this trend continued in winter (Table 5.2.). There was inadequate sample size to determine male winter travel distances. Females made more short movements (less than 2km/day) in winter than summer (Figure 5.3.).

Table 5.2. Median daily travel (km) of female and male wood bison during different seasons (see text for dates). The values in parentheses represent ·the number of travel distances calculated. Different superscripts show significant differences (p<0.05) between seasons. P-values show significance between the sexes. Significance values based on Mann Whitney U test results.

	Females	Males	P
Pre-rut	2.06^a (45)	2.37^a (18)	0.373
Rut	2.16^a (40)	1.76^a (26)	0.420
Post-rut	1.18^b (28)	0.74^b (16)	0.085
Summer	2.15^a (78)	2.27^a (43)	0.695
Fall	1.27^{ab} (42)	0.66^b (23)	0.005
Winter	1.08^b (42)	0.20 (2)	- - -
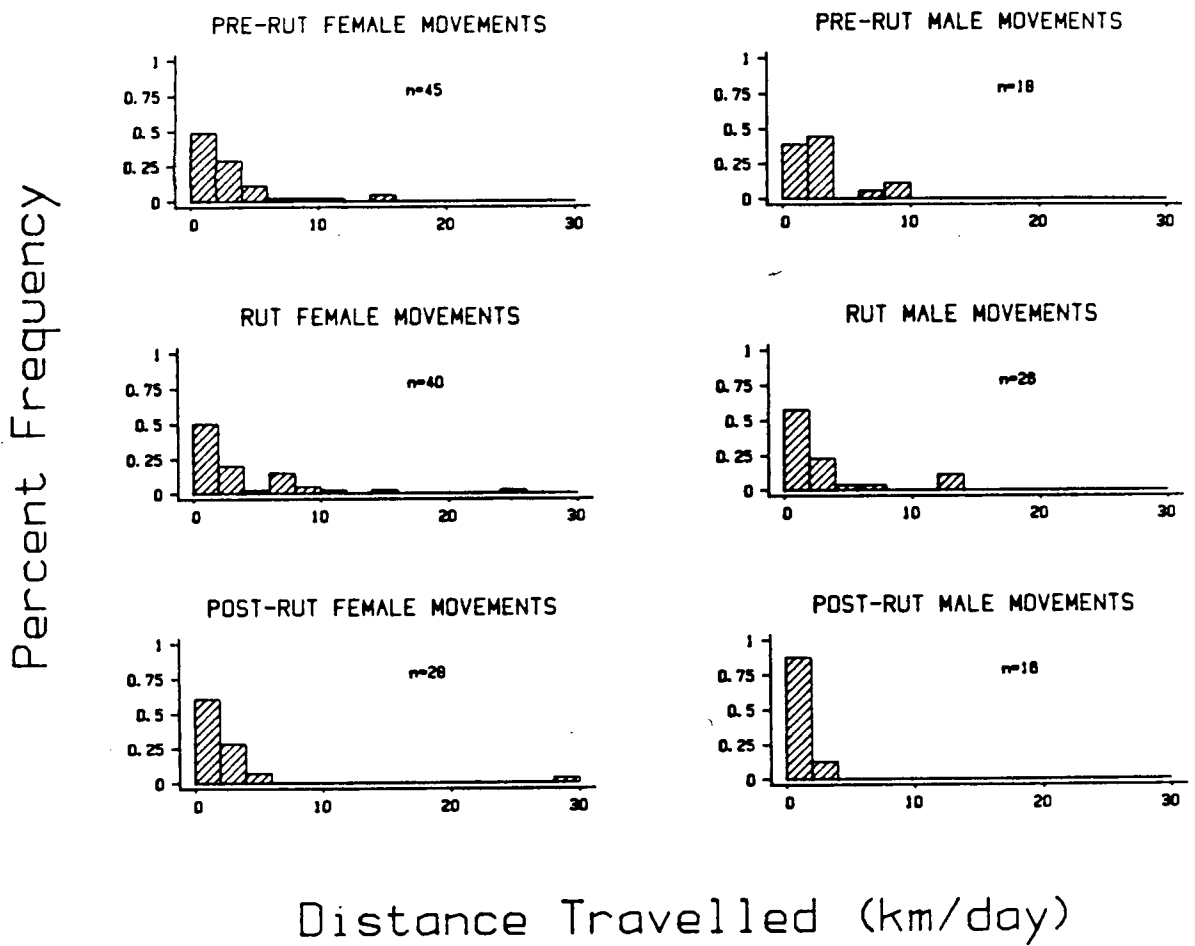
Figure 5.2. Percent frequency of male and female daily travel distances during pre-rut, rut, and post rut (see text for dates).
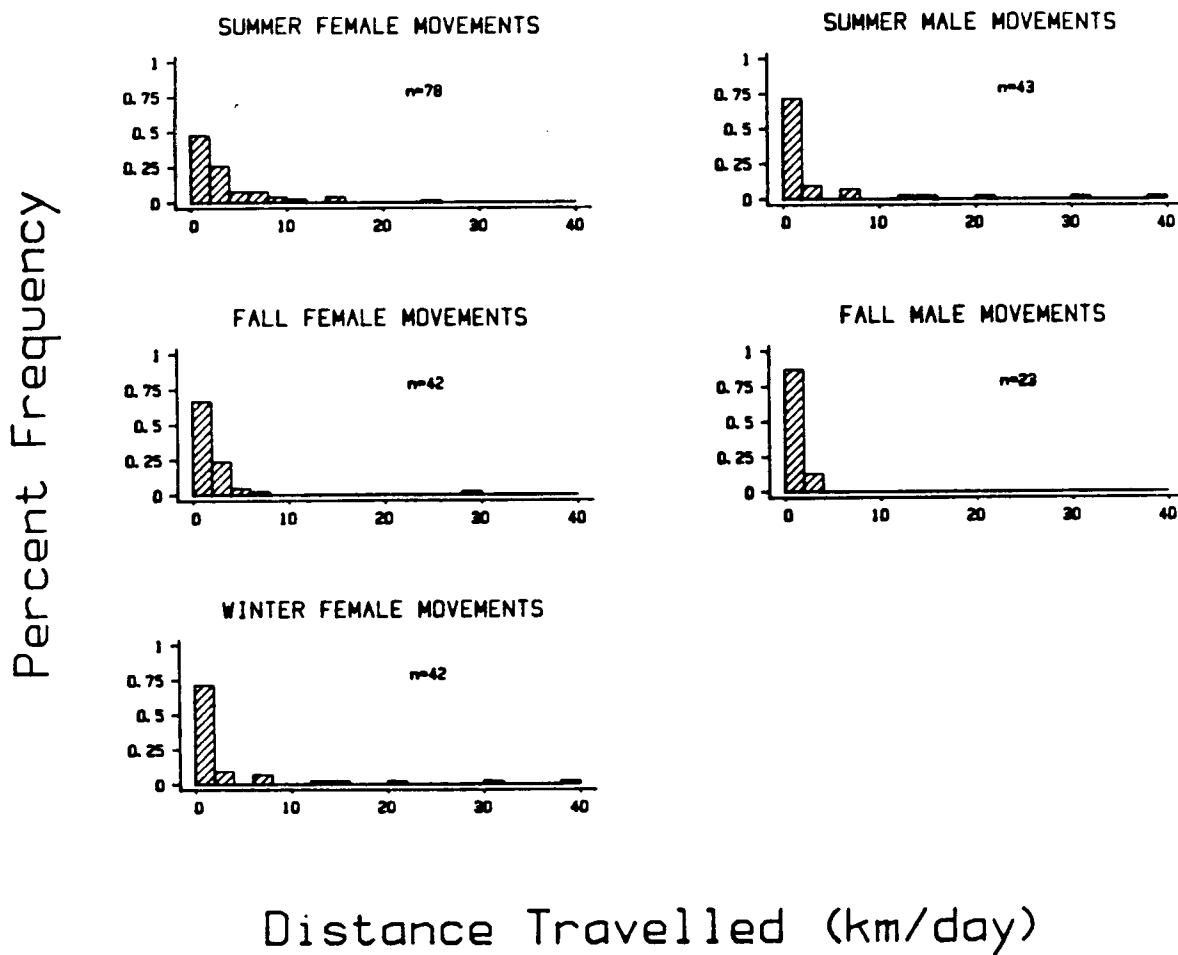
Figure 5.3. Percent frequency of male and female daily travel distances during summer, fall, and winter (see text for dates).

DISCUSSION

Home Range

Home ranges of wood bison were 5 to 100 times larger than those of other North American ungulates (Table 5.3.). In addition, the smallest wood bison home range (178.5km^2) far exceeds that predicted by the home range-body weight relationships calculated from data by McNab (1963) or Harestad and Bunnell (1979). Using 590kg as the mean weight of a female wood bison (C. Gates, unpubl. data), the predicted home range size of a female wood bison is 1.5km^2 following McNab (1963) and 18.2 km^2 following Harestad and Bunnell (1979). Harestad and Bunnell (1979) and Lindstedt et al. (1986) mentioned that habitat productivity can potentially confound home range-body mass relationships. Van Vuren (1983) suggested that low habitat productivity may be the reason plains bison summer home ranges in Utah are three times larger than predicted by Harestad and Bunnell (1979), and I would suggest that habitat productivity may also determine wood bison home range size. Because savanna and meadow habitats are widely scattered and represent such a small area of the Sanctuary (see chapters 1 and 4), bison may have to travel over large areas in order to acquire adequate forage.

Bison home ranges in the Mink Lake expansion area were significantly smaller (p<0.05) than those in the Sanctuary. A recent fire has created a series of large homogeneous meadows around Mink Lake. Lush growth, perhaps because of nutrients released by the fire, has occurred in these

Table 5.3. Home ranges (km^2) of some North American ungulates.

Species	HomeRange[1]	Reference
Alces alces	14-18 (M)	Phillips et al., 1973
	6-40 (M)	Van Ballenberghe & Peek, 1971
B. b. bison	27-71 (C)	Lott & Minta, 1983
	32-82 (C)	Van Vuren, 1983[2]
B. b. athabascae	179-1442 (C)	This study
Cervus canadensis	6-400 (C)	J. Woods, 1988 pers. comm.
	15-30 (M)	Craighead et al., 1973
	2-46 (M)	Knight, 1970

[1] Letters in parentheses indicate methodologies for computing home range:

M = minimum area, C = minimum convex polygon.

[2] Summer home range calculation only.

meadows. With the habitat patches less dispersed in the Mink Lake area than in the Sanctuary, one would expect the smaller home ranges found in the Mink Lake area. With less than one third of the bison population (N. Larter, unpubl. data) inhabiting the Mink Lake area, decreased competition for food may also play a role in smaller home ranges.

Individual migratory tendencies may be another reason why wood bison home ranges are so much larger than predicted by body weight-home range size relationships. Both McNab (1963) and Harestad and Bunnell (1979) omit caribou and include only non-migrant elk in their relationships. Harestad and Bunnell (1979) calculated mean home range size for all species, possibly masking the effects of any individual migrants. Individual elk in Banff show great variablility in home ranges because some are migrant, others non-migrant, and some switch migratory tendencies (J. Woods, pers. comm.).

Most free-ranging bison appear to be seasonally migratory; movements being directional and also altitudinal in some regions (Soper, 1941; McHugh, 1958; Meagher, 1973; Van Vuren, 1983). Wood bison in the Sanctaury also show seasonal movement patterns; moving into forested habitats during fall and returning to open habitats during winter and summer. However, rarely are these seasonal movements directed into distinct areas of the yearly home range. Movements between the major lakebeds occur in both summer and winter and generally create the outer home range boundaries. Forested habitats between the lakebeds are occupied in the fall. Only three of 16 radio-collared bison used areas outside of their summer and winter range during fall.

During February, 1988, four radio-collared bison were amongst approximately 250 animals occupying an area 25km east of the traditional

winter bison range. This area was dominated by a combination of small open meadow and small treed patches. As mentioned in chapter 4, snow conditions during this winter may have adversely affected forage availability. Possibly the vegetation characteristics in this new area modified snow conditions making the forage more accessible. These animals remained until mid-April before returning to the traditional area. This type of movement had not been seen previously.

Contrary to expectations based upon body size and hence forage requirements, males had smaller home ranges than females. This result may be an artifact of fewer male relocations, and a lack of relocations during early summer. Harestad and Bunnell (1979) found females to have home ranges as large as, or larger than, males in only two of the 27 species studied. Interestingly, both species (moose and elk) were large herbivores. Additionally, small samples precluded statistical comparisons of the differences they show between male and female home range size for many of the species they studied.

It seems reasonable for females to have larger home ranges, if they always maximize food intake and food quality in order to maximize reproductive success as proposed by Clutton-Brock and Harvey (1978). Females are further burdened in their search for quantity and quality of forage by being associated with larger groups (see chapter 4). Melton et al. (in prep. a) and Coppock and Detling (1986) suggest that females require larger food patches than males and therefore imply that females must require larger home ranges to find such food patches. Daily movements should increase in order to meet their foraging requirements in the larger home range.

In order to maximize encounters with females, males would be expected to move more during the rut than during the pre- or post-rut. My data partially agree with this prediction. The larger pre-rut movements I found may have resulted from being gathered late in the season just prior to the rut. Virgl (1988) found that solitary bulls, and bulls in bull groups spent more time walking during the rut than during pre-rut. However Melton et al. (in prep. b), found that bulls in herds spent less time walking during the the rut than during pre-rut. Both studies were conducted on the Mackenzie population during 1987. Bulls freely move in and out of mixed herds, but social ranking of individual bulls may be an important factor affecting movements associated with mixed herds. These conflicting results indicate that more data are required to determine if male wood bison movement patterns agree with the prediction of being greatest during the rut.

Female movements were: 1) generally larger than males in all seasons, 2) significantly larger than males during fall, and 3) shorter and more frequent in winter than in summer. These movement patterns would be expected if females maximized their intake of superior quality forage throughout the year. Melton et al. (in prep. a) showed that females had greater overall movement rates, and greater within patch movement rates (steps/minute) than males, suggesting females are more selective feeders than males. Increased movements are implied by more selective feeding.

Competition for resources may also be an important factor in determining female movement patterns. Melton et al. (in prep. a) suggest that females require larger food patches than males because they are

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associated with larger groups. Males in small groups can utilize resource patches too small for the larger mixed herds. Sinclair (1977) suggested that male African buffalo can use smaller habitat patches than females for the same reasons. These findings suggest that foraging females will move through habitat patches faster than foraging males. Movements should decrease from summer to winter because of increased metabolic constraints.

All animals showed significantly shorter daily movements just after the rut and throughout the fall. This may be due to the relatively homogenous quality and available biomass of forage found in all habitats (see chapter 2) (Figure 5.4). Large daily movements then would probably not lead animals to better forage. During the fall, mixed herds split into smaller groups (see chapter 4), presumably this allowed females to utilize the smaller resource patches they had previously overlooked. Mixed groups remained small until winter when large mixed groups formed again.

Daily movements of all bison were smaller in winter than in summer, but there were occassionally very large daily movements (Figure 5.3). These large movements may be necessary if localized grazing pressure has severely depleted the forage biomass in the habitat patch. Winter freezing provided access to vast sedge stands in wet sedge meadows. Once these patches were found, little movement may be needed to secure adequate forage because of local forage abundance, and reduced energy costs and food intake. Winter forage has high fiber content causing a reduction in the rate of passage, consequently less feeding is required to fill the rumen. Bison have adapted to survive on forages of high fiber and reduced crude protein (Hawley et al., 1981; Hawley, 1987).
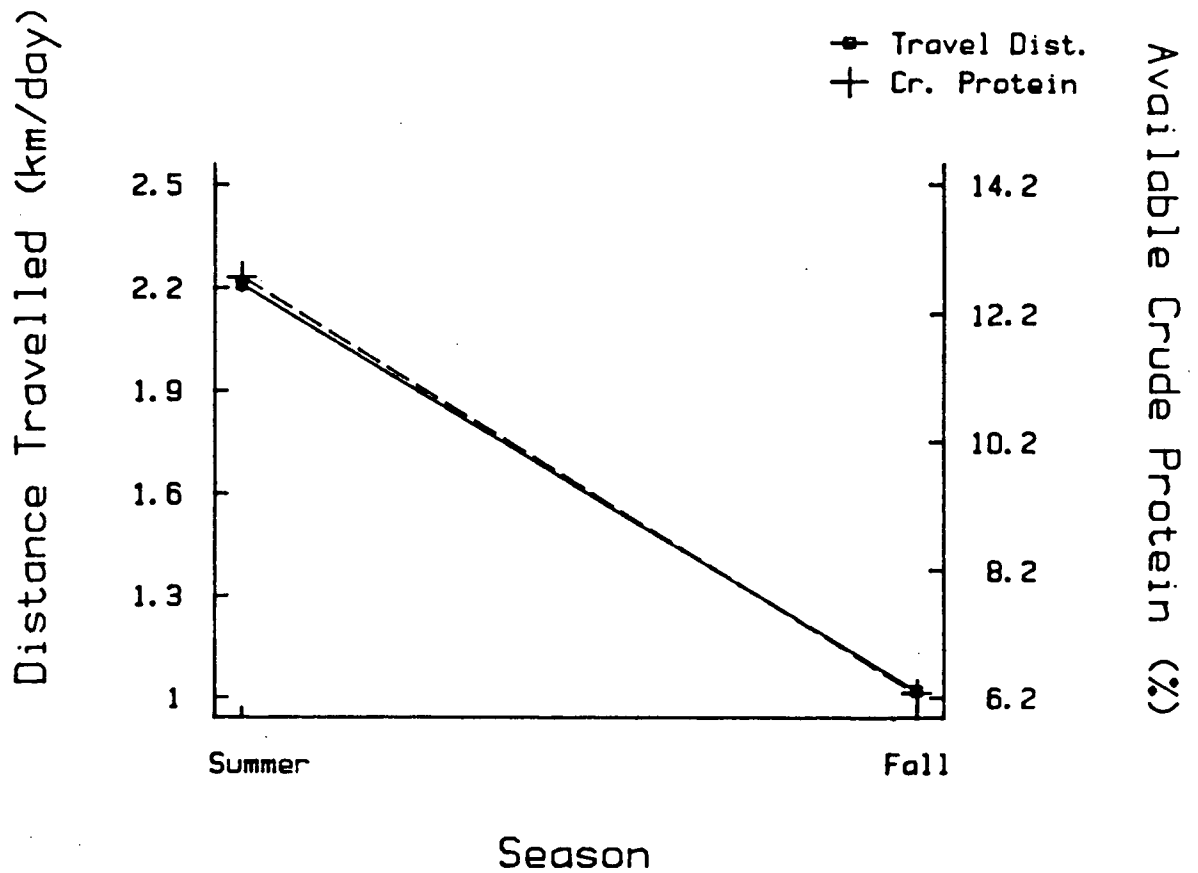
Figure 5.4. Median daily travel distance (km/day) and mean forage crude protein (%) values for summer and fall. Travel distances include both male and female data. Crude protein values represent the mean of all forages. Summer = 1 June to 7 August, fall = 8 August to 31 October.

SUMMARY

1) Wood bison home ranges were not adequately predicted by the home range-body weight relationships proposed by McNab (1963) or Harestad and Bunnell (1979). Home range sizes were much larger than predicted. Habitat productivity and food distribution appear to be the major factors confounding these relationships. However, competition for resources and the possibility of migrant individuals cannot be discounted.

2) Female home ranges were larger than male home ranges. Although small sample size may have affected this result, larger female home ranges may not be as rare as suggested by Harestad and Bunnell (1979), and may not be uncommon in ungulates. More information on ungulate home ranges will be required in order to address this issue.

3) Home ranges were smaller for bison inhabiting the Mink Lake expansion area than for those inhabiting the Mackenzie Bison Sanctuary. Less dispersed habitat patches and decreased competition for forage may have caused these differences in home range size.

4) The main factors underlying female movement patterns cannot be clearly determined from my results. The constant search for the best quantity and quality of forage in order to maximize reproductive success may explain the results. Predator avoidance could explain why the largest daily movements are made when calves are young and most vulnerable. However, seasonal fluctuations in forage distribution and availability combined with interspecific competition for forage could explain the results.

CHAPTER 6. GENERAL DISCUSSION

Food limitation has been proposed as a population regulating mechanism for large ungulate populations (Caughley, 1970; McCullough, 1979). Sinclair et al. (1985) documented evidence identifying the lack of food during the dry season as the regulating mechanism in Serengeti wildebeest. Evidence from this study indicates that forage distribution and availability play an important role in habitat selection, home range size, and seasonal movements of wood bison, and that there is the potential for food limitation to act as a population regulating mechanism.

Most wild ungulates face undernutrition each winter due to the seasonality and unreliability of food supplies (Sinclair, 1977; White et al., 1981). However, ungulates typically store less fat than other herbivores (Pond and Mattacks, 1985), and the fat stored does not fully substitute for winter forage (Tyler, 1987b). Thus ungulates must forage constantly in order to survive; they cannot rely on fat storage.

Tyler (1987a) suggests abundance of winter forage as the ultimate factor determining abundance of Svalbard reindeer. Given scarce winter forage, he suggests animals should minimize energy costs as an important means of survival. This will prolong the time that can be spent surviving on poor forage. Hence there should be a decrease in energetically costly non-feeding activities, like walking, rolling and aggressive behavior. European bison decreased the time spent in such non-feeding activities during winter (Cabon-Raczynska et al., 1983). Wood bison decreased daily travel movements in winter and spent most of their time inhabiting wet sedge meadows which provide the highest forage biomass. Their winter activity patterns consisted

mostly of feeding or lying, with little walking. Walking was more prevalent in summer activity patterns (N. Larter, unpubl. data). However, wood bison still lost body fat reserves over the course of the winter (C. Gates, unpubl. data).

The availability of winter forage is affected by three things: 1) changes in snow and ice cover, 2) changes in primary production from the previous summer, and 3) changes in competition for resources. Lower primary production during the 1987 summer, in comparison to the previous summer, may have caused lower forage availability during the 1987-88 winter than during the previous winter. Adverse snow conditions during the 1987-88 winter caused bison to switch from foraging in higher biomass wet sedge meadows to foraging in willow savannas that provided a much more limited food supply. Body fat and animal condition measured in the fall of 1987 was at the lowest levels recorded from two previous fall and spring measurements, and it continued to decline over the winter to even lower levels when measured in the 1988 spring (C. Gates, unpubl. data). I would suggest that changes in available forage during the 1987 summer and 1987-88 winter were factors in the poorer condition exhibited by bison.

Summer forage is less likely to limit the bison population, and wood bison can switch from an almost exclusive sedge diet to a mixed diet (including in excess of 30% browse). However, a summer diet high in browse may not provide the necessary energy and nutrients required to maintain body conditions when forage is poor. Wood bison prefer a summer diet high in sedge (C. atherodes in particular), and actively forage on it when it is available. Comparative in vitro digestibility trials on all forages would provide information on what bison actually derive from the different forages.

The acid-detergent lignin analyses may provide information on the proportion of cellulose and lignin found in the indigestible forage fiber. Results from these analyses would provide more insights into forage quality as percieved by the animal, and may help determine whether the change in diet was a factor involved in the observed poorer body condition of the 1987 fall.

Other potential factors causing poor body condition could be increased competition, increased predatory harassment, insect harassment, or parasite loads. Increased competition cannot be dismissed because the population increased between 1986 and 1987 with a corresponding decrease in primary production. Detailed behavioural observations and activity patterns for both years would be required to address competition. Some of these data are available, but there may be inadequate information to rule one way or the other on the effects of increased competition. Harassment by wolves would appear to be quite negligible, especially when compared to the almost constant harassment experienced by bison in Wood Buffalo National Park (L. Carbyn, pers. comm.). Qualitatively, wolf harassment was low during both years I conducted field work. Insect harassment was more severe during a two week period in early July, 1987. Increased harassment does cause reduce time spent feeding (Melton et al., in prep. b) however it did not cause a noticeable shift in habitat use. It is possible that feeding disruptions over this period decreased forage intake. It is also possible that the decreased time spent feeding during a foraging bout was compensated for by longer overall foraging bouts or more foraging bouts per day. Data on this is lacking. Parasite loads in the Mackenzie wood bison were low to negligible when measured in both winters (P. Daoust, pers. comm.).

To determine if decreases in food availability have affected population

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dynamics, measures of population estimates, survival rates, and recruitment rates are required. The last population census was conducted in April 1987, prior to the decrease in forage availability, and showed that the population was still increasing. However, cow to calf ratios showed a large drop in 1988, and suggested that recruitment for bison inhabiting the Sanctuary was low compared to previous years. Recruitment in the Sanctuary was similar to levels found in the rapidly declining Slave River Lowlands bison population. Recruitment for bison inhabiting the Mink Lake expansion remained high and was similar to levels recorded in past years in the Sanctaury (C. Gates, pers. comm.). Snow conditions and primary production were not noticeably different between Mink Lake and the Sanctuary. Competition for available forage may have been reduced in the Mink Lake expansion zone, and the amount of travel required to move between habitat patches is probably lower, and these may have improved recruitment.

It is possible that the decrease in food availability in the Sanctuary will represent a minor inflection on the population growth curve. Wood bison range is expanding with the recent dispersal of animals into newly found habitat patches to the west of the Sanctuary. If this eruption continues one might be able to determine population regulating mechanisms at the original liberation point by back calculating the demographic characteristics (following Caughley 1970). This situation provides the opportunity to determine populating regulating mechanisms for an expanding endemic ungulate population, and is the next step in future research.

LITERATURE CITED

Abaza, R.H., J.T. Blake and E.J. Fischer. 1967. Chemical analyses of nutritional elements and toxic oxalate compounds of sedges, rushes, and certain broad leafed plants typifying inter-mountain meadowland forage. Utah Agric. Exp. Stn., Mimeo Ser. 504.

Adamczewski, J.Z., C.C. Gates, R.J. Hudson and M.A. Price. 1987. Seasonal changes in body composition of mature female caribou and calves (Rangifer tarandus groenlandicus) on an arctic island with limited winter resources. Can. J. Zool. 65: 1149-1157.

Arnold, G.W., E.S. De Boer and C.A.P. Boundy. 1980. The influence of odour and taste on the food preferences and food intake of sheep. Aust. J. Agric. Res. 31: 571-587.

Audette, R.C.S., H.M. Vijayanagar and J. Bolan. 1970. Phytochemical investigation of Manitoba plants. I. A new indole alkaloid and associated alkaloids from Phalaris arundinacea. Can. J. Chem. 48: 149-155.

Baltzi, G.O. and H.G. Jung. 1980. Nutritional ecology of microtine rodents: resource utilization near Atkasook, ALaska. Arc. Alp. Res. 12: 483-499.

Barker, R.D 1986. An investigation into the accuracy of herbivore diet analysis. Aust. Wildl. Res 13: 559-568.

Bell, R.H.V. 1969. The use of the herb layer by grazing ungulates in the Serengeti. In: Animal populations in relation to their food resources (Watson, A. ed.). p. 111-123. Symp. Brit. Ecol. Soc. (Aberdeen). Blackwell Sci. Pub., Oxford.

Bell, R.H.V. 1971. A grazing ecosystem in the Serengeti. Sci. Amer. 225: 86-93.

Bergerud, T.A. 1971. The population dynamics of Newfoundland caribou. J. Wildl. Manage. 25: 1-55.

Bergerud, T.A. 1974. The role of environment in the aggregation movement and distribution behaviour of caribou. In: The behaviour of ungulates and its relation to management (Geist, V. and F. Walther eds.). p. 552-583. I.U.C.N. Publ. Ser. 24, Morges, Switzerland.

Bobek, B. 1977. Summer food as the factor limiting roe deer population size. Nature 268: 47-49.

Boertje, R.D. 1981. Nutrirional ecology of the Denali caribou herd. Unpublished M.Sc. thesis, Univ. of Alaska, Fairbanks.

Borowski, S. and S. Kossak. 1972. Natural food preferences of the European bison in seasons free of snow cover. Acta Theriol. 17: 151-159.

Byers, C.R., R.K. Steinhorst, and P.R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48: 1050-1053.

Cabon-Raczynska, K., M. Kraskinska and Z. Krasinski. 1983. Behaviour and daily activity rhythm of European bison in winter. Acta Theriol. 28: 273-299.

Cairns, A.L. and E.S. Telfer. 1980. Habitat use by 4 sympatric ungulates in boreal mixed wood forest. J. Wildl. Manage. 44: 849-857.

Calef, G.W. and J. Van Camp. 1987. Seasonal distribution, group size and structure, and movements of bison herds. In: Bison ecology in relation to agricultural development in the Slave River lowlands, N.W.T. (Reynolds, H.W. and A.W.L. Hawley eds.). p. 15-20. Can. Wildl. Serv. Occasional Pap. No. 63. Ottawa.

Campbell, B.H. and M. Hinkes. 1983. Winter diets and habitat use of Alaskan bison after wildfire. Wildl. Soc. Bull. 11: 16-21.

Case, T.J. 1979. Optimal body size and an animals diet. Acta Biotheoretica 28: 54-69.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himilayan thar in New Zealand. Ecology 51: 53-72.

Christian, J.J., V. Flyger and D.E. Davis. 1960. Factors in the mass mortality of a herd of Sika deer, Cervus nippon. Chesapeake Sci. 1: 79-95.

Clutton-Brock, T.H., F.E. Guinness and S.D. Albon. 1982. Red deer: behavior and ecology of two sexes. Edinburgh Univ. Press, Edinburgh.

Clutton-Brock, T.H. and P.H. Harvey. 1978. Mammals, resources and reproductive strategies. Nature 273: 191-195.

Coppock, D.L. and J.K. Detling. 1986. Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning. J. Wildl. Manage. 50: 452-455.

Craighead, J.J., F.C. Craighead, Jr., R.L. Ruff and B.W. O'Gara. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by biotelemetry. Wildl. Monog. 33: 1-50.

Damuth, J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. Biol. J. Linnaen Soc., 15: 185-193.

Downes, C.M., J.B. Theberge and S.M. Smith. 1986. The influence of insects on the distribution, microhabitat choice, and behavior of the Burwash caribou herd. Can. J. Zool. 64: 622-629.

Fuller, W.A. 1961. The ecology and management of the American bison. Terre et la Vie 2: 286-304.

Fuller, W.A. 1966. The biology and management of the bison in Wood Buffalo National Park. Can. Wildl. Serv. Wildl. Manage. Bull. Ser. 1., No. 16.

Gallagher, C.H., J.H. Koch, R.M. Moore and J.D. Steel. 1964. Toxicity of Phalaris tuberosa for sheep. Nature 204: 542-545.

Gasaway, W.C., R.O. Stephenson, J.L. Davis, P.E.K. Shepherd, and O.E. Burris. 1983. Interrelationships between wolves, prey, and man in interior Alaska. Wildl. Monog. 84: 1-50.

Gates, C.C. and N.C. Larter. in prep. Growth and dispersal of an introduced large herbivore population: the Mackenzie wood bison.

Gibson, R.M. and F.E. Guiness. 1980. Behavioral factors affecting male reproductive success in red deer. Anim. Behav. 28: 1163-1174.

Hagman, J.L., G.C. Marten and A.W. Hovin. 1975. Alkaloid concentration in plant parts of reed canarygrass of varying maturity. Crop Sci. 15: 41-43.

Hanley, T.A. 1982. The nutritional basis for food selection by ungulates. J. Range Manage. 35: 146-151.

Hanley, T.A. and K.A. Hanley. 1982. Food resource partitioning by sympatric ungulates on Great Basin rangeland. J. Range Manage. 35: 152-158.

Hansen, R.M., T.M. Foppe, M.B. Gilbert, R.C. Clark and H.W. Reynolds. 1976. The microhistological analyses of feces as an estimator of herbivore diet. Unpublished report. Composition Analysis Laboratory, Colorado State Univ., Ft. Collins.

Hansen, R.M., D.G. Peden, and R.W. Rice. 1973. Discerned fragments in feces indicates diet overlap. J. Range Manage. 26: 103-105.

Harestad, A.S. and F.L. Bunnell. 1979. Home range and body weight -- a reevaluation. Ecology 60: 389-402.

Hawley, A.W.L. 1987. Bison and cattle use of forages. In: Bison ecology in relation to agricultural development in the Slave River lowlands, N.W.T. (Reynolds, H.W. and A.W.L. Hawley eds.). p. 49-52. Can. Wildl.Serv. Occasional Pap. No. 63. Ottawa.

Hawley, A.W.L., D.G. Peden, H.W. Reynolds and W.R. Stricklin. 1981. Bison and cattle digestion of forages from the Slave River Lowlands, Northwest Territories, Canada. J. Range Manage. 34: 126-130.

Herrig, D.M. and A.O. Haugen. 1969. Bull bison behavior traits. Iowa Acad. Sci. 76: 245-262.

Holechek, J.L., B. Gross, S.M. Dabo, and T. Stephenson. 1982. Effects of sample preparation, growth stage, and observer on microhistological analysis of herbivore diets. J. Wildl. Manage. 46: 502-505.

Hudson, R.J. and S. Frank. 1987. Foraging ecology of bison in aspen boreal habitats. J. Range Manage. 40: 71-75.

Johnson, M.K., H. Wofford, and H.A. Pearson. 1983. Digestion and fragmentation: influence on herbivore diet analysis. J. Wildl. Manage. 47: 877-879.

Knight, R.R. 1970. The Sun River elk herd. Wildl. Monog. 23: 1-66.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. In: Behavioural ecology: an evolutionary approach (Krebs, J.R. and N.B. Davies eds.). p. 23-63. Blackwell Sci. Publ., Oxford.

Larter, N.C. and C.C. Gates. 1987. Seasonal selection of resources by wood bison in the Mackenzie Bison Sanctuary, Northwest Territories, Canada. 18th Congress International Union Game Biologists, Krakow, Poland.

Leslie, D.M. Jr., M. Vavra, E.E. Starkey, and R.C. Slater. 1983. Correcting for differential digesibility in microhistological analyses involving common coastal forages of the Pacific Northwest. J. Range Manage. 36: 730-732.

Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, New Jersey.

Lindstedt, S.L., B.J. Miller and S.W. Buskirk. 1986. Home range, time and body size in mammals. Ecology 67: 413-418.

Lott, D.F. and S. Minta. 1983. Home ranges of American bison cows on Santa Catalina Island, California. J. Mammal. 64: 161-162.

MacArthur, R.H. and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. Proc. Nat. Acad. Sci. (USA) 51: 1207-1210.

MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. Amer. Nat. 100: 603-609.

McCullough, D.R. 1979. The George Reserve deer herd. Univ. of Michigan Press, Ann Arbor.

McHugh, T. 1958. Social behavior of the American buffalo (Bison bison bison). Zoologica 43: 1-40.

McInnis, M.L., M. Vavra, and W.C. Krueger. 1983. A comparison of four methods used to determine diets of large herbivores. J. Range Manage. 36: 302-306.

McNab, B.K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97: 133-140.

McNaughton, S.J. 1979. Grassland-herbivore dynamics. In: Serengeti: dynamics of an ecosystem (Sinclair A.R.E. and M. Norton-Griffiths, eds.). p. 46-81. Univ. of Chicago Press, Chicago.

Maher, C.R. and J.A. Byers. 1987. Age-related changes in reproductive effort of male bison. Behav. Ecol. Sociobiol. 21: 91-96.

Marten, G.C., R.M. Jordan and W. Hovin. 1976. Biological significance of reed canarygrass alkaloids and associated palatability variation to grazing sheep and cattle. Agron. J. 68: 909-914.

Meagher, M.M. 1971. Snow as a factor influencing bison distriburion and numbers in Pelican Valley, Yellowstone National Park. In: Proc. Snow Ice Symp. p. 63-67. Iowa State Univ., Ames.

Meagher, M.M. 1973. The bison of Yellowstone National Park. Natl. Park Serv. Sci. Monogr. Ser. No. 1. 161pp.

Meagher, M.M. 1976. Winter weather as a population-regulating influence on free-ranging bison in Yellowstone National Park. Trans. Natl. Parks Centennial Symp. Ser. No. 1: 29-38.

Mech, L.D. and P.D. Karns. 1977. Role of the wolf in a deer decline in the Superior National Forest. U.S. Dept. Agric. Serv. Res. Pap. NC-148, North Cent. For. Exp. Stn., St. Paul, Minnesota.

Melton, D.A., C.C. Gates, N.C. Larter and J.A. Virgl. in prep a. Foraging behaviour of wood bison in an expanding population.

Melton, D.A., N.C. Larter, C.C. Gates and J.A. Virgl. in prep b. Aspects of the behaviour of wood bison in an expanding population.

Messier, F. and M. Crete. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65: 503-512.

Mychaisw, L. 1987. Primary range survey of the Mackenzie Bison Sanctuary. Unpublished report. Dept. Renewable Res., Yellowknife, N.W.T.

National Academy of Sciences - National Research Council. 1976. Nutrient requirements of beef cattle. Nutrient requirements of domestic animals, No. 4. 5th ed. Natl. Acad. Sci., Washington, D.C.

Nelson, D.W. and L.E. Sommers. 1973. Determination of total nitrogen in plant material. Agron. J. 65: 109-112.

Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38: 541-545.

Peden, D.G. 1976. Botanical composition of bison diets on shortgrass plains. Am. Midl. Nat. 96: 225-229.

Person, S.J. 1975. Digestibility of indigenous plants utilized by *Rangifer tarandus*. Ph. D. thesis, Univ. of Alaska, Fairbanks.

Phillips, R.D., W.E. Berg and D.B. Siniff. 1973. Moose movement patterns and range use in northwestern Minnesota. J. Wildl. Manage. 37: 266-278.

Pond, C.M. and C.A. Mattacks. 1985. Body mass and natural diet determinants of the number and volume of adipocytes in Eutherian mammals. J. Morph. 185: 183-193.

Putman, R.J. 1984. Facts from faeces. Mammal Rev. 14: 79-97.

Pyke, G.H., H.R. Pulliam and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Reynolds, H.W., R.M. Hansen, and D.G. Peden. 1978. Diets of the Slave River lowland bison, Northwest Territories, Canada. J. Wildl. Manage. 42: 581-590.

Reynolds, H.W. and A.W.L. Hawley. 1987. Seasonal variation in forage quality. In: Bison ecology in relation to agricultural development in the Slave River lowlands, N.W.T. (Reynolds, H.W. and A.W.L. Hawley eds.). p. 45-48. Can. Wildl. Serv. Occasional Pap. No. 63. Ottawa.

Reynolds, H.W. and D.G. Peden. 1987. Vegetation, bison diets, and snow cover. In: Bison ecology in relation to agricultural development in the Slave River lowlands, N.W.T. (Reynolds, H.W. and A.W.L. Hawley eds.). p. 39-44. Can. Wildl. Serv. Occasional Pap. No 63. Ottawa.

Rochelle, J.A. 1980. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. Unpublished Ph. D. thesis, Univ. of British Columbia, Vancouver.

Rosenzweig, M.L. 1974. On evolution of habitat selection. In: Proc. First International Congress Ecology. p. 401-404. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv. Publ. 1300, Ottawa.

Rutberg, A.T. 1984. Competition and reproduction in American bison cows. Unpublished Ph. D. thesis, Univ. of Washington, Seattle.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Schwartz, C.C. and N.T. Hobbs. 1985. Forage and range evaluation. In: Bioenergetics of widl herbivores (Hudson, R.J. and R.G. White eds.). p. 21-51. CRC Press, Boca Raton, Florida.

Shackleton, D.M. 1968. Comparative aspects of social organization of

American bison. Unpublished M.Sc. thesis, Univ. Western Ontario, London.

Sinclair, A.R.E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. J. Anim. Ecol. 44: 497-520.

Sinclair, A.R.E. 1977. The African buffalo. Chicago Univ. Press, Chicago.

Sinclair, A.R.E., H. Dublin and M. Borner. 1985. Population regulation of Serengeti wildebeest: a test of the food hypothesis. Oecologia 65: 266-268.

Sinclair, A.R.E. and M. Norton-Griffiths. 1979. Serengeti: dynamics of an ecosystem. Univ. of Chicago Press, Chicago.

Skoog, R.O. 1968. Ecology of the caribou (Rangifer tarandus granti) in Alaska. Unpublished Ph. D. thesis, Univ. California, Berkley.

Smith, A.D. and L.J. Shandruk. 1979. Comparison of fecal, rumen and utilization methods for ascertaining pronghorn diets. J. Range Manage. 32: 275-279.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry: The principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, 776pp.

Soper, J.D. 1941. History, range and home life of the northern bison. Ecol. Monog. 11: 347-412.

Sparkes, D.R. and J.C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. J. Range Mgmt. 21: 264-265.

Stuwe, M. and C.E. Blohowiak. 1985. MCPAAL: Micro-computer Programs for the Analysis of Animal Locations, version 1.21. Conservation and Research Cent., Nat. Zoological Park, Smithsonian Institution, Washington D.C.

Sullivan, J.T. 1962. Evaluation of forage crops by chemical analysis: A critique. Agron. J. 54: 511-515.

Tessaro, S.V. 1988. A descriptive and epizootioologic study of brucellosis and tuberculosis in bison in northern Canada. Unpublished Ph. D. thesis, Univ. of Saskatchewan, Saskatoon.

Todd, J.W. and R.M. Hansen. 1973. Plant fragments in feces of bighorns as indicators of food habits. J. Wildl. Manage. 38: 363-366.

Tucker, C.J., L.D. Miller and R.L. Pearson. 1973. Measurement of the combined effect of green biomass chlorophyll, and leaf water on canopy spectroreflectance of the short-grass prairie. Proc. of the Second Annual Remote Sensing of Earth Resources Conf., Univ. of Tennesee, Tullahoma.

Tyler, N.J.C. 1987a. Natural limitation of the abundance of the high arctic Svalbard reindeer. Unpublished Ph. D. thesis, Univ. of Cambridge.

Tyler, N.J.C. 1987b. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. In: Reproductive energetics in mammals (Loudon, A.S.I. and P.A. Racey eds.). p. 203-229. Oxford Univ. Press.

Van Ballenberghe, V. and J.M. Peek. 1971. Radio-telemetry studies of moose in northern Minnesota. J. Wildl. Manage. 35: 63-71

Van Camp, J. 1975. Snow conditions and the winter feeding behaviour of Bison bison in Elk Island National Park. Can. Wildl. Serv. Rep. CWS-53-75.

Van Den Brink, W. 1980. The behavior of wisent and bison in large enclosures. Acta Theriol. 25: 115-130.

Van Soest, P.J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. J. Assoc. Off. Agr. Chem. 46: 829-835.

Van Soest, P.J. 1967. Development of a comprehensive system of feed analyses and its application to forages. J. Anim. Sci. 26: 119-128.

Van Vuren, D. 1983. Group dynamics and summer home range of bison in Southern Utah. J. Mammal. 64: 329-332.

Vavra, M. and J.L. Holechek. 1980. Factors influencing microhistological analysis of herbivore diets. J. Range Manage. 33: 371-374.

Vavra, M., R.W. Rice and R.M. Hansen. 1978. A comparison of esophageal fistula and fecal material to determine steer diets. J. Range Manage. 31: 11-13.

Virgl, J.A. 1988. Foraging strategies of male and female wood bison (Bison bison athabascae) in relation to reproductive fitness. Unpublished B.Sc. Honors thesis, Univ. of British Columbia, Vancouver.

Voth, E.H. and H.C. Black. 1973. A histological technique for determining feeding habits of small herbivores. J. Wildl. Manage. 37: 223-231.

Waggoner, V. and M. Hinkes. 1986. Summer and fall browse utilization by an Alaskan bison herd. J. Wildl. Mgmt. 50: 322-324.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Nat. 108: 290-304.

White, R.G., F.L. Bunnell, E. Gaare, T. Skogland and B. Hubert. 1981. Ungulates on arctic ranges. In: Tundra ecosystems: A comparative analysis (Bliss, L.C., J.B. Cragg, D.W. Heal and J.J. Moore eds.). p. 397-483. Intl. Biol. Prog., No. 25. Cambridge Univ. Press.

Woods, D.L. and K.W. Clark. 1971. Genetic control and seasonal variation of some alkaloids in reed canarygrass. Can. J. Plant Sci. 51: 323-329.

APPENDIX 1.

REGRESSIONS OF NITROGEN CONCENTRATION (%) VERSUS TIME

Habitat	Forage	Regression	R^2Value	P-Value
Wet Sedge	C. atherodes	2.448-0.232x	0.8908	0.0000
	C. aquatilis	2.327-0.181x	0.8704	0.0000
Willow Sav.	C. atherodes	3.356-0.326x	0.9703	0.0000
	C. aquatilis	2.670-0.221x	0.8416	0.0000
	Grass	3.773-0.373x	0.9448	0.0000
	P. arundinacea	4.159-0.404x	0.9448	0.0000
	Salix spp.	3.092-0.240x	0.8649	0.0000
Willow-Asp.	C. atherodes	2.756-0.228x	0.9311	0.0000
	C. aquatilis	3.578-0.300x	0.8912	0.0000
	Grass	3.440-0.353x	0.9774	0.0000
	P. arundinacea	4.041-0.385x	0.9653	0.0000
	Salix spp.	3.456-0.262x	0.9444	0.0000
Marl	C. atherodes	3.143-0.276x	0.9555	0.0000
	Grass	2.862-0.280x	0.9602	0.0000
	Salix spp.	2.724-0.209x	0.8959	0.0000

Habitat	Forage	Regression	R^2Value	P-Value
Mixed Forest	<u>C</u>. <u>atherodes</u>	3.071-0.229x	0.8532	0.0000
	<u>C</u>. <u>aquatilis</u>	2.427-0.184x	0.8639	0.0000
	Grass	2.777-0.282x	0.9298	0.0000
	<u>Salix</u> spp.	2.818-0.202x	0.9159	0.0000
Dry Conifer	Grass	3.427-0.341x	0.9849	0.0000
Wet Conifer	<u>Carex</u> spp.	2.705-0.238x	0.8888	0.0000
	<u>Salix</u> spp.	3.456-0.262x	0.9458	0.0000

APPENDIX 2.

REGRESSIONS OF ACID-DETERGENT FIBER (%) VERSUS TIME

Habitat	Forage	Regression	R^2Value	P-Value
Wet Sedge	C. atherodes	30.942+1.717x	0.8245	0.0003
	C. aquatilis	33.128+1.813x	0.8272	0.0003
Willow Sav.	C. atherodes	25.139+1.925x	0.8497	0.0002
	C. aquatilis	31.207+1.863x	0.7600	0.0011
	Grass	27.587+2.321x	0.8494	0.0002
	P. arundinacea	19.286+3.283x	0.5663	0.0120
	Salix spp.	27.460+1.701x	0.2482	0.1428
Willow-Asp.	C. atherodes	25.516+2.219x	0.9517	0.0000
	C. aquatilis	31.558+1.767x	0.7019	0.0048
	Grass	28.851+2.773x	0.8952	0.0000
	P. arundinacea	18.639+3.052x	0.5663	0.0120
	Salix spp.	27.824+1.416x	0.3246	0.0855
Marl	C. atherodes	26.742+1.892x	0.9434	0.0000
	Grass	29.073+2.768x	0.9073	0.0000
	Salix spp.	24.650+1.628x	0.5858	0.0099

Habitat	Forage	Regression	R^2 Value	P-Value
Mixed Forest	C. atherodes	27.166+1.787x	0.9088	0.0000
	C. aquatilis	36.065+1.312x	0.6584	0.0044
	Grass	33.998+2.272x	0.6633	0.0041
	Salix spp.	19.417+2.948x	0.8756	0.0001
Dry Conifer	Grass	26.680+1.846x	0.6925	0.0028
Wet Conifer	Carex spp.	26.913+1.944x	0.7601	0.0010
	Salix spp.	25.017+1.454x	0.3589	0.0882

APPENDIX 3.

REGRESSIONS OF N/ADF VERSUS TIME

Habitat	Forage	Regression	R^2Value	P-Value
Wet Sedge	C. atherodes	7.142-0.711x	0.9605	0.0001
	C. aquatilis	6.351-0.552x	0.9178	0.0001
Willow Sav.	C. atherodes	11.338-1.186x	0.9847	0.0000
	C. aquatilis	7.706-0.721x	0.8894	0.0001
	Grass	12.098-1.329x	0.9452	0.0000
	P. arundinacea	15.963-1.771x	0.9191	0.0001
	Salix spp.	10.528-0.985x	0.7461	0.0027
Willow-Asp.	C. atherodes	9.219-0.882x	0.9655	0.0000
	C. aquatilis	10.175-0.945x	0.8891	0.0001
	Grass	10.129-1.139x	0.9302	0.0000
	P. arundinacea	15.413-1.648x	0.9715	0.0000
	Salix spp.	11.872-1.077x	0.7952	0.0012
Marl	C. atherodes	10.396-1.033x	0.9785	0.0000
	Grass	8.866-0.994x	0.8880	0.0001
	Salix spp.	10.577-0.991x	0.8693	0.0003

Habitat	Forage	Regression	R^2 Value	P-Value
Mixed Forest	C. atherodes	10.084-0.899x	0.9166	0.0001
	C. aquatilis	6.428-0.551x	0.8702	0.0002
	Grass	7.478-0.822x	0.8707	0.0002
	Salix spp.	11.326-1.102x	0.8832	0.0002
Dry Conifer	Grass	11.066-1.166x	0.9795	0.0000
Wet Conifer	Carex spp.	8.808-0.871x	0.8818	0.0002
	Salix spp.	9.247-0.809x	0.9604	0.0000