

Summer feeding and resting behaviour of wood bison
and the effects of fire on fen vegetation near
Waterhen, Manitoba.

by

Dean J. Berezanski

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Zoology

Winnipeg, Manitoba

(c) Dean J. Berezanski, 1986

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-33886-5

SUMMER FEEDING AND RESTING BEHAVIOUR OF WOOD BISON AND THE EFFECTS
OF FIRE ON FEN VEGETATION NEAR WATERHEN, MANITOBA

BY

DEAN J. BEREZANSKI

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

© 1986

Permission has been granted to the LIBRARY OF THE UNIVERSITY OF MANITOBA to lend or sell copies of this thesis, to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film, and UNIVERSITY MICROFILMS to publish an abstract of this thesis.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

I hereby declare that I am the sole author of this thesis.

I authorize the University of Manitoba to lend this thesis to other institutions or individuals for the purpose of scholarly research.

Dean J. Bereżanski

I further authorize the University of Manitoba to reproduce this thesis by photocopying or by other means, in total or in part, at the request of other institutions or individuals for the purpose of scholarly research.

Dean J. Bereżanski

The University of Manitoba requires the signatures of all persons using or photocopying this thesis. Please sign below, and give address and date.

ABSTRACT

Summer diets of a confined herd of wood bison, as indicated by fecal analyses, showed sedges and grasses to dominate each month, but vary in proportion of total plant composition. However, observations of the herd indicated that forbs were the dominant plants grazed, and were taken in successively decreasing proportions each month.

Age-sex classes of bison did not differ in choice of plant species eaten during June, as indicated by observed behaviour. The classes differed in July, with cow diets differing from bull and spikehorn diets. Only bulls and spikehorns differed in August.

Fire-treated sedge fens were little used by the bison because these areas were difficult to travel through. In high-water fens, biomass of vegetation from burned fen was greater than fen only in June and July. Fire removed litter and allowed for rapid solar heating. The ash was thought not to provide a significant nutrient flush, as calcium content was more often less in burned fen sedges than in unburned ones. In addition, in low-water fen, biomass in burned fen was greater only in July. High-water fen always had greater vegetation biomass than low-water fen. Certain quality parameter suggested earlier maturation of vegetation in burned and high-water level fens.

Resting habitats were chosen in different proportions between months in response to tabanid fly harassment. Open habitats were the dominant choices in June and July, but accounted for less than half the choices in August. Tabanid fly activity was greatest in June and July, and almost nil in August. The bison were thought to seek open habitats to escape these flies. The age-sex classes used habitats in different proportions during June and in July. Cows avoided open habitats, while spikehorns used open habitats the most. All classes used habitats in similar proportions during August.

Feeding activity of the bison was crepuscular in June and July, but more diurnal in August. The increase in diurnal activity coincided with the decrease in tabanid activity.

ACKNOWLEDGEMENTS

I am indebted to my advisor Rick Riewe for his support, enthusiasm, and friendship. Much appreciation goes to W. O. Pruitt, Jr., who was my acting advisor in Rick's absence, and to R. M. Evans and J. M. Stewart who were committee members.

My thanks to the Board of Directors of Waterhen Wood Bison Ranches Ltd. for allowing research to be carried out on the herd. A special thanks goes to Harvey Nepinak and to Nelson Contois and his work crew for their assistance and friendship.

Special thanks and love to my parents who gave me the opportunity and encouragement to go to college and university.

Dennis Houle and Ken Catcheway of Skownan were invaluable help in the vegetation collection. Richard Zieba from NRI and Bev Hathaway of Zoology assisted in sorting and weighing the vegetation.

My appreciation goes to several branches of the Department of Natural Resources. Harvey Payne and the Wildlife Branch provided much support and advice for the study. Natural Resources Officer Chris Ruhr of Gypsumville and his crew carried out the prescribed burns. Tom Marchant of Gimli and the Forestry Branch provided a survey flight over the site.

Hal Reynolds of the Canadian Wildlife Service, Edmonton, gave advice on the study and constructive criticism of several drafts.

My heartfelt thanks to Jill Oakes who flew me around Wood Buffalo National Park and to Waterhen, and graciously loaned me the "Green Hornet" for the summer.

A special thanks to Bernie McIntyre who helped transport and store my bags of "grass", and to Jim "Che-bek" Briskie who put up with three different cars in our 2.5 years of car-pooling.

Much appreciation to Rick Riewe, Bill Jones, Kelly Leavesley, and Cathy Shields for loaning me their drafting equipment. Special commendations to Greg Kelly and the many people who "borrowed me" money for late-night unwinding sessions in the pub.

This study was funded by a Wildlife Branch Grant and a Wildlife Society (Manitoba Chapter) Bursary to myself, and by grants to R. Riewe from Environment Canada (Environment 2000 Program) and Employment and Immigration Canada (Work-study Program).

In memory of my dad

CONTENTS

ABSTRACT	iv
ACKNOWLEDGEMENTS	vi
	<u>page</u>
INTRODUCTION	1
Subspecific History	1
Feeding Habits	5
Foraging Strategies of Age-Sex Classes	7
Fire Effects	8
Bison and Their Habitat	8
Other Bovids and Their Habitat	9
Emergent Plants Other Than Sedges	11
Habitat Selection By Resting Bison	13
Objectives	14
METHODS	16
Site Description	16
Animal Behaviour Study	21
Vegetation Study	24
RESULTS-ANIMAL BEHAVIOUR STUDY	28
Feeding Differences Between Months	28
Observed Fire-treated Habitat Preferences	34
Observed Feeding Differences Between Classes	
Within Months	34
Observed Resting Habitat Choices	36
RESULTS-VEGETATION STUDY	41
Biomass	41
Crude Protein (CP)	44
Acid Detergent Fibre (ADF)	47
Total Digestible Nutrients (TDN)	50
Calcium:Phosphorus (Ca:P)	53
Calcium (Ca)	57
Phosphorus (P)	59
DISCUSSION-ANIMAL BEHAVIOUR STUDY	61
Feeding Differences Between Months	61
Fecal Analyses	61

Plant Phenology	61
Habitat Availability	62
Prior Foraging Experience	63
Observed Behaviour	64
Sample Times	65
Biomass Per Bite	66
Sample Size	67
Sample Frequency	69
Other Observations	69
Observed Fire-Treated Feeding Habitat	
Preferences	71
Observed Feeding Differences Between Classes	
Within Months	71
Observed Resting Habitat Choices	74
Differences Between Months	74
Daily Feeding Activity Cycle	78
DISCUSSION-VEGETATION STUDY	80
Biomass	80
Statistical Analysis of Quality Parameters	82
Crude Protein (CP)	83
Acid Detergent Fibre (ADF)	85
Total Digestible Nutrients (TDN)	85
Calcium:Phosphorus (Ca:P)	86
Calcium (Ca)	88
Phosphorus (P)	89
CONCLUSIONS	90
Conclusions to Hypotheses	90
Other Conclusions	94
RECOMMENDATIONS	96
LITERATURE CITED	98
PERSONAL COMMUNICATIONS	107
<u>Appendix</u>	<u>page</u>
A. SEXES AND AGES OF WATERHEN WOOD BISON 1984	108
B. PARTIAL VEGETATION LIST FOR WATERHEN SITE	110
C. DESCRIPTION OF HABITAT TYPES	115
D. TEMPERATURES AND PRECIPITATION, CFS GYPSUMVILLE	116

E.	DESCRIPTION OF QUALITY PARAMETERS	117
F.	DIETS OF WOOD BISON PRIOR TO MANITOBA TRANSFER . .	120
G.	DAILY FEEDING TIMES OF WOOD BISON	122
H.	SAMPLE SIZE FREQUENCY DISTRIBUTION BY HABITAT TYPES	123
I.	FREQUENCY OF SPIKEHORNS OBSERVED FEEDING BY HABITAT	124
J.	FREQUENCY OF OBSERVED FEEDING OF EACH CLASS BY HABITAT	125
K.	FREQUENCY OF OBSERVED COMFORT AND OTHER BEHAVIOURS	126
L.	RELATIONSHIP OF TEMPERATURE AND BISON FEEDING ACTIVITY	127

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
1. Historical distribution and range of bison.	2
2. Morphology of male wood and plains bison.	3
3. Waterhen wood bison site in the Interlake District of Manitoba.	17
4. Vegetation cover types in Waterhen wood bison site.	18
5. Location of vegetation transects.	25
6. Observed herd food choices between months.	31
7. Observed age-sex class food choices between months.	33
8. Observed monthly food choices between age-sex classes.	35
9. Herd resting habitat choices between months.	37
10. Age-sex class resting habitat choices between months.	38
11. Monthly resting habitat choices between age-sex classes.	39
12. Crude protein content of sedge samples.	45
13. Acid detergent fibre content of sedge samples.	48
14. Total digestible nutrient content of sedge samples.	51
15. Calcium:Phosphorus ratios of sedge samples.	54
16. Calcium and phosphorus contents of sedge samples.	56

LIST OF TABLES

<u>Table</u>	<u>page</u>
1. Mean surface to substrate water depths.	20
2. Mean percent plant fragment composition of bison feces.	29
3. Food choices of the Waterhen wood bison herd. . . .	30
4. Current year's biomass (kg/ha) in the Waterhen sedge fens.	42
5. Comparison of CP content of sedges samples.	46
6. Comparison of ADF contents of sedge samples.	49
7. Comparison of TDN contents	52
8. Comparison of Ca:P ratios.	55
9. Comparison of Ca contents of sedge samples.	58
10. Comparison of P content of sedge samples.	60

INTRODUCTION

SUBSPECIFIC HISTORY

Novakowski (1979) stated that wood bison (Bison bison athabascae Rhoads) were once distributed throughout the coniferous forests of western and northern Alberta, north to Lac la Martre and the Horn Mountains in the Mackenzie Valley, west to the lower Liard and Peace Rivers and the Upper Mackenzie River (Figure 1). Early sighting records indicate a type of "wood bison" inhabiting the forests around Lakes Manitoba and Winnipeg. These individuals were apparently smaller than the plains bison (B. b. bison [Linnaeus]) (Roe 1970), so were probably not B. b. athabascae. Individuals of today's wood bison are about 20% heavier than B. b. bison (Reynolds pers. comm.) with a different body morphology (Geist and Karsten 1977; Figure 2).

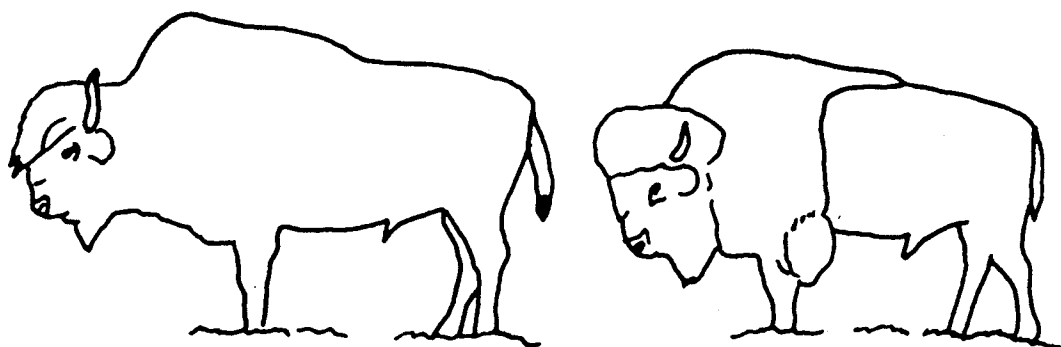
Wood bison are an endangered subspecies (Cook and Muir 1984). The last remnants of B. b. athabascae herds ranged in the region between the Caribou Mountains of Wood Buffalo National Park (WBNP), and Great Slave Lake and were subsequently given legal protection by the Canadian government in 1893. By then, their numbers were estimated at not more than 500. In 1922, an Order-in-Council created Wood Buffalo Na-

Figure 1. Historic and prehistoric distribution of bison.

1. Prehistoric range of wood bison, with subfossil athabasca identified here. 2. Historical range of wood bison. 3. Taxonomic identity unknown, possible subspecies intergradation. 4. Historical range of plains bison (after van Zyll de Jong 1985 in press).



Figure 2. Morphology of male wood (left) and plains (right)
bison (after Reynolds et al. 1982).



tional Park (WBNP) to give greater protection to these bison, at which time 1500 were estimated to exist (Leonard 1982).

Between 1925 and 1926, 6673 plains bison from Wainwright, Alberta were introduced into the park. Cross-breeding between the two subspecies occurred over the years and the pure wood strain was thought lost. In 1957, about 200 individuals of what were believed to be B. b. athabasca were discovered in the upper Nyarling River part of the park. Of this herd, eighteen were relocated to the Mackenzie Bison Sanctuary in 1963, and 23 went to Elk Island National Park (EINP) in 1965 (Leonard 1982). Although an overlap exists in blood protein characteristics between plains and wood bison (Ying and Peden 1977, Peden and Kraay 1979), van Zyll de Jong (1985 in press) recognized B. b. athabasca as a valid subspecies. The Mackenzie population is estimated at 1200-plus and still growing (Government of the N.W.T. 1983) while the EINP population stands at about 200 (Blythe pers. comm.). In 1980, 28 wood bison from EINP were released near Nahannni Butte, Northwest Territories (NWT) (Reynolds et al. 1982). In early 1984, over 30 bison were released into an enclosure near Hay-Zama, Alberta (Reynolds pers. comm.).

In late February 1984, 34 wood bison were transported from various zoos and game farms in western Canada to a 2.59 km² enclosure near Waterhen Lake, Manitoba. Appendix A gives the age- and sex- class breakdown of the transfer herd. This

was the cooperative effort of numerous federal, provincial, and private organizations along with the Waterhen Indian Band.

FEEDING HABITS

Grasses and sedges are the main forages used by bison, although proportions used are dependent upon habitat. Bison in the Slave River Lowlands, NWT, show slight to moderate selection of slough sedge (C. atherodes Spreng) throughout the year, followed by reedgrasses (Calamagrostis spp.)(Reynolds et al. 1978). Van Vuren and Bray (1983) found bison feces on seeded range in southern Utah to contain 94% grasses (86% Agropyron spp.) and sedges. He concluded that this was the results of forage availability. Van Vuren (1984) found summer diets in shrub-steppe communities to be 99% grasses (66% Poa spp.) and sedges. In short-grass plains of northeastern Colorado, blue grama (Bouteloua gracilis [HBK.] Lag.) and buffalo grass (Buchloe dactyloides [Nutt.] Engelm.) were dominant, but crested wheatgrass (A. cristatum [L.] Gaertn.) was preferred over blue grama (Peden in Reynolds et al. 1982). Bison in Colorado National Monument fed mostly on four-wing saltbush (Atriplex canescens, nomenclature from Wasser 1977), with speargrass (Stipa comata Trin.&Rupr.) used next in abundance (Wasser 1977). Forbs and browse may be substituted if grasses and sedges are not available (Soper 1941, Fuller 1966, Meagher

1973, Reynolds et al. 1978, Wydeven and Dahlgren 1985). Thus, bison can be described as having a mixed feeding strategy, thereby subsisting on high- and low-quality diets (forbs and sedges, respectively, for example).

Peden et al. (1974) showed that sedges and grasses are lower than forbs in protein content and digestibility. Many forbs are high in protein and palatability (as seen in Looman 1983) but are usually less abundant. A two-fold explanation for selection of sedges and grasses exists. First, these are usually the more abundant and easily collected foods (especially in the Waterhen area). The amount of biomass per bite is probably greater in sedge communities than in aspen forest floor communities. Second, and more important, bison can efficiently digest and assimilate low quality forage. (Richmond et al. 1977, Hawley et al. 1981). Peden et al. (1974) hypothesized this to be the result of more efficient nitrogen recycling but Reynolds et al. (1982) stated that this was an untested hypothesis. Wales et al. (1975) summarized that urea recycled from blood to rumen has a significant contribution to nitrogen metabolism. Nitrogen is essential for animal growth and rumen microbe activity. Hawley (in Reynolds et al. 1982) reported high blood urea nitrogen (BUN) values in bison compared to domestic cattle (Bos taurus L., nomenclature from this author) under various diets and environmental conditions. Keith (in Reynolds et al. 1982) stated that rumen ammonia and salivary urea levels also influence nitrogen recycling.

The diets of large ungulates change over the season. For example, changes in the diets of moose (Alces alces [L.]) are attributed to a difference in energy and nutrient requirements throughout the growing season (Belovsky 1978, Stewart et al. 1976). McCaffery et al. (1974) stated that white-tailed deer (Odocoileus virginianus borealis Miller) use of aspen in Wisconsin coincided with maximum protein content of that aspen. Reindeer (Rangifer tarandus tarandus [L.]) in southern Norway graze along a phenological gradient of Salix spp. and Deschampsia spp. (Skogland 1975). Free-land and Janzen (1974) suggested that mammalian herbivores optimize food choice to decrease the intake of toxic plant secondary compounds. For example, saskatoon (Amelanchier alnifolia Nutt) contains prussic acid in the early stages of leaf growth (Looman 1983, Quinton 1985).

FORAGING STRATEGIES OF AGE-SEX CLASSES

Separate age-sex classes of several ungulate species have different nutrient requirements and foraging strategies. Church and Pond (1974) stated that more nutrients are required by lactating female domestic mammals than by males. For example, Belovsky (1978) showed that, to meet their greater sodium requirements, moose cows with calves consume more aquatic vegetation than do bulls or barren cows. Rice and Church (1974) noted a difference in browse preference between sexes of black-tailed deer. Geist (1982) discussed

the different foraging strategies of wapiti (Cervus elaphus L. 1758) bulls, cows, and calves, relating energy and nutrient requirements and competition between these age-sex classes. Willms and McLean (1978) proposed a feeding strategy for mule deer (O. h. hemionus [Rafinesque]) juveniles based also on nutrient requirements. Church and Pond (1974) stated that domestic bovid stomachs are developed by 6 to 9 months of age, so one may assume that spikeshorn (immature individual of any sex) digestive functions, including urea recycling, are as efficient as adults', and that they can use the less digestible forage.

FIRE EFFECTS

Bison and Their Habitat

Fire is recognized as a useful tool for improving sedge and grass habitats, although water, not fire, is generally thought of as the limiting factor to emergent plant distributions (Dane 1959, Harris and Marshall 1963, Walker and Coupland 1970, Millar 1973, and Thompson 1982). Little research has been done on the effects of fire on sedge habitats. A fall fire in sedge meadows in the Slave River Lowlands, N.W.T., showed greater production in the two years post-burn. The higher production was insignificant, however, due to a large variance (Jalkotzy and Van Camp unpublished

report). Campbell and Hinkes (1983) documented an increase in bison winter range due to habitat changes following a 1977 wildfire at Farewell Lake, Alaska. The habitat burned contained sedge (Carex spp. and Eriophorum spp.), ash (Fraxinus sp.), and willow. In the two to five years following the fire, the bison population increased from 33 to 98 in the burned habitat. The primary habitats of grassland and sedgeland increased from a pre-fire level of 38% of accessible range to 97%. Similar behavior was noted in the Slave River Lowlands where bison tended to use burned areas more often in the summer (V. Hawley pers. comm.). In WBNP, bison feces counts in forested jackpine stands were significantly different from burned stands. Forested stands had greater counts, indicating preference for that habitat. The best explanation for this preference was that more cover was available in the forested areas to hide from the sun and from predators (Berezanski unpublished data). Moose were found to also use forested stands more often than burned stands (Neu et al. 1974).

Other Bovids and Their Habitat

Stelfox (in Viereck 1973) stated that, between 1916 and 1936, fire in the Rockies reduced much conifer area to grassland. Mountain sheep (Ovis canadensis Shaw) populations rose threefold in the area in that period of time. Hobbs and Spowart (1984) and Hobbs and Swift (1985) showed that

mountain sheep have higher quality winter diets when using burned grassland. However, individual forage protein and digestibility improve only a few percentage points. Hobbs and Spowart (1984) stated that the improved diets are the result of selection of more green grasses, which are more nutritious. Selection is attributed to less litter obscuring these grasses and to warmer soil conditions. Warmer soil conditions promote growth of cool season grasses during winter.

Riggs and Peek (1980) examined use by bighorns of long-lived seral vegetation resulting from fire in spruce-fir stands in Glacier National Park. Forage species in seral stands were partially green throughout winter and climax grassland was cured by November 15 in their study. Use of seral communities tended to decline through winter, but they were always preferred. Climax bunchgrass communities were selected by the by the sheep and seral stages avoided during full green-up in April. Seip and Bunnell (1985a) found that yearling Stone's sheep (O. dalli stonei J.A. Allen) on burned ranges had greater horn growth, indicating superior range. In addition, the incidence of lungworm (Protostrongylus spp.) decreased and lamb production increased. They concluded that the better condition of the sheep was the result of greater forage quantity during the winter on burned ranges. Forage quality did not differ between burned and unburned areas. They also concluded that range burning ben-

efitted sheep only marginally in spring and summer. While Seip and Bunnell did not elaborate on it, the reduction in lungworm on burned ranges may have been the result of loss of the intermediate gastropod host to the parasite. This has been observed with black-tailed deer (Odocoileus hemionus columbianus [Richardson]; Isaac in Wright and Bailey 1982).

Seip and Bunnell (1985b) showed foraging Stone's sheep ewes to have the same bite rates when feeding in spring on burns and natural clearings despite greater herbage quantity and tiller (above-ground root) density of grasses on burns. In addition, there was no difference in foraging time of rams or ewes on burned and natural clearings.

Duvall and Whitaker (1964) documented domestic cattle weight gains on Louisiana grassland burned on a 3-year rotation basis. Cows with unweaned calves gained 25.9kg between May and August, compared to no gain under normal range conditions. Willms et al. (1980) showed domestic cattle in British Columbia to prefer forage from autumn-burned wheatgrass (Agropyron spicatum [Pursh] Scribn & Smith) communities. Reduced litter and increased palatability were suggested as influencing factors there, also.

Emergent Plants Other Than Sedges

While little research has been done on the effects of fire on sedges, other emergent plant species have been in-

vestigated. Marsh wetlands were burned 1 to 4 times over 13 years during a study in Saskatchewan. Present were C. atherodes, Scolochloa festuacea (Willd.) Link, Eleocharis palustris (L.) R.&S. No changes in species composition occurred (Millar 1973). Increased quality is attributed to a release of nutrients from ash into the soil, and to the removal of litter, thus permitting more rapid warming of the substrate and nutrient availability, thus permitting earlier growth (Daubenmire 1968). Hoffpauir (in Thompson 1982) found short-lived increases in soil calcium, phosphate, and potassium immediately after a burn in Louisiana Spartina marshes. Nutrients released by the fire were hypothesized to be taken up by growing plants. Thompson (1982) stated that nutrient release may stimulate growth and contribute to more rapid phenological development. Early emergence may also be a factor favouring selection by bison of one habitat over another (Hobbs and Spowart 1984, Reynolds pers. comm.). In addition, loss of litter makes the emerging grass shoots easier to find (Hobbs and Spowart 1984). Following spring burning at Delta Marsh, Manitoba, reedgrass (Phragmites australis [Cav.] Trin. ex Steudel, from Thompson 1982) flowering stem biomass did not increase, but density did. No change in substory composition or production occurred. Mineral compositions of shoots were greater in burned stands than published values (Thompson 1982). Burning favours P. australis because it provides earlier emergence and earlier shading power, removes litter, and increases density. The effect is

temporary as associate species are usually unaffected or unharmed (Haslam 1971).

HABITAT SELECTION BY RESTING BISON

Several factors affect habitat choice and behaviour of wild and domestic ungulates. Harassment by biting flies, especially "bulldogs" or "horse flies" (Diptera:Tabanidae), has been implicated as a major factor (Bauer in Stormer and Bauer 1980, numerous authors in Danks 1981, Collins and Urness 1982, S. Cantor pers. comm.). Cantor (pers. comm.) identified the following horsefly species in the Waterhen area: Hybomytra epistates, H. lasiophthalmus, H. nuda, H. arpodii, H. affinis, H. illiota, Chrysops excitans, Chrysops spp., and Tabanus similis. Being primarily grazers, the bison may choose to rest and ruminate near or in feeding areas (open grass/sedge meadows) to reduce travel time to them (Mloszewski 1983). Ambient air temperature is also a factor (Bauer in Stormer and Bauer 1980, Kirby and Stuth 1982). Fuller (1960) theorized that forests are used as refuges by bison from predators to crush attackers against trees. Geist (1982) suggested habitat choice by different age-sex classes of wapiti, for example, may be related to vulnerability to predators.

OBJECTIVES

Waterhen Wood Bison Ranches Ltd., managers of the herd at Waterhen, are attempting to increase the herd size. To do this, information is required as to the forage needs of wood bison and to the use of fire and changing water levels to manage the Waterhen site. In addition, data regarding the use of habitats for activities other than feeding (in this case, resting activity) should be collected. Such data will allow managers to evaluate sites for future transfer herds of wood bison.

This study set out to collect the above information and data, as a minimal amount exists in the literature. This objective was met by testing several hypotheses which were put forth after the literature review. The hypotheses are:

1. proportions of plant species eaten by the herd differed between months;
2. proportions of unburned and burned fen sedges grazed by bison were different between months;
3. proportions of grazed plant species within months differed between age-sex classes of bison;
4. biomass of current year's vegetation differed between unburned and burned fens within months;

5. biomass of current year's vegetation differed between high- and low-water level sedge fens within months;

6. quality of sedges differed between unburned and burned transects, between high- and low-water transects, and between C. aquatilis and Carex spp.

7. proportions of habitats chosen by resting bison differed between months when bulldog flies were present;

8. proportions of habitats chosen by resting bison differed between age-sex classes.

Hypothesis 1 was examined using both fecal analyses and observations of feeding. Hypotheses 2, 3, 7, and 8 were tested using observed behaviour only. Hypotheses 4, 5, and 6 were tested by clipping fen vegetation.

METHODS

SITE DESCRIPTION

The 2.59 km² Waterhen enclosure is situated at 52° 00' N., 99° 40' W. (Figure 3). The site is in the Interlake subdivision of the Manitoba Lowlands and is between 254 and 261m above sea level. The Lowlands constitute part of the Interior Plains physiographic region and were covered by glacial Lake Agassiz. The bedrock dates from the Ordovician, Silurian, and Devonian periods. Several advances of the continental ice sheet scoured the Precambrian Shield and deposited particles of all sizes onto the sedimentary strata of the Lowlands. Shale and limestone material deposited on preglacial surfaces formed a mantle of ground moraine. Those areas containing shale quickly weathered, but areas with limestone did not do so as fast. This created an undulating surface of swales (depressions) and ridges. The swales collect run-off water and create large areas of fen (Shaykewich and Weir 1965).

Soils of the study site vary. The swales include loamy brunisols, dark gray chernozems, and peaty humic gleysols. The ridges are made up mainly of humic mesosols (Mills and Smith 1981). Vegetation in the swales is a characteristic

Figure 3. Waterhen wood bison site (star) in the Interlake
District of Manitoba.

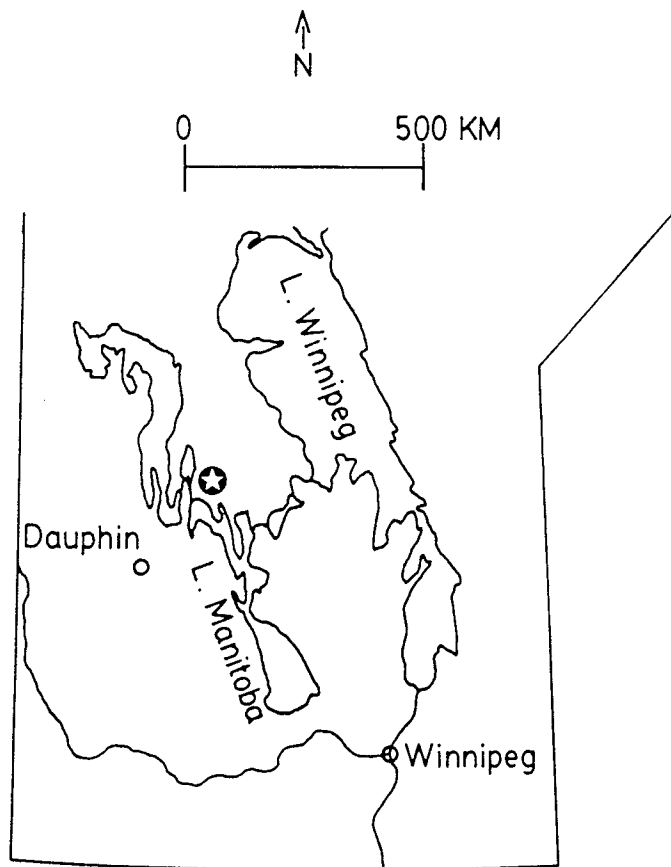
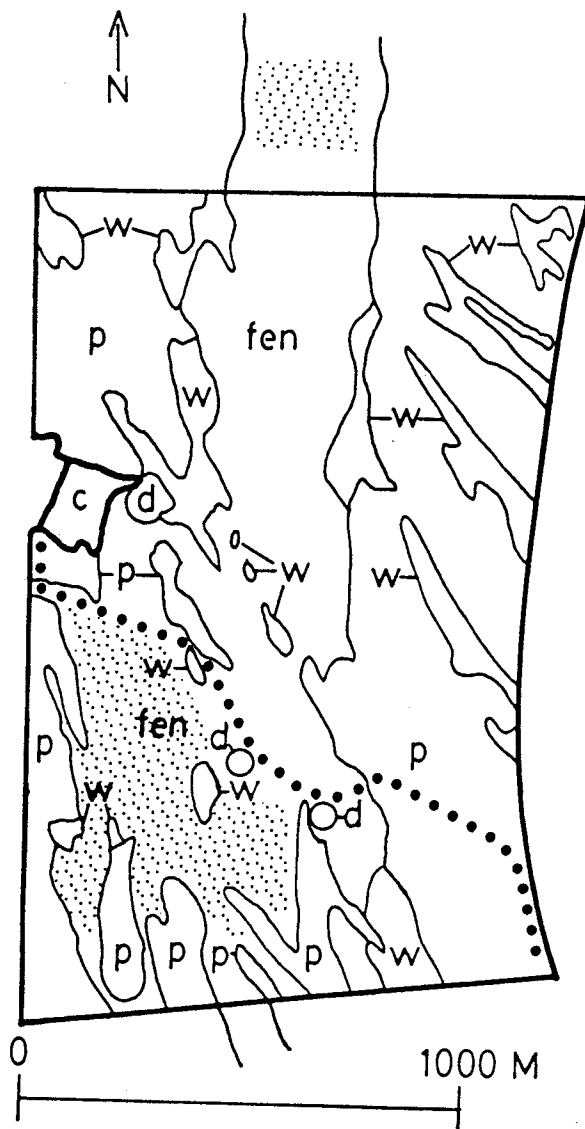


Figure 4. Vegetation cover types in the Waterhen wood bison site. Map is based on cover typing done by Don Forrester, Department of Natural Resources.



c = corral d = dugout p = poplar (aspen)
w = willow

— Fence
 .. Enclosure road
 ▨ Burned area

Carex fen community, dominated by water sedge (Carex aquatilis Wahl) (Figure 4). Aspen (Populus tremuloides Michx.) communities dominate ridges, but small stands of jackpine (Pinus banksiana Lamb), black spruce (Picea mariana [Mill] BSP), white spruce (P. glauca [Moench] Voss), and paper birch (Betula papyrifera Marsh) are present. A partial list of plant species in the area is given in Appendix B.

The study site drains north into Waterhen Lake. A road running across the main sedge fen divides it into north and south halves. Prior to mid-July 1984, a beaver dam blocked the drainage of the fen, creating a higher water level on the north side of the fen relative to the south side. After mid-July, the dam was removed and the north fen allowed to drain. The drop in water level was considerable, but still remained relatively higher on the north side. Water levels were significantly different between July and August in all areas (Table 1; an F-test was first performed to meet requirements for t-tests).

Table 1. Mean surface to substrate water depths (cm \pm S.D.) in 1984. A significant difference ($P < 0.05$) from July in an F- or t-test is indicated by "F" or "T", respectively.

WATER LEVEL	TREATMENT	JULY DEPTH	AUGUST DEPTH	SIG.
High	Unburned	22.5 \pm 2.37	16.1 \pm 2.39	T
High	Burned	24.2 \pm 3.05	8.11 \pm 4.00	F
Low	Unburned	13.8 \pm 3.15	6.31 \pm 2.80	T
Low	Burned	18.7 \pm 5.18	3.83 \pm 1.80	F

ANIMAL BEHAVIOUR STUDY

From late May to late August 1984, individuals or groups of bison were located at opportunistic times between dawn and dusk in the Waterhen enclosure. Total numbers of individuals by age-sex class, when distinguishable, and other parameters were recorded at 20 min intervals using the scan sampling technique (after Altmann 1974). Other parameters were activity, location, and habitat type. Temperature (in certain cases), cloud cover, and wind direction were also recorded.

Age-sex classes were defined as bull (mature male), cow (mature female), spikehorn (immature individual more than one year old of any sex), and calf (immature individual less than one year old of any sex). The sexes of spikehorns and calves could not be reliably determined. Behaviour categories were based on McHugh (1958) and included feeding (on forbs and burned or unburned sedges and grasses, hay, or other), licking salt, drinking, ruminating, resting, standing, alert, comfort movement, walking, dominance behavior, and playing. For the purposes of analysis, resting and ruminating observations were combined as resting behaviour. Habitat types, defined as open, edge, and closed and are further described in Appendix C. Temperature during each observation in June and July was measured using a hand-held "Fisherbrand" Thermometer #14-985-5B (-20° to 110°C). August temperatures were recorded on a Short and Mason #37

Temperature recorder (0° to 100°F) set in a Stevenson screen in an open area on the ground. Wind direction was estimated in cardinal terms (ie. north, south, east, etc.). Cloud cover was estimated as a percentage of sky covered. Climate and monthly temperatures and precipitation in the study period are given in Appendix D.

Observations of bison were made by eye or with 7X35 binoculars. Data were recorded onto a cassette tape recorder. Although the herd was habituated to human presence, observations were made usually from inconspicuous or concealed locations so as not to affect behavior. Sampling was stopped when vehicles or people suddenly approached the herd. Bison typically responded to an approach by flight to or from the cause. Sampling was resumed when the animal or animals appeared to behave "naturally". Every effort was made to sample in a location that afforded the best view of as many habitat types as possible.

In late May and in June, a total of 307 scan samples were taken during 25 days. May data were included with June data. The number of samples in a day ranged from 1 to 32 (mean \pm S.D., 12.3 ± 9.34), and the number of consecutive samples ranged from 2 to 17 (2.75 ± 3.08). In July, 361 samples were taken during 24 days. The number of samples taken in a day ranged from 1 to 33 (15.0 ± 9.49), and the number of consecutive samples ranged from 2 to 15 (3.72 ± 2.88). In August, 317 samples were taken over 19 days. The number of

samples per day ranged from 6 to 36 (16.7 ± 8.45), and the number of consecutive samples ranged from 2 to 28 (6.82 ± 6.76).

All data were transcribed onto MANTES files in the University of Manitoba (UM) Amdahl computer. Statistical chi-square (X^2) analyses were performed using APL (CONT program in the UM APL library) and SAS (TABLES) (SAS Institute 1982) programs.

Samples of bison feces not more than one day old were collected during the summer. A dropping more than one day old generally had a crust formed on the outside. A plastic spoon was drawn through the middle of each feces until about 30g were collected. Samples were opportunistically selected from bull, cow, and spikehorn feces. Calf feces were distinguishable by their shape and light tan colour and were not selected. Total samples collected were 35 over four days in June, 50 over five days in July, and 58 over five days in August. Samples were transported to Winnipeg (transit time of about 24hrs) and frozen. Ten grams of each sample collected within a month were composited into one sample for that month. Fifty grams of each composite were preserved with an equal volume of table salt and sent by airmail to the Composition Analysis Laboratory, Colorado State University, Fort Collins. The compositing procedures were done in March 1985, and results received in October 1985. Plant cuticle fragment composition by genera (and species,

in some cases) of each composite was determined using the methods described by Hansen et al. (undated). For each composite, 20 microscope fields per slide using 5 slides were analyzed. Holechek et al. (1982) identified differential digestibilities of forbs as a problem, but Reynolds et al. (1978) had acceptable results using this method to estimate proportions of food ingested by bison.

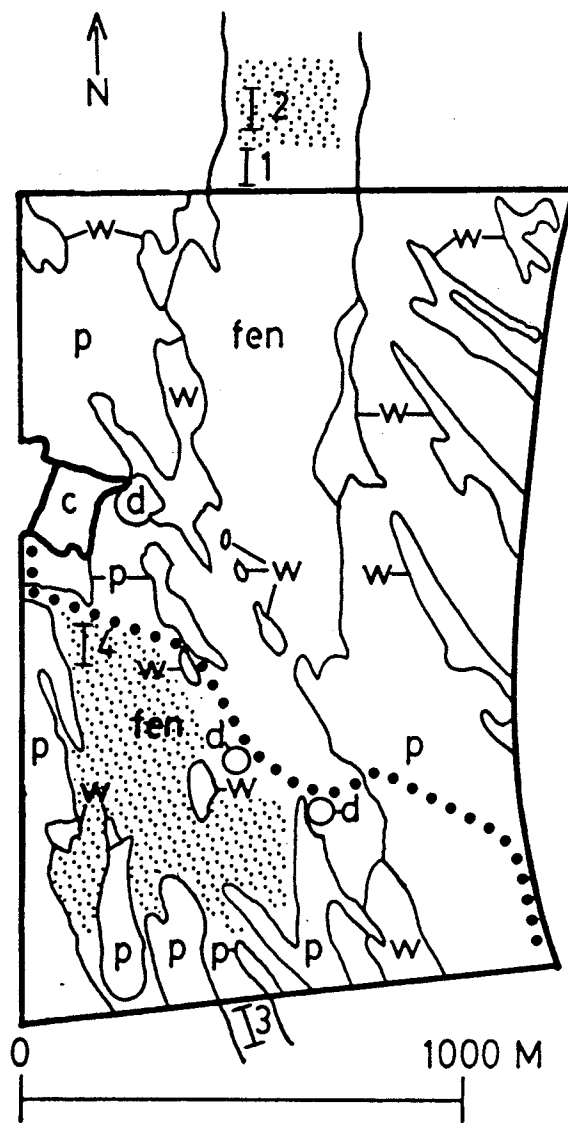
Mammalian nomenclature follows Banfield (1981), unless otherwise indicated.

VEGETATION STUDY

A high-water and a low-water fen were subjected to free-running headfires on April 1 and April 9, 1984, respectively, by DNR personnel. Spot burns of about 1ha were requested but the fires could not be controlled and larger areas were burned (Figure 4). Ice was still present on the fens.

Single unburned and burned fen transects were established in both high- and low-water level fens (Figure 5). June and July plots were 1m x 1/2m in size, except for June low-water burned plots, which were 1m x 1m. These latter plots had been sampled first, and large biomasses prompted smaller plot sizes in subsequent sampling. August plots were further reduced to 1/2m x 1/2m, again because of unexpectedly large biomasses. Forty-five to 50 plots per transect were sampled in the second weeks of June, July, and August. All

Figure 5. Location of vegetation transects.



1. HIGH-WATER LEVEL UNBURNED
2. HIGH-WATER LEVEL BURNED
3. LOW-WATER LEVEL UNBURNED
4. LOW-WATER LEVEL BURNED

plots with a transect were 2 m apart. Vegetation was clipped to about two cm above the water surface. Only current year's leaves and the immediate twig were clipped off birch and willow. Samples were shipped to Winnipeg (transit time of about 24hrs) and frozen, with the exception of August high-water samples, which were air-dried on-site. All samples were eventually oven-dried to between 60° and 70° C prior to analyses.

Total biomass of each plot in each transect was calculated. Ten random plots in each transect were sorted into C. aquatilis, Carex spp., and "other" plant species, and biomass determined. These "other" species are listed in Appendix B. These two sedge categories were used because C. aquatilis was the easiest to distinguish of the sedges. Each sedge type was analyzed for food quality (eg. one composite sample of C. aquatilis and one composite sample of Carex spp. was used for June high-water burned fen). Quality parameters were crude protein (CP), acid detergent fibre (ADF), calcium (Ca), phosphorus (P), Ca:P, and estimated total digestible nutrients (TDN; estimated from ADF). TDN can be converted to total digestible energy by multiplying TDN by 4.409 Mcal/kg-%. Ca:P was calculated from the Ca and P values provided. Quality of browse species was not examined because preliminary observations indicated little use of browse in the study site by the bison in summer. An explanation of quality parameters and analysis methods is given

in Appendix E. Vegetation was sorted and weighed to the nearest 0.1g between November and August 1985.

Biomass of each vegetation type was compared using t-tests on transformed data, as biomass does not have a normal distribution. Transformations were calculated using Taylor's Power Law and simple regression (Elliot 1977). To meet t-test requirements, an F-test was first performed to ascertain if the two samples were from the same population. If the F-test was significant, a t-test was not performed (Zar 1974). F-tests, t-tests, and simple regressions were performed using programs in the APL library, UM Amdahl computer.

Quality analyses were done by the Feed Analysis Section, Manitoba Department of Agriculture, and followed AOAC (1970) procedures. Quality analyses were performed between June and August 1985, and were compared using Wilcoxon's paired-sample test (Zar 1974).

The nomenclature of plant species follows Budd (1979) and Scoggan (1978).

RESULTS-ANIMAL BEHAVIOUR STUDY

FEEDING DIFFERENCES BETWEEN MONTHS

As indicated by feces analyses, grasses and sedges dominated the diet each month, with means of 84.47%, 98.00%, and 90.00% of all fragments in June, July, and August samples, respectively (Table 2). Carex spp. made up the largest means of any taxa, with respective monthly means of 69.13%, 87.17%, and 80.00%. Only two other taxa had major changes between respective months: Juncus, which averaged 6.20%, 2.07%, and 2.68%; Salix, which averaged 8.33%, 0%, and 1.15%. In addition, Carex, Juncus, and Salix were the only taxa to exceed 5.00% composition at any time.

Diet, as indicated by fecal analyses, differed completely from the diet indicated by observed feeding behaviour, both in rank and relative change between months (Table 3). According to the observed feeding behaviour, the herd (bulls, cows, and spikehorns, collectively) grazed foods in different proportions between months during the summer ($X^2 = 817$, $df=8$, $P<0.001$; Figure 6). Forbs constituted the greatest proportion of foods taken each month, but were taken in significantly different proportions between months ($X^2 = 52.3$, $df=2$, $P<0.001$). In August, they shared dominance with un-

Table 2. Mean percent composition of plant fragments in bison feces. Means are based on counts of 20 microscope fields of five slides per month (ie. a total of 100 fields per month). Browse plants are indicated by (B), and hay-composing plants are indicated by (H).

PLANT	JUNE	JULY	AUGUST
Monocots			
<u>Agrostis</u> (H)	2.18	3.13	2.22
<u>Bromus</u> (H)	4.53	2.22	2.24
<u>Carex</u>	69.13	87.12	80.00
Grass seed and glume			.42
<u>Hordeum</u>	.88	1.00	
<u>Juncus</u>	6.20	2.07	2.68
<u>Koeleria cristata</u> (H)			.42
<u>Muhlenbergia</u>	.85	1.18	1.35
<u>Phragmites communis</u>	.70	.80	1.43
<u>Stipa comata</u> (H)		.28	
	84.47	98.00	90.76
Dicots			
<u>Cornus</u>		.27	1.30
<u>Fragaria</u>	1.48	.28	2.36
<u>Rosa</u>	.49		
<u>Rubus</u>		.67	
<u>Salix</u> (B)	8.33		1.15
<u>Shepherdia</u> (B)	.47		.88
<u>Spiraea alba</u>	3.98	.25	2.18
<u>Symphoricarpos</u>	.49		.49
<u>Trifolium</u>	.29		
<u>Vicia</u>			.88
Unknown forb		.53	
	15.53	2.00	9.24

Table 3. Food choices of the Waterhen wood bison herd.

"Observed" diet is expressed as percent of all individuals observed feeding that month (except calves). "Fecal" diet is from data given in Table 2. June results for both observed and fecal diet were based on data collected after June 10, 1984.

PLANTS	JUNE	N	JULY	N	August	N
<u>Observed</u>						
Forbs	58.42		58.92		45.15	
Grasses and sedges	10.39		19.91		49.83	
Hay	30.82		20.76			
Other	0.36	493	1.41	1132	3.98	1732
<u>Fecal</u>						
Forbs	6.24		2.00		6.72	
Grasses and sedges	76.91		90.99		85.53	
Hay	7.56		7.01		6.23	
Other	9.29				2.52	

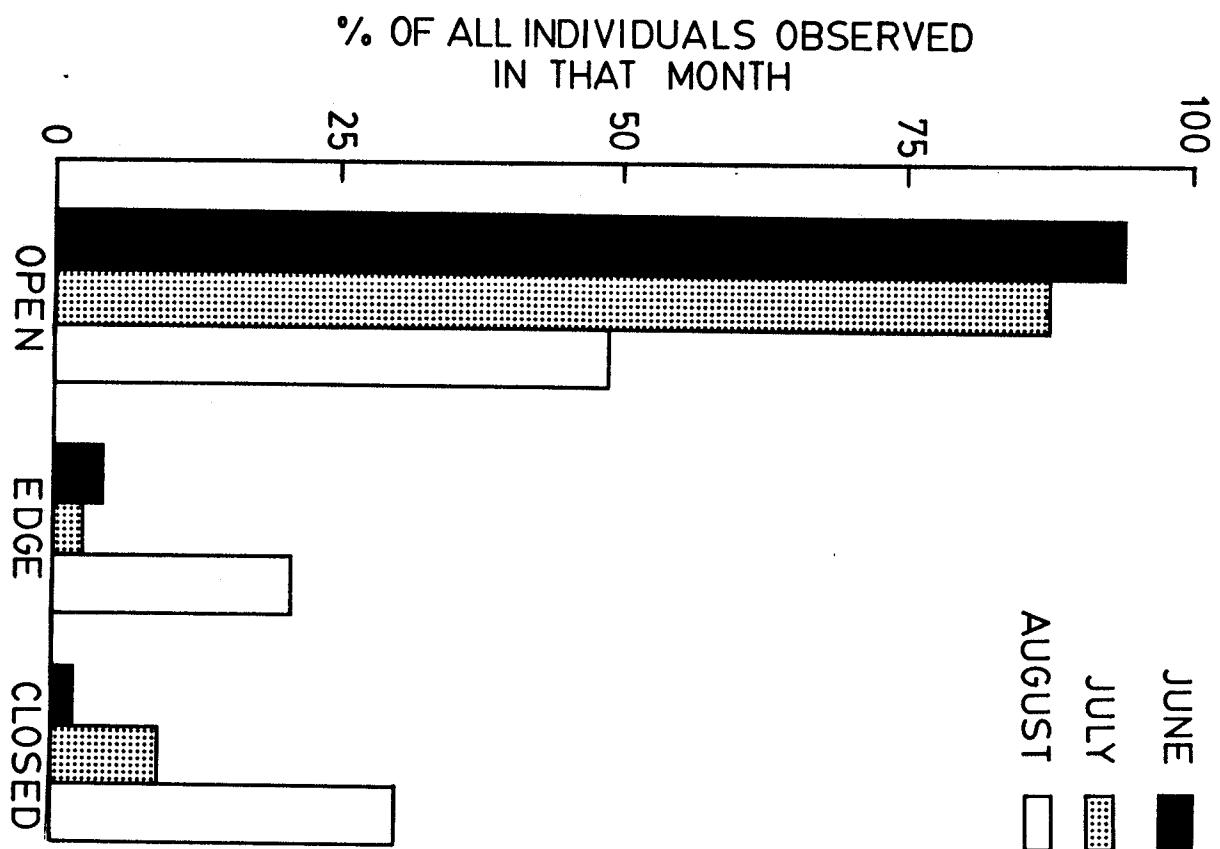
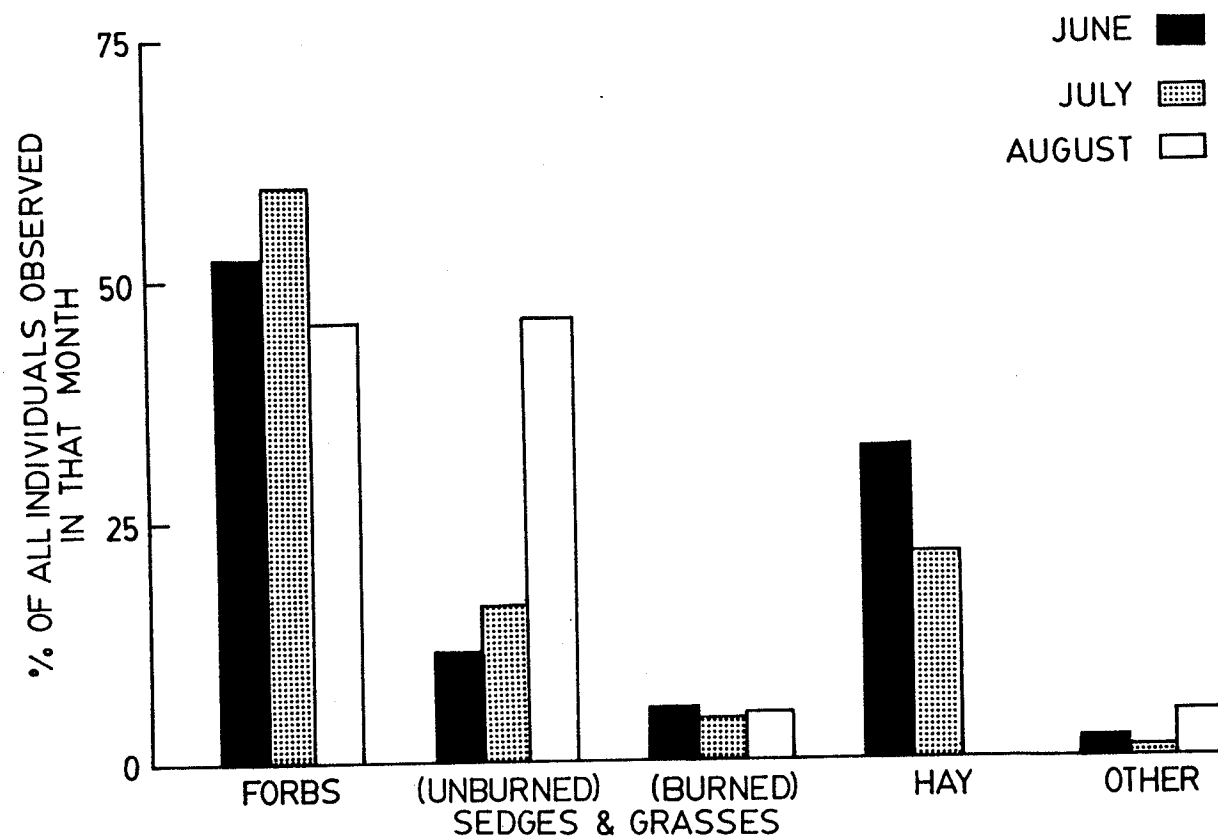


Figure 6. Observed herd food choices between months.
June N=493, July N=1132, August N=1732.



burned grasses and sedges (45.0% of all choices each). Hay decreased from 32.1% of all choices in June to 0% in August. In August, hay was eaten whenever brought to the herd in a truck, but was not used when foraging "naturally", that is, if the animal came across it during a feeding expedition, the hay was ignored. Burned grasses and sedges and other vegetation were taken in minor proportions of 5.3% or less.

Observed herd food choices between individual months were significantly different: June and July ($\chi^2 = 18.3$, $df=4$, $P<0.001$); June and August ($\chi^2 = 706$, $df=4$, $P<0.001$); July and August ($\chi^2 = 623$, $df=4$, $P<0.001$).

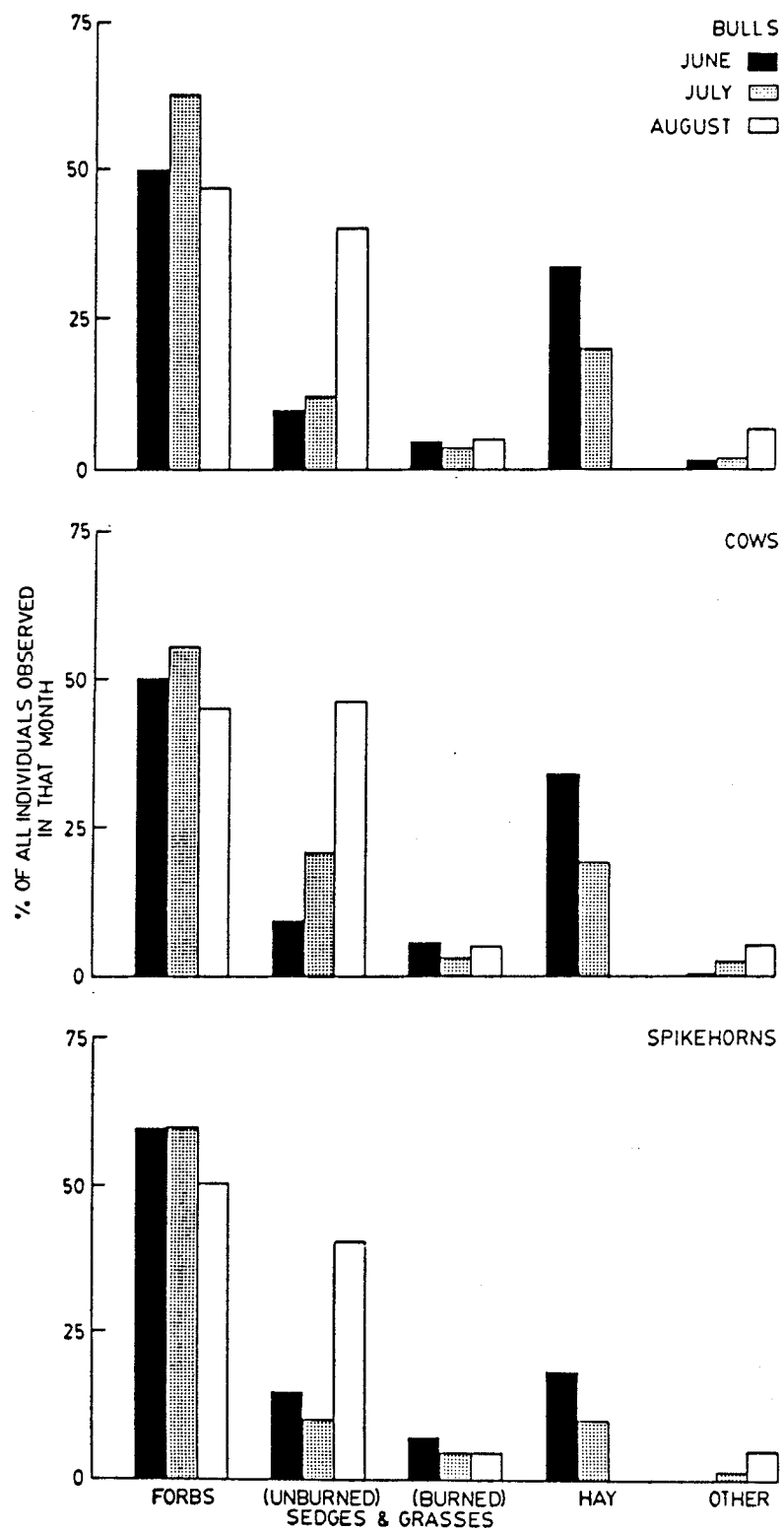
When food choices of each class were analyzed between months, bulls and cows had a similar trend in proportions of forbs used each month, although a significant difference existed between the two classes ($\chi^2 = 17.9$, $df=2$, $P<0.001$; Figure 7). Forb use by adults increased from June to July and dropped again in August. However, spikehorns consistently used forbs the most each month (60.0%, 60.0%, and 50.2%, respectively), and were the only class that decreased their take of unburned sedges and grasses in July (from 14.3% to 9.9%; Figure 7).

Figure 7. Observed age-sex class food choices between months.

Bulls: June N=222, July N=395, August N=516

Cows: June N=201, July N=473, August N=772

Spikehorns: June N=70, July N= 264, August N=444



OBSERVED FIRE-TREATED HABITAT PREFERENCES

Proportions of grasses and sedges taken each month by the herd differed significantly between burned and unburned types ($X^2 = 610$, $df=2$, $P<0.001$; Figure 6). The burned types consisted of 5.3% or less each month and were taken in similar amounts between months ($X^2 = 3.13$, $df=2$, $P=0.393$).

OBSERVED FEEDING DIFFERENCES BETWEEN CLASSES WITHIN MONTHS

In June, no significant differences in food choice between the three age-sex classes existed ($X^2 = 7.87$, $df=6$, $P=0.248$; Figure 8). In addition, each class was similar to the others: bulls and cows ($X^2 = 0.244$, $df=3$, $P=0.970$); bulls and spikehorns ($X^2 = 7.26$, $df=3$, $P=0.064$); cows and spikehorns ($X^2 = 6.48$, $df=3$, $P=0.091$). However, spikehorns tended to feed the least on hay ("dead" vegetation), compared to other classes.

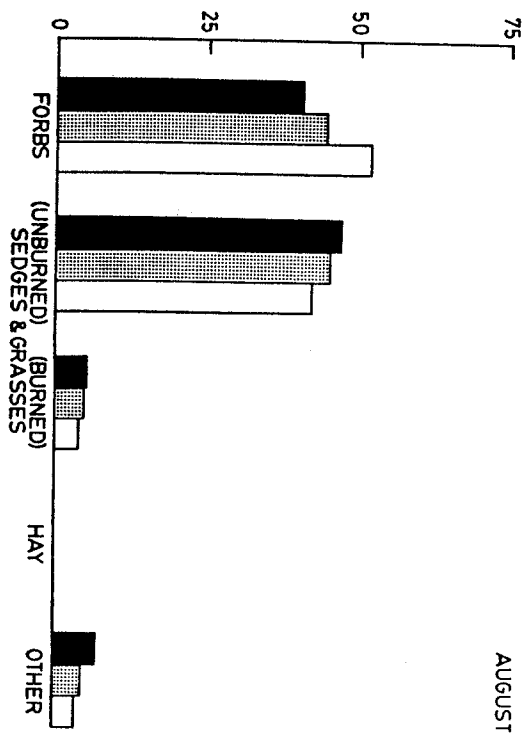
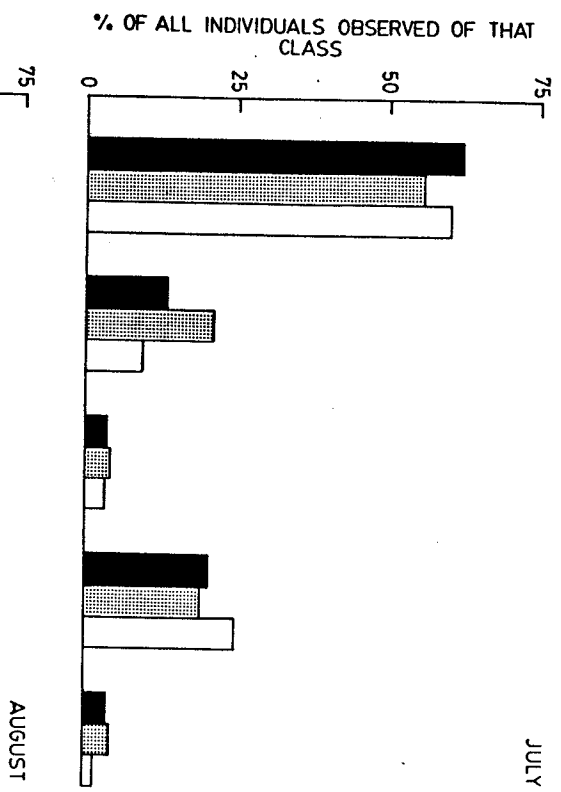
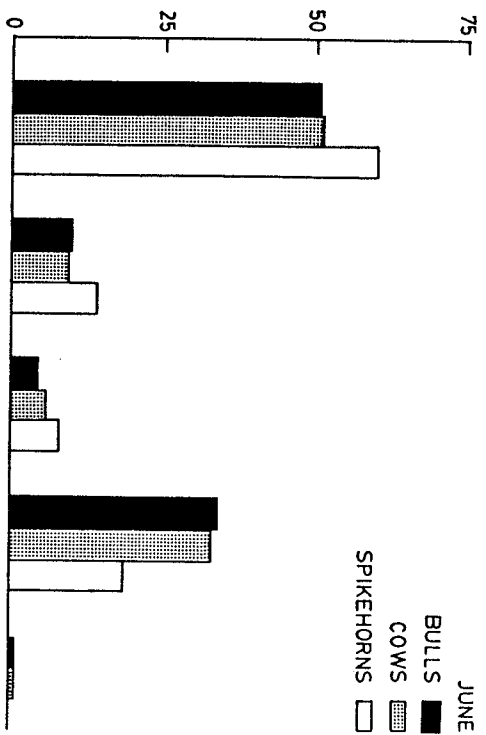
July feeding choices were significantly different between the three classes ($X^2 = 28.6$, $df=8$, $P=0.003$; Figure 8). Cows differed from bulls ($X^2 = 10.5$, $df=4$, $P<0.033$) and from spikehorns ($X^2 = 23.6$, $df=4$, $P=0.001$). Cows tended to feed more on grasses and sedges (burned and unburned together) than bulls and spikehorns combined, although forbs still dominated. Bulls and spikehorns did not differ significantly ($X^2 = 7.93$, $df=4$, $P=0.094$).

Figure 8. Observed monthly food choices between age-sex classes.

June: Bulls N=222, Cows N=201, Spikehorns N=70

July: Bulls N=395, Cows N=473, Spikehorns N=264

August: Bulls N=516, Cows N=772, Spikehorns N=444



The proportions of foods taken in August were similar between the three classes ($\chi^2 = 9.52$, $df=6$, $P=0.147$; Figure 8). Comparisons between individual classes showed no difference between bulls and cows ($\chi^2 = 1.94$, $df=3$, $P=0.585$) nor between cows and spikehorns ($\chi^2 = 4.37$, $df=3$, $P=0.224$). Bulls and spikehorns were, however, significantly different, ($\chi^2 = 9.15$, $df=3$, $P=0.027$). A large proportion of the difference was attributed to the use of forbs. Bulls grazed them 41.3% of the time and the spikehorns' 50.2%.

OBSERVED RESTING HABITAT CHOICES

Proportions of resting habitats chosen by the herd differed significantly between the three months ($\chi^2 = 1663$, $df=4$, $P<0.001$; Figure 9). June and July were the months with bulldog flies present. Each month was significantly different from the other: June and July ($\chi^2 = 252$, $df=2$, $P<0.001$), June and August ($\chi^2 = 1352$, $df=2$, $P<0.001$); July and August ($\chi^2 = 994$, $df=2$, $P<0.001$). Open habitats were preferred in June and July (95.3% and 88.3% respectively), but dropped drastically in August (48.6%). In August, edge and closed habitats accounted for 21.0% and 30.4%, respectively, of all choices. Each age-sex class showed a similar pattern in habitat choice over these months (Figure 10).

Analyses of resting habitat choices in June showed a significant difference between the three classes ($\chi^2 = 15.2$, $df=4$, $P=0.004$; Figure 11). Bulls were similar to cows (χ^2

Figure 9. Herd resting habitat choices between months.

Calves are not included.

June N=3058, July N=4359, August N=1207.

RESULTS-VEGETATION STUDY

BIOMASS

In overall review of the monthly biomass of each plant group, high-water (unburned and burned) and low-water unburned transects increased continuously, whereas the low-water burned fen stabilized after July (Table 4). Sedges began to senesce by August.

The June biomass ($768 \text{ kg/ha} \pm 264$, mean \pm S.D.) of the unburned fen with high-water level differed from the burned fen ($1208 \text{ kg/ha} \pm 278$, $t=8.262$, $df=98$, $P<0.001$). Low-water unburned and burned transects appeared to have similar biomasses ($407 \text{ kg/ha} \pm 142$ and $409 \text{ kg/ha} \pm 250$, respectively), but no statistical comparison was done because the two transects had different plot sizes. Biomass of vegetation from low-water unburned fen was different from that of the high-water unburned ($t=9.112$, $df=98$, $P<0.001$). High-water burned fen had a greater biomass ($1208 \text{ kg/ha} \pm 278$) than low-water burned ($409 \text{ kg/ha} \pm 250$), although a t-test was not performed.

In July, biomass ($1894 \text{ kg/ha} \pm 312$) variance of the high-water unburned fen differed from the high-water burned fen ($2082 \text{ kg/ha} \pm 476$, $F=4.449$, $df=48,48$, $P<0.001$). Mean biom-

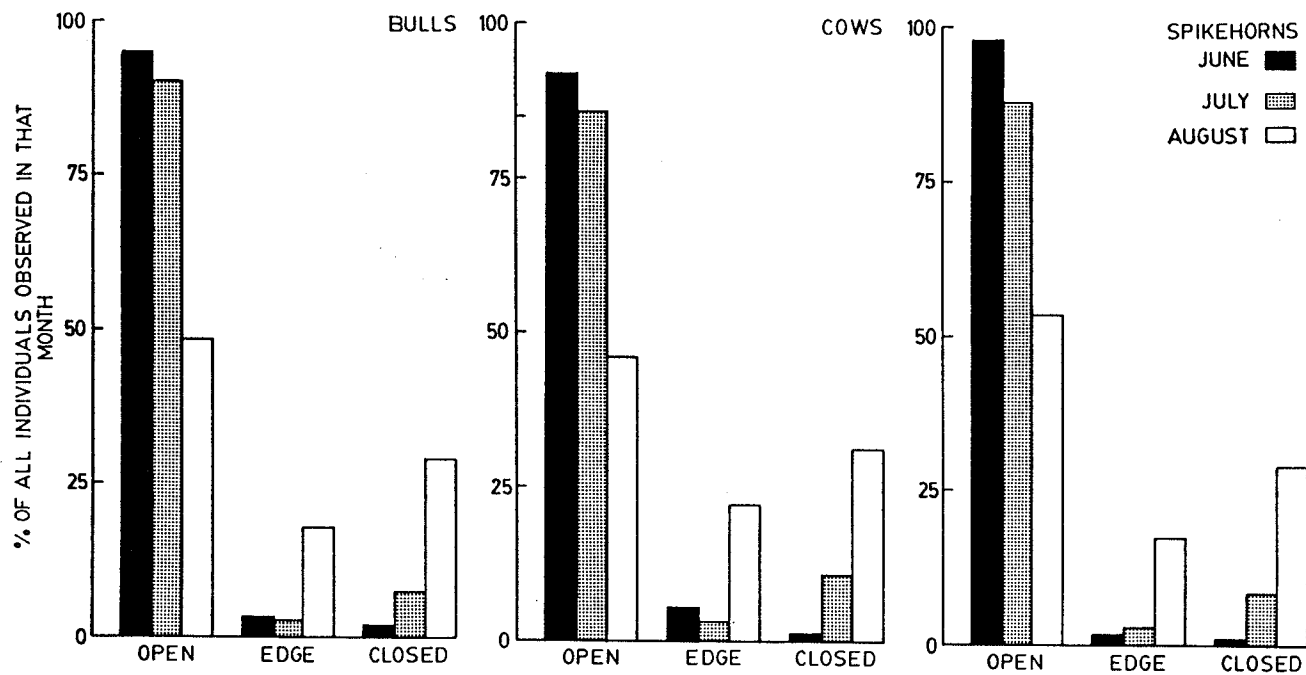


Figure 10. Age-sex class resting habitat choices between months.

Bulls: June N=1191, July N=1643, August N=411

Cows: June N=1258, July N=1899, August N=583

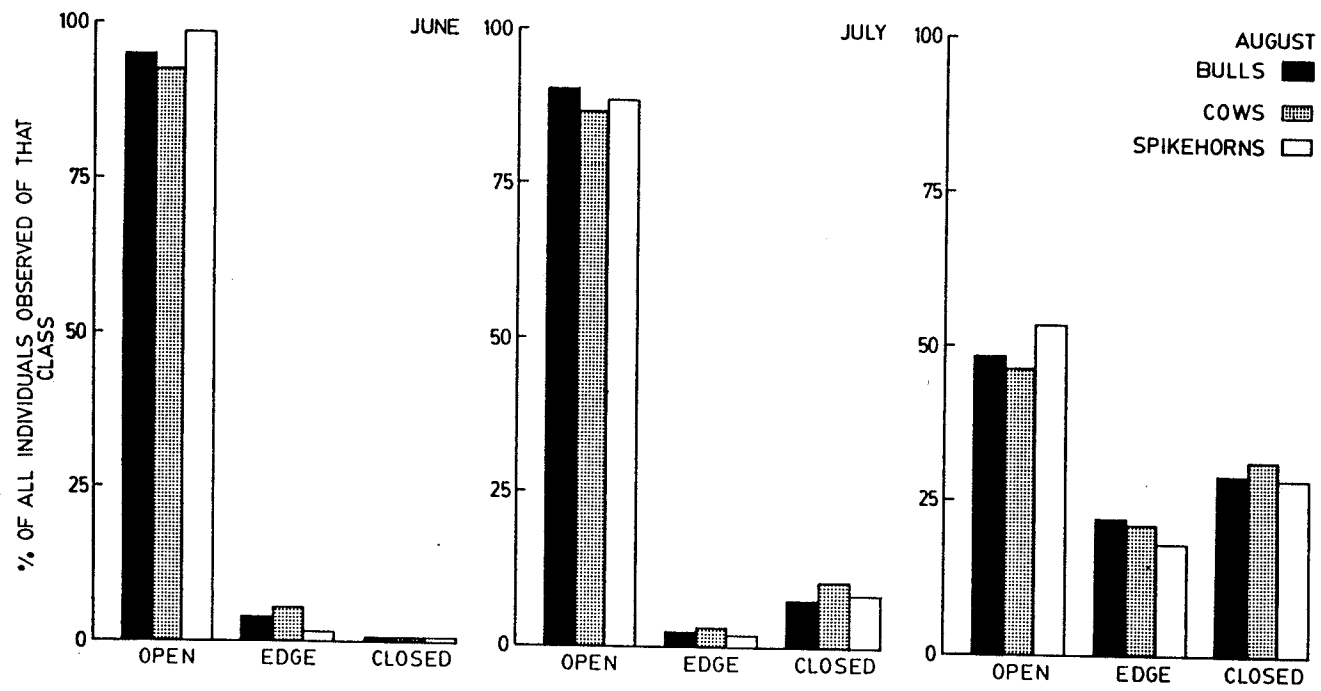
Spikehorns: June N=585, July N=817, August N=213

Figure 11. Monthly resting habitat choices between age-sex classes.

June: Bulls N=1191, Cows N=1283, Spikehorns N=584

July: Bulls N=1643, Cows N=1899, Spikehorns N=817

August: Bulls N=411, Cows N=583, Spikehorns N=213



=3.04, $df=2$, $P=0.219$). Spikehorn choices differed significantly from bulls ($X^2 = 6.75$, $df=2$, $P=0.034$) and from cows ($X^2 = 14.6$, $df=2$, $P<0.001$), as spikehorns used the open habitats more than the other two classes.

A significant difference existed between classes regarding resting habitat choices in July ($X^2 = 12.4$, $df=4$, $P=0.015$; Figure 11). Bulls used the greatest proportion of open habitats (90.0%) and were significantly different from cows ($X^2 = 11.9$, $df=2$, $P=0.003$). Spikehorns were intermediate in proportions used and were similar to bulls ($X^2 = 1.36$, $df=2$, $P=0.507$) and cows ($X^2 = 2.80$, $df=2$, $P=0.246$).

August resting habitat choices between all three classes were similar ($X^2 = 3.47$, $df=4$, $P=.483$; Figure 11). Each class was similar to the other: bulls and cows ($X^2 = 0.625$, $df=2$, $P=0.732$); bulls and spikehorns ($X^2 = 1.82$, $df=2$, $P=0.404$); cows and spikehorns ($X^2 = 3.08$, $df=2$, $P=0.215$).

An interesting observation was that, of all classes, cows consistently chose open habitats the least each month. When compared to bulls and spikehorns combined (into one class), use of open habitats was similar between months ($X^2 = 4.48$, $df=2$, $P=0.239$). Cows used closed areas during July and August more than did both bulls and spikehorns (combined into one class) despite the two months being similar ($X^2 = 0.038$, $df=1$, $P=0.862$). Closed habitats were virtually unused in June (<1.00% for each class).

RESULTS-VEGETATION STUDY

BIOMASS

In overall review of the monthly biomass of each plant group, high-water (unburned and burned) and low-water unburned transects increased continuously, whereas the low-water burned fen stabilized after July (Table 4). Sedges began to senesce by August.

The June biomass ($768 \text{ kg/ha} \pm 264$, mean \pm S.D.) of the unburned fen with high-water level differed from the burned fen ($1208 \text{ kg/ha} \pm 278$, $t=8.262$, $df=98$, $P<0.001$). Low-water unburned and burned transects appeared to have similar biomasses ($407 \text{ kg/ha} \pm 142$ and $409 \text{ kg/ha} \pm 250$, respectively), but no statistical comparison was done because the two transects had different plot sizes. Biomass of vegetation from low-water unburned fen was different from that of the high-water unburned ($t=9.112$, $df=98$, $P<0.001$). High-water burned fen had a greater biomass ($1208 \text{ kg/ha} \pm 278$) than low-water burned ($409 \text{ kg/ha} \pm 250$), although a t-test was not performed.

In July, biomass ($1894 \text{ kg/ha} \pm 312$) variance of the high-water unburned fen differed from the high-water burned fen ($2082 \text{ kg/ha} \pm 476$, $F=4.449$, $df=48,48$, $P<0.001$). Mean biom-

Table 4. Current year's biomass (kg/ha) in the Waterhen sedge fens. Figures in brackets were calculated using N=10 random plots from that transect. Statistical analyses were based on transformed data (described in the text). A significant difference ($P < 0.05$) from the burned or high-water transect in that month is designated by "a" or "b", respectively.

WATER LEVEL & TREATMENT		JUNE			JULY			AUGUST		
(SPECIES)		mean	sd	N	mean	sd	N	mean	sd	N
		(% of mean)			(% of mean)			(% of mean)		
HIGH UNBURNED		768	264	50	1894	312	49	2852	660	45
(C. aquatilis)		(78.1)			(63.2)			(76.1)		
(Carex spp.)		(19.9)			(27.1)			(24.1)		
(Other species)		(2.00)			(9.80)			(0)		
HIGH BURNED		1208	278	50 a	2082	476	49 a	2896	776	50
(C. aquatilis)		(93.1)			(90.8)			(84.8)		
(Carex spp.)		(6.40)			(7.25)			(3.54)		
(Other species)		(0.60)			(1.95)			(11.6)		
LOW UNBURNED		407	142	50 b	1170	306	49 b	1672	408	49 b
(C. aquatilis)		(80.1)			(56.3)			(56.1)		
(Carex spp.)		(16.6)			(21.2)			(23.9)		
(Other species)		(3.30)			(22.5)			(20.2)		
LOW BURNED		409	250	49	1420	276	50 ab	1504	294	49 ab
(C. aquatilis)		(51.6)			(19.0)			(18.0)		
(Carex spp.)		(23.8)			(74.2)			(74.9)		
(Other species)		(24.6)			(6.80)			(7.10)		

asses of the two unburned transects ($1894 \text{ kg/ha} \pm 312$ and $1170 \text{ kg/ha} \pm 306$, high- and low-water, respectively) also differed ($t=12.116$, $df=97$, $P<0.001$). Biomass variances of the two burned transects ($2082 \text{ kg/ha} \pm 476$ and $1420 \text{ kg/ha} \pm 276$, high- and low-water, respectively) were different ($F=2.147$, $df=49,48$, $P=0.004$).

In August, mean biomass ($2852 \text{ kg/ha} \pm 660$) of the high-water level unburned transect was similar to the high-water burned transect ($2896 \text{ kg/ha} \pm 776$, $t=0.176$, $df=93$, $P>0.50$), but the low-water unburned and burned differed ($1672 \text{ kg/ha} \pm 408$ and $1504 \text{ kg/ha} \pm 294$, respectively; $t=2.124$, $df=98$, $P=0.025$). The two unburned transects differed ($t=10.465$, $df=92$, $P<0.001$) as did the two burned transects ($t=13.168$, $df=97$, $P<0.001$).

Percent biomass composition by species was variable (Table 4) and statistical analyses were not performed because of the low sample size and high variability. Composition was similar during only 2 of 3 months in each transect type (eg. high-water unburned, high-water burned, etc.). The largest discrepancy between the three months was in the low-water burned type: June composition was 51.6% C. aquatilis, 23.8% Carex spp., and 24.6% other species. Respective July and August compositions were 18% and 19% C. aquatilis, 74.2% and 74.9% Carex spp., and 6.8% and 7.1% other species. Of the two water levels, high-water always had the greatest C. aquatilis proportions. When this water level was delineated

by treatment, the unburned transect had a smaller proportion of C. aquatilis than the burned. Conversely, the low-water unburned transects had greater C. aquatilis proportions than burned transects.

CRUDE PROTEIN (CP)

The CP content of C. aquatilis in the four transect types dropped from a range of 10.7%-12.0% dry matter weight in June to 7.2%-8.5% in July (Figure 12). CP levelled out by August, with the range being 6.7%-8.2%. High-water level burned fen consistently had the lowest values each month, and the other three varied in relative rank. Carex spp. samples had a similar trend in CP, but relative ranks of transect types varied each month. The June range was 11.4%-13.4%, the July range was 6.8%-8.1%, and the August range was 6.4%-6.8%.

The CP content of sedges from burned transects was greater than that of unburned transects even though the latter dominated in 9 of 12 comparisons (Table 5). When examined at the species level, unburned transects had CP contents greater than or equal to burned ones for both C. aquatilis and Carex spp. samples. Low-water sedges were greater than high-water sedges, and C. aquatilis had contents greater than or equal to Carex spp. Species differences were not affected by fire treatment or water level.

Figure 12. Crude protein content of sedge samples. Values are expressed as % dry matter weight (%DMW).

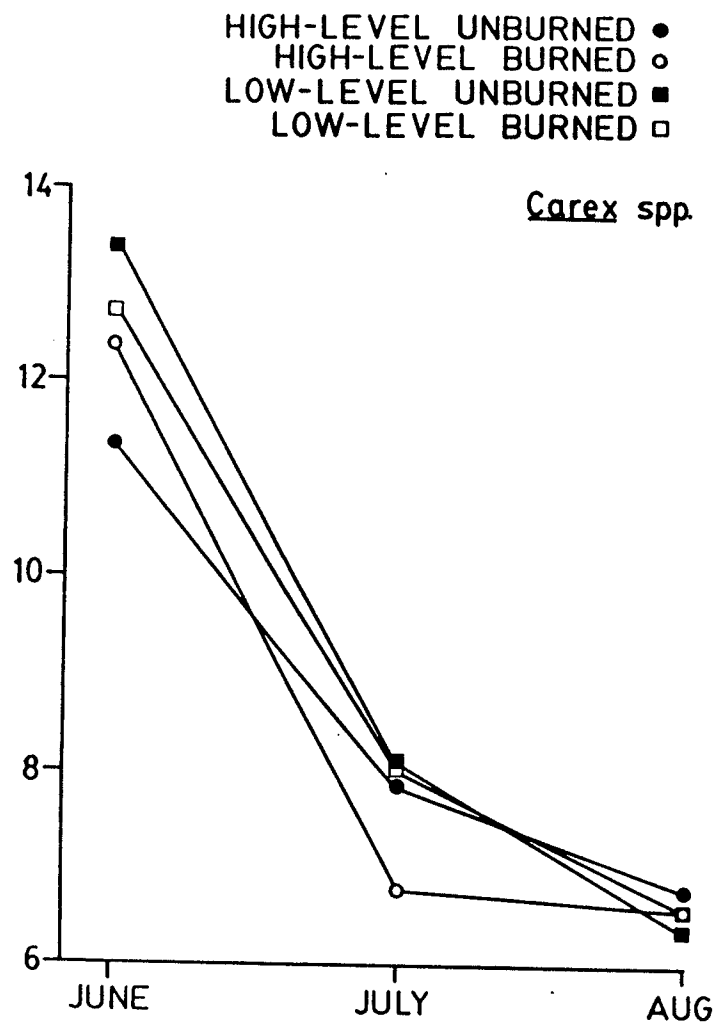
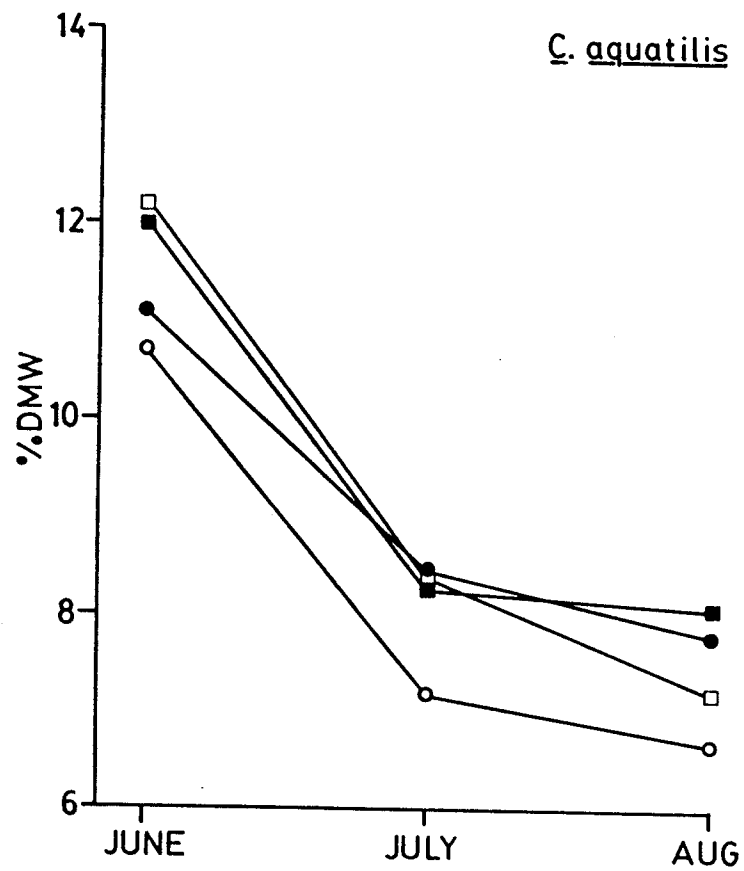


Table 5. Comparison of CP content of sedge samples. *-indicates a significant Wilcoxon T. x-indicates the comparison was affected by irregular differences (see "Discussion- Quality Parameter Analysis").

VARIABLES COMPARED	N	T	PROB a(1)
Unburned and Burned	12	14.5	0.03 *x
<u>C. aquatilis</u> only	6	3.0	0.10
<u>Carex</u> spp. only	6	5.0	0.20
High- and Low-Water	12	3.5	<0.01 *
<u>C. aquatilis</u> only	6	1.0	0.04 *
<u>Carex</u> spp. only	6	0.0	0.03 *
<u>C. aquatilis</u> and <u>Carex</u> spp.	12	32.5	>0.25
Unburned only	6	8.0	>0.25
Burned only	6	10.5	>0.25
High-water only	6	8.0	>0.25
Low-water only	6	9.5	>0.25

ACID DETERGENT FIBRE (ADF)

ADF content of C. aquatilis samples increased each month in all but one of the transects (Figure 13). Relative ranks changed each month. Analyses of June transects gave a range of 42.6%-43.1% dry matter weight, July had a range of 45.0%-47.6%, and August had a range of 46.2%-51.2%. ADF of Carex spp. samples had trends similar to C. aquatilis over the summer, but greater June and August ranges and a similar July range. June ADF ranged from 41.0%-44.6%, July was 45.9%-47.2%, and August was 47.2%-54.0%. Carex spp. in low-water unburned and high-water burned did not level out by August. Relative ranks of Carex spp. samples varied each month, but August ranks were the same as C. aquatilis.

ADF of sedges from unburned transects was greater than or equal to those from burned transects. (Table 6). When high-water and low-water levels were compared, high-water samples were greater than or equal to low-water samples. However, when only C. aquatilis samples were analyzed, high-water was still greater even though it dominated in only 2 of 6 comparisons. When species were compared, C. aquatilis was greater than or equal to Carex spp.. However, when only low-water samples were tested, Carex aquatilis was statistically greater even though it dominated in only 2 of 6 comparisons.

Figure 13. Acid detergent fibre content of sedge samples.

Values are expressed as % dry matter weight (%DMW).

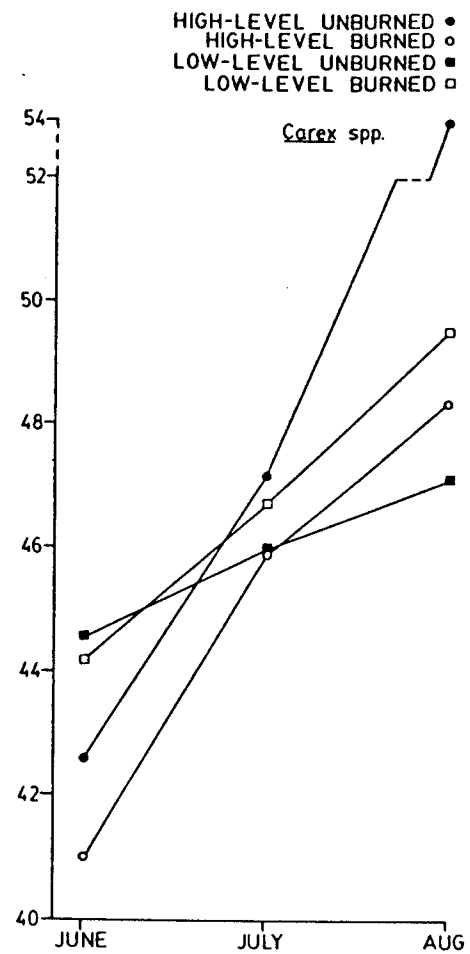
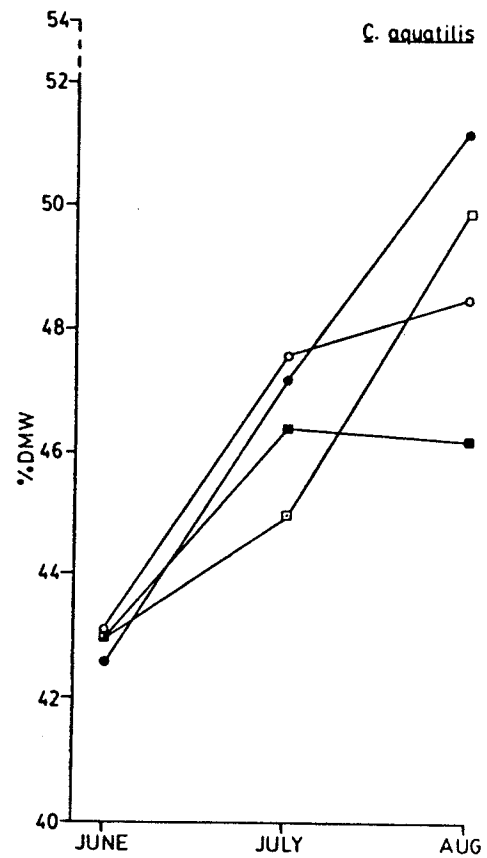


Table 6. Comparison of ADF content of sedge samples. *-indicates a significant Wilcoxon T. x-indicates the comparison was affected by irregular differences.

VARIABLES COMPARED	N	T	PROB a(1)
Unburned and Burned	11	21.5	0.20
<u>C. aquatilis</u> only	5	5.0	>0.25
<u>Carex</u> spp. only	6	7.0	>0.25
High- and Low-Water	11	35.0	>0.25 x
<u>C. aquatilis</u> only	5	5.0	>0.25
<u>Carex</u> spp. only	6	8.5	>0.25 x
<u>C. aquatilis</u> and <u>Carex</u> spp.	11	19.0	0.15
Unburned only	5	3.0	0.18
Burned only	6	8.0	>0.25
High-water only	5	9.0	>0.25
Low-water only	6	3.0	0.10 x

TOTAL DIGESTIBLE NUTRIENTS (TDN)

The TDN is inversely proportional to ADF content. TDN of C. aquatilis, therefore, decreased from June to August in three transect types (Figure 14). The June range was 55.0%-55.8% dry matter weight, July was 52.9%-54.1%, and August was 50.0%-53.3%. Relative ranks by TDN were generally inverse to ADF ranks in the same month. TDN of Carex spp. samples were also inversely related to ADF and range trends were similar to ADF trends: June range was 54.0%-56.8%, July range was 52.6%-53.5%, and August range was 48.0%-52.7%. Relative ranks were generally the inverse of ADF ranks.

Sedges from unburned transects had TDN values greater than or equal to burned ones (Table 7). However, when only Carex spp. samples were used, unburned ones were still greater than or equal to burned, despite the latter dominating in 4 of six comparisons. High-water transects were greater than or equal to low-water ones, although both dominated in 3 of 6 comparisons when C. aquatilis samples were compared. When species were compared, C. aquatilis had TDN values greater than or equal to Carex spp. When species were examined using only high-water samples, C. aquatilis was still statistically greater despite dominating in only 1 of 6 comparisons.

Figure 14. Total digestible nutrient content of sedge samples.
Values are expressed as % dry matter weight (%DMW).

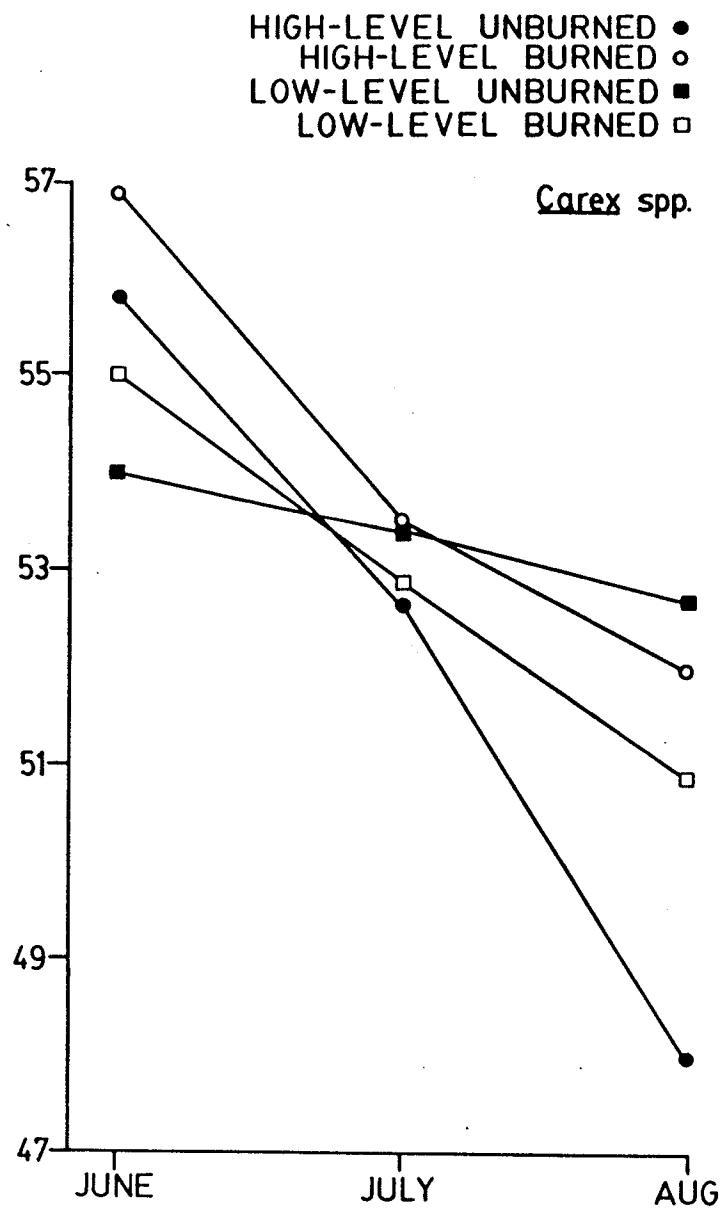
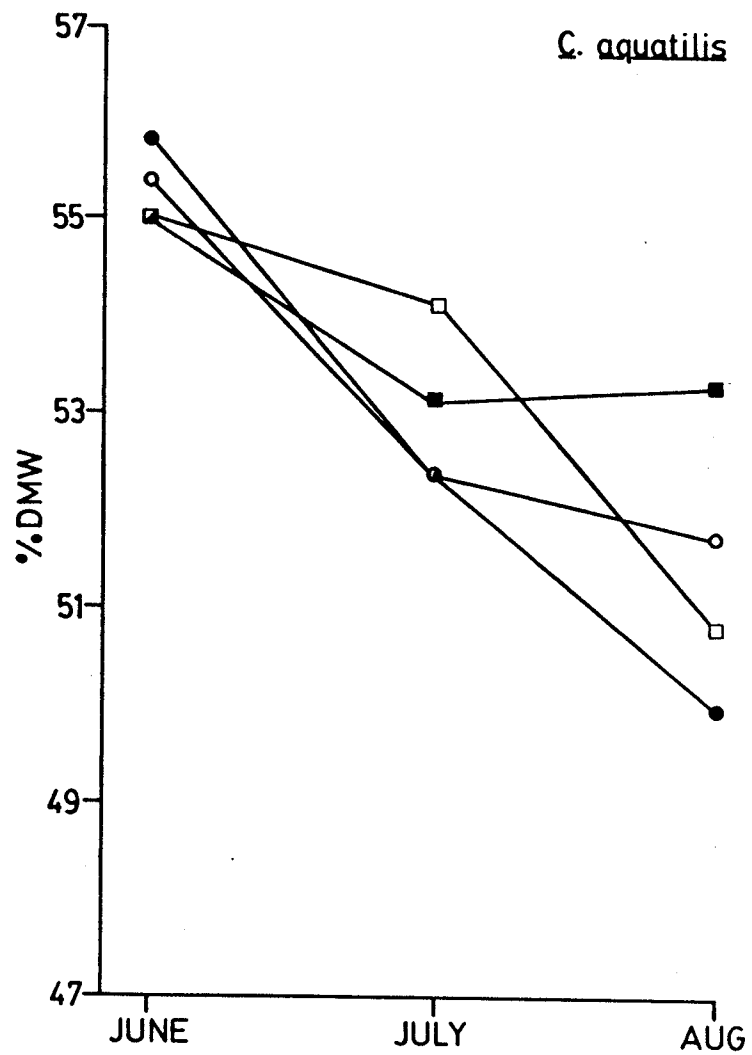


Table 7. Comparison of TDN content of sedge samples. *-indicates a significant Wilcoxon's T. x-indicates the comparison was affected by irregular differences.

VARIABLES COMPARED	N	T	PROB a(1)
Unburned and Burned	10	19.0	0.23
<u>C. aquatilis</u> only	4	5.0	>0.25
<u>Carex</u> spp. only	6	6.0	0.25 x
High- and Low-Water	12	39.0	>0.25
<u>C. aquatilis</u> only	6	7.5	>0.25 x
<u>Carex</u> spp. only	6	8.0	>0.25
<u>C. aquatilis</u> and <u>Carex</u> spp.	9	25.0	>0.25
Unburned only	6	7.5	>0.25
Burned only	6	8.0	>0.25
High-water only	4	6.0	>0.25
Low-water only	5	3.5	0.18

CALCIUM:PHOSPHORUS (CA:P)

The Ca:P ratio increased from June to August in each transect (Figure 15). Ranges of Ca:P for C. aquatilis samples were 0.77-1.50 in June, 1.39-2.00 in July, and 2.33->4.60 in August. Carex spp. ranges were 1.00-1.75 in June, 2.22-4.20% in July, and <0.05->6.20 in August.

Sedges from unburned transects had ratios greater than or equal to burned transects (Table 8). High-water transects were greater than or equal to low-water transects. Carex spp. had greater Ca:P ratios than C. aquatilis.

Increases in Ca:P are the result of increases in %Ca dry matter weight and/or decreases in %P dry matter weight between June and August (Figure 16). Changes in % composition were greater for P than Ca in 6 of 8 transect types.

Figure 15. Ca:P ratios of sedge samples. Values are derived from %DMW Ca:%DMW P.

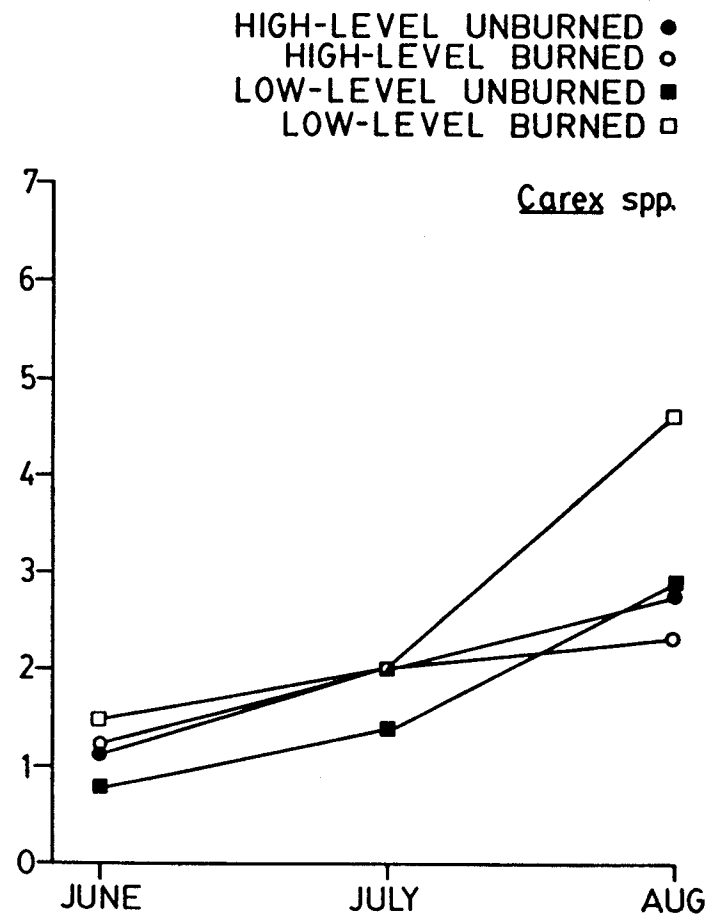
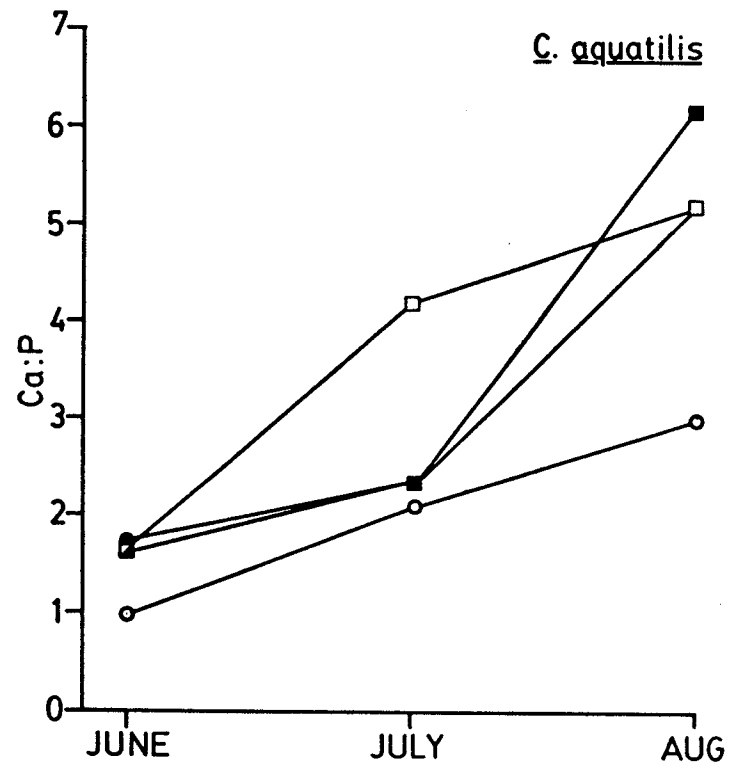
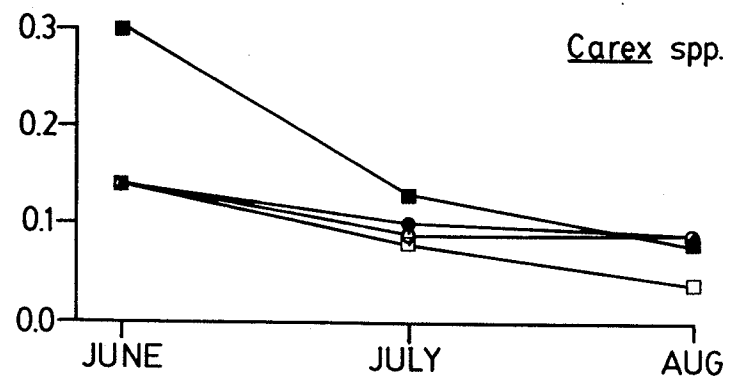
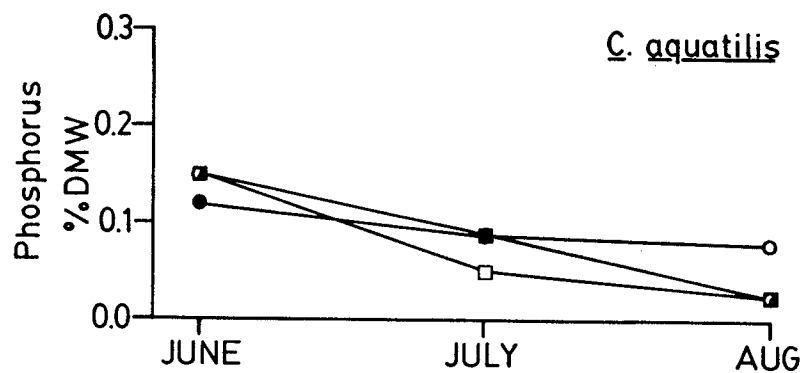
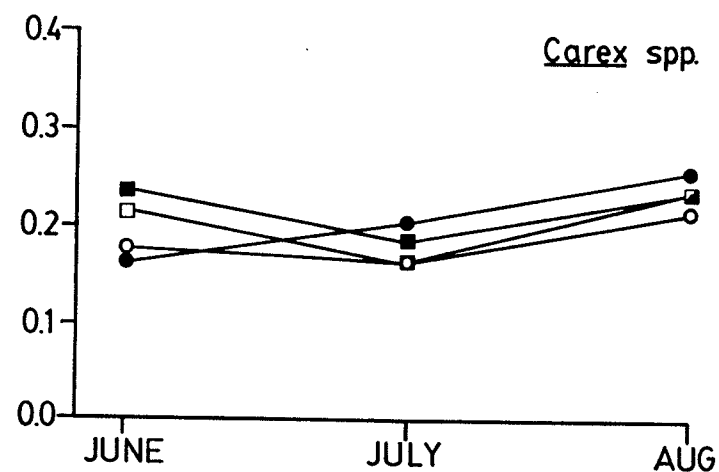
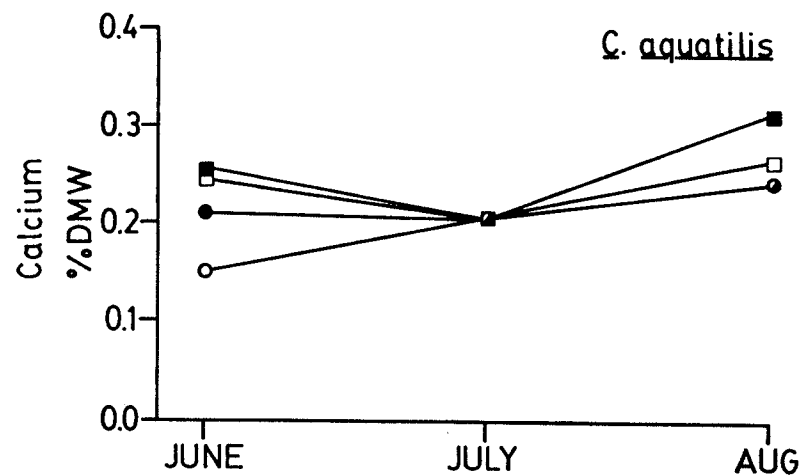


Table 8. Comparison of Ca:P contents of sedge samples. *-indicates a significant Wilcoxon T.

VARIABLES COMPARED	N	T	PROB a(1)
Unburned and Burned	11	31.5	>0.25
<u>C. aquatilis</u> only	5	2.0	0.10
<u>Carex</u> spp. only	6	5.0	0.20
High- and Low-Water	11	15.5	0.08
<u>C. aquatilis</u> only	5	7.0	0.25
<u>Carex</u> spp. only	6	3.0	0.10
<u>C. aquatilis</u> and <u>Carex</u> spp.	12	2.0	0.01 *
Unburned only	6	0.0	0.03 *
Burned only	6	2.0	0.05 *
High-water only	6	1.0	0.04 *
Low-water only	6	0.0	0.03 *

Figure 16. Calcium and phosphorus contents of sedge samples.
Values are % dry matter weight (%DMW).

HIGH-LEVEL UNBURNED ●
 HIGH-LEVEL BURNED ○
 LOW-LEVEL UNBURNED ■
 LOW-LEVEL BURNED □



CALCIUM (CA)

Ca concentration ranges for C. aquatilis were 0.16%-0.23% in June, 0.16%-0.20% in July, and 0.21%-0.25% in August. Ranges for Carex spp. were 0.15%-0.21% in June, 0.20%-0.21% in July, and 0.24%-0.31% in August.

Statistically, sedges from unburned transects had Ca contents less than burned transects, even though the former was greater in 9 of 12 comparisons (Table 9). When only Carex spp. samples were used, Ca content of unburned transects was statistically less even though they dominated in 5 of 6 comparisons. High-water transects were less than low-water ones, except when only C. aquatilis samples were compared. In that case, high-water was statistically greater even though both dominated in 3 of 6 comparisons. When species were compared, Carex spp. was greater than C. aquatilis. However, when only high-water samples were examined, C. aquatilis was greater, despite it being dominant in only 1 of 6 comparisons with Carex spp.

Table 9. Comparison of Ca content of sedge samples. *-indicates a significant Wilcoxon T. x-indicates the comparison was affected by irregular differences.

VARIABLES COMPARED	N	T	PROB a(1)
Unburned and Burned	11	5.0	0.01 *x
<u>C. aquatilis</u> only	5	1.0	0.08
<u>Carex</u> spp. only	6	2.0	0.05 *x
High- and Low-Water	12	16.5	0.05 *
<u>C. aquatilis</u> only	6	12.5	>0.25 x
<u>Carex</u> spp. only	6	1.5	0.04 *
<u>C. aquatilis</u> and <u>Carex</u> spp.	12	4.5	<0.01 *
Unburned only	6	0.0	0.03 *
Burned only	6	1.5	0.04 *
High-water only	6	3.5	0.13 x
Low-water only	6	0.0	0.03 *

PHOSPHORUS (P)

Phosphorus values for C. aquatilis were 0.14%-0.30% dry matter weight in June, 0.08%-0.13% in July, and <0.05%-0.09% in August. The range of values for Carex spp. samples were 12.0%-15.0% in June, 5.00%-9.00% in July, and <5.00%-8.00% in August.

The P contents of sedges from unburned transects were greater than or equal to those from burned transects (Table 10). High-water transects were greater than or equal to low-water transects. Samples of C. aquatilis were statistically less than Carex even though the former dominated in 8 of 12 transects. When only unburned transects were examined, Carex spp. was greatest even though it did not dominate in any comparisons.

Table 10. Comparison of P content of sedge samples. *-indicates a significant Wilcoxon T. x-indicates the comparison was affected by irregular differences.

VARIABLES COMPARED	N	T	PROB a(1)
Unburned and Burned	6	2.5	0.08
<u>C. aquatilis</u> only	4	0.0	0.10
<u>Carex</u> spp. only	2	—	—
High- and Low-Water	7	14.0	>0.25
<u>C. aquatilis</u> only	5	8.0	>0.25
<u>Carex</u> spp. only	2	—	—
<u>C. aquatilis</u> and <u>Carex</u> spp.	10	4.0	0.01 *x
Unburned only	6	0.0	0.03 *x
Burned only	4	3.0	>0.25
High-water only	5	1.5	0.06
Low-water only	5	1.0	0.08

DISCUSSION-ANIMAL BEHAVIOUR STUDY

FEEDING DIFFERENCES BETWEEN MONTHS

Fecal Analyses

The Waterhen wood bison herd used sedges as their main food as expected, according to the fecal analyses. Major differences in proportions of sedges were observed between months, and several possible explanations exist for this. These include plant phenology, habitat availability, and prior foraging experience.

Plant Phenology

The first influencing factor may have been the the phenological nature of plants. Stewart et al. (1976) showed in certain browse species that quality parameters (eg. crude protein) are generally highest at the leaf enlargement stage in June but decline somewhat by August. Chapin and Kendrowski (1983) had similar results with evergreen and deciduous taiga trees. The bison may have chose for this higher quality in the forbs during June and July. Bison at Colorado National Monument appeared to select forage with a high protein content year-round (Wasser 1977). Towards August, the quality would have decreased, causing the Waterhen animals

to use sedges. However, Looman (1983) stated that sedges can be quite nutritious. Crude protein content of beaked sedge (Carex rostrata Stokes), for example, can be up to 18% until midsummer. Crude protein of sedges within the enclosure were as high as 12.7% in June. Bison were, thus, still expected to eat sedges most often in June and July, and, in fact, they did. Forbs may have been selected in order to meet certain nutrient demands for that time of year. Lactating cows, especially, would require increased nutrient levels, as has been observed with lactating moose (Belovsky 1978). The increase in sedge and grass proportions in July may have reflected an end to the need for digestible forage. The bison would have used sedges most often by this point in time, so a drop in sedge and grass proportions in August may have reflected overgrazing. Sedges were available only at the fen edges and were quickly used up. This would cause the animals to switch back to the remaining forbs.

Habitat Availability

Habitat availability was one possible cause for greater forb use in June, relative to the rest of the summer. Travel through the fens was quite energy-demanding owing to the muskeg-like nature of this habitat. Borowski and Kossak (1972) suggested that European wisent (B. bonasus L., nomenclature from ibid) avoid marshy areas even though a rich supply of food may be there. On an occasion when the Water-

hen herd had to be baited across a fen with pelletized alfalfa (Medicago sativa L.), the animals followed the person with the bait only to the edge of the fen and refused to cross for several minutes. Clearly, they knew that the fen should be avoided.

On several occasions in mid April, the bison were observed to feed in the middle of the burned sedge fen. Young sedges began to emerge at that time and were easy to find because no litter was present to hide them. The fen itself was easy to walk on as the substrate below the shoot meristems was frozen. By May, the substrate lost its firmness and was difficult to walk over. As the water levels dropped and edges of the fen dried after mid-July, sedge use increased.

Prior Foraging Experience

Regelin et al. (in Thill 1984) and Bartmann et al. (1982) showed that lack of foraging experience did not influence diet selection by tame mule deer. Markgren (in Bartmann et al. 1982) showed tame moose calves to select diets different from wild moose. Neff (in ibid) stated that stress conditions could force wild deer to choose some forages undesirable to tame deer. Bartmann and Carpenter (1982) stated that tame deer need time to develop new feeding habits in new habitats. The amount of time is difficult to ascertain due to changes in individual preferences, plant

phenology, and plant availability. Bartmann et al. (1982) recommended using large numbers of deer and using animal conditioning prior to, and during a study, to minimize bias. Natural feeding preferences of the bison were probably not affected by the fact that many of the Waterhen bison fed on prepared or artificial diets prior to their relocation to the site (Appendix F). The herd may not have had enough time to get conditioned to the habitat and phenological events, but did graze sedges when available. They probably made these choices inherently or were able to determine palatability, as seen with mule deer (Krueger et al. 1974, Wallmo and Neff in Thill 1984, and Neff in Thill 1984). However, more work should be done to ascertain whether prior foraging experience affects bison diet selection.

Observed Behaviour

The diet indicated by feces analyses was completely different from the diet indicated by observed behaviour, both in rank and relative change between months. Grasses and sedges and hay, collectively, dominated each month in the feces, but observed behaviour showed them to dominate in August only. Their proportion increased from June to July and dropped in August in the feces, but increased from July to August only as indicated in the observed behaviour. This discrepancy has two possible explanations, including: a) time of sampling, b) amounts of biomass per bite in differ-

ent habitats, c) sample sizes, and d) sampling frequency. Therefore, unless animals are observed at all times of the day, and in every habitat, observations of feeding are not accurate indicators of diet. The first two explanations probably accounted for most of the discrepancies. Differential digestibilities between plants and inconsistent cuticle fragmentation in vivo were also factors (as discussed by Holechek et al. 1982). However, the great magnitude of difference between fecal and observed diets suggests that these two factors were minor ones.

Sample Times

Proportions of animals feeding increased greatly at dawn and dusk (Appendix G). Plains bison and captive wisent feed during the night (numerous authors in Cabon-Raczynska et al. 1983). Sampling is difficult in darkness, and only the initial and final stages of feeding were observed at dusk and dawn, respectively, for the first two months. Choice of habitat was limited only by accessibility, however, and not distance from resting areas. If the bison wanted to choose sedges if available, as they did later on in summer, they could have used them immediately at dusk or dawn. The duration and location of night feeding is still unknown but the animals, indeed, fed extensively on sedges as indicated by feces analyses, and this added greatly to the proportions of sedges observed to be taken in this study. Belovsky and

Jordan (1978) plotted an activity graph for moose showing feeding peaks at times very similar to those of the Waterhen herd (Appendix G). Brink's (1980) relationship between time of day and behaviour of plains bison and wisent resembles that of the Waterhen herd. Roath and Krueger (1982) noted that domestic cattle feed immediately after sunrise and immediately before sunset. If the Waterhen herd had the same evening feeding patterns as moose, then they fed for an additional 4 to 5 hours at night. A considerable proportion of the feeding schedule of bison had yet to be sampled.

Biomass Per Bite

A second major source of bias was the amount of biomass available to the herd in different habitats. As early as June, the aspen forest floor biomass was low. Forbs and browse had their highest use in that month possibly because of fen inaccessibility and/or plant phenology. The herd would have spent relatively more time searching for a scarce food source, and showed a lower rate of biomass per bite. This would cause the observational results to show a large amount of forbs consumed when, in fact, very little was taken. Collection time of forbs would have also increased. Greater search time per unit of food in depleted range has been documented for domestic heifers (Scarnecchia et al. 1985), wapiti, mule deer (Parker et al. 1984, Wickstrom et al. 1984, Hudson and Nietfeld 1985), and reindeer (Trudell and White 1981).

Sample Size

Sample size, or the number of animals observed in each scan sample, was affected by inherent herd size fluctuation. A larger group of grazing bison moved along much faster from one location to another than did a smaller group. Nelson (1965) noted this in a Utah herd. This may tend to increase the diversity of foraging habitats, species, and locations, and hide true diet preferences. However, the number of animals per sample per habitat may be equal for few animals spending a long time in one habitat and for many animals spending little time in the same habitat: this would nullify any differences between large and small group sizes when data are pooled. This does not preclude obtaining as many samples on as many different days in as many different habitats as possible, of course. Social facilitation plays a role in feeding behaviour: in the enclosure, a single bison feeding usually attracted other individuals to that feeding place and numbers of animals feeding in one habitat gradually increased. No analyses were done to determine if a feeding rate difference existed in one feeding habitat between a large and small group size per sample per habitat.

Fluctuation may have been caused by sex, relating to the fact that male bison tend to form smaller herds separate from the mixed or matriarchal herds (cows, calves, and spikehorns; Soper 1941, Fuller 1966, Reynolds et al. 1982). A small group of animals is harder to locate in initial

search efforts than a large one, and a lack of data on male groups may weight overall herd habits in favour of mixed groups. The Waterhen bulls occasionally exhibited this behaviour, but usually stayed with the matriarchal group. The reason for males joining the matriarchal group may be related to horsefly attacks. Duncan and Vigne (1979) showed that horse (Equus sp.) group size increases during tabanid season. The rate of tabanid attack per individual decreases with increasing group size. Thus, a bison may attempt to reduce its own probability of attack by getting into a larger congregation.

Fluctuation was also caused by different visibility in different habitat types. Sampling in two different habitats produced two different sample size frequency distributions (Appendix H). Observations in open habitats produced a distribution with more large groups than in closed habitats (aspen forest, in particular). Only animals close to the observer could be sampled within the aspen, leaving the unseen, more distant individuals unaccounted for in the sampling, and possibly in other habitat types. Therefore, the results of forage selection may have been over-inflated towards foods in aspen communities. A good observation position was often difficult to find due to disturbance towards the moving bison by the observer and towards the observer by the herd.

Sample Frequency

The 20 min intervals used between sampling were adequate, as the herd's behaviour was more or less dominated by two lengthy behaviour activities: feeding and resting. The total number of sampling days was adequate because the range the bison used was relatively small (2.59 km^2). Most of the areas could potentially be visited by the herd many times over the sampled days, and any differences in locations and habitats within the month would be noted. In other words, if the animals were in a much larger area, no change in observed location may have been due to size of the range rather than to choice by the herd. In such a case, more sampling days would be required.

Sampling of behaviour on more days with rain was desired. Daily activity patterns on rainy days was different from non-rainy days. This is further discussed in "Daily Feeding Activity Cycle".

The number of samples taken in total for each month was adequate, as the bison had enough time to visit all types of habitats within the range.

Other Observations

Even though forbs were used the least as food (as seen in fecal samples), changes in use of aspen habitat may have, indeed, reflected habitat (as opposed to feeding) preferenc-

es. The consistently high proportions of forbs in the observed spikehorn diet may have been caused by selection for more digestible forage or for cover. A theory for selection of more digestible forage is based on Geist's (1982) proposed foraging strategy for wapiti calves, and Willms and McLean's (1978) theory for juvenile mule deer. The calf or juvenile would graze more digestible forage than adults because it has a relatively large surface:mass ratio, higher metabolic rate, and greater food requirements. However, as mentioned before, domestic bovid stomachs reach mature size by 6 to 9 months of age (Church and Pond 1974). Spikehorns were expected to use sedges when available, but their tendency to feed less on hay ("dead" vegetation) than adults still suggested a need for high quality or moisture content forage. Ideally, fecal analyses should be done on each age-sex class to identify their respective diets.

Spikehorns may also have been selecting for cover, rather than for food quality, resulting in a preference for the aspen forest. Spikehorns may be more susceptible to predation than full-grown adults, and may select for cover even though they are travelling with a herd. Aspen cover contains mainly forbs and shrubs which would be fed on. Cover selection was doubtful, however, as discussed later in the August "Observed Feeding Differences Between Classes Within Months".

Still another explanation for spikehorns' greater use of forbs is displacement. Sedges, a limited food resource, were

available only at the periphery of the fens and dominant adults may have displaced the spikehorns from the sedge patches. The spikehorns kept up with the herd, but would have spent relatively less time feeding on sedges and more on forbs. No surveys were taken of spikehorn position in the herd for this study, however.

OBSERVED FIRE-TREATED FEEDING HABITAT PREFERENCES

The extremely small use of burned habitat was undoubtedly due to inaccessibility, as the burned habitats were far into the sedge fen. The herd was observed feeding on several occasions in the burned habitat in late April, when the sedges were the only vegetation emerging in the area. At the same time, the substrate was still frozen and could support a bison. Early emergence is the reason for feeding in the burned areas at that time. Little evidence was found of the animals extensively using the middle of the fens from June to August.

OBSERVED FEEDING DIFFERENCES BETWEEN CLASSES WITHIN MONTHS

Observed behaviour was shown to be inaccurate in determining diets. Despite this, it may be useful in determining shifts in diet or shifts in habitat use. For this reason, plant choice differences between classes within months will be discussed.

Each of the age-sex classes except calves were expected to select sedges when available for forage, but to differ in relative proportions of each diet item. In June, any true differences in food choice between classes were masked by inaccessibility of the sedge fens, and decreased observation times. Spikehorns appeared to prefer "live" forage over hay, as they consumed live vegetation more than the other age-sex classes and hay the least. Geist's (1982) feeding strategy for wapiti calves may apply in this case (more digestible forage used due to greater food requirements). The hay was cut in the previous year and was probably less palatable than live forage. As discussed previously, selection for cover is another possible explanation for use of forbs. Most of the observed June feeding activity took place in closed aspen habitat (40.6% of all choices, Appendix I). Forbs are the most abundant forage in closed aspen communities and were used the most as a result. August results dispute cover selection, though, as discussed later.

Forbs remained the major observed forage of all classes in July. A few more sedge areas were available and were used, but high water levels still posed problems. Cows used sedges and grasses the most of all the classes (25.0%), and forbs the least (55.0%). This further suggests a separation of food choice between classes. Geist (1982) stated that wapiti bulls should not compete with mothers or prospective mothers and offspring. As proof, Dzieciowski (1969 in Geist

1982), showed that wapiti bulls use more fibrous forage than do cows. Bison may have used a reverse of the wapiti strategy in this case of limited availability: bulls allowed cows to feed on the fibrous sedges which were easier and less time-consuming to gather. Such a reversal seems unlikely, however.

Spikehorns used sedges and grasses the least of all the classes in July and hay the most, opposite to June's results. Displacement by adults from the sedge areas (a limited food resource) may have been a cause, as discussed in "Feeding Differences Between Months". Furthermore, August results suggest food niche separation by spikehorns not to be a factor, as discussed in the next paragraph. The lower use of sedges and grasses combined with a dwindling distribution of forbs would force the spikehorns to use more hay to supplement their diet. Hay supplied in July was freshly cut and was probably more nutritious than that left over from the previous year. Therefore, it would be more palatable.

Bulls and spikehorns were the only two classes that differed significantly in August. The spikehorns used predominantly forbs (50.2%) while the bulls used sedges and grasses the most (52.7%). Cows also took advantage of the more accessible sedges and grazed them 50.3% of the time. In light of this increase, spikehorns were probably not using a different feeding strategy in August. They used mostly sedges

as originally expected. Displacement from the sedge patches by dominant adults may have been the reason for lower relative sedge use compared to adults. Cover selection is disregarded because the majority of their feeding was in open habitats (41.9%) whereas bulls and cows used primarily edge habitat (39.2% and 39.0%, respectively; Appendix J).

OBSERVED RESTING HABITAT CHOICES

Differences Between Months

The dominance of open habitats chosen by the herd in June and July (95.3% and 88.3% of all choices, respectively) is attributed to extreme bulldog fly annoyance. S. Cantor (pers. comm.) captured over 8700 tabanids in a 24 hr period in July 1985. This was much more than the amount trapped by Hanec and Bracken (1964) in surveys around Manitoba. Tabanid activity was insignificant at Waterhen in August 1984 and 1985. Darling (in Collins and Urness 1982) and Collins and Urness (1982) noted that wapiti seek open habitats to escape tabanids. When the bulldog season ended at the beginning of August 1984 at Waterhen, habitat choices changed drastically. Edge and closed habitats together comprised a total of 51.5%, as compared to 4.7% in June and 11.7% in July. June, July, and August were hot months and the bison would absorb much solar radiation during the day. They should have sought shade in the edge and closed areas to prevent overheating. Bauer (in Stormer and Bauer 1980) postulated that

white-tailed deer spend more time in mature stands as the summer approaches because of the presence of fewer biting insects or lower temperatures. This was not the case with the Waterhen herd, however, as choice was apparently dependent upon wallowing capability. Soper (1941) stated that a bison's primary source of relief from biting flies is wallowing in the dirt and dust, although Reinhardt (1985) found no evidence for this. McHugh (1958) observed bulls to use established wallows most of the time; at the Waterhen site, disturbed ground such as that in the corral and on the road simulate established wallow conditions. While these places are much windier than closed habitats, wind has a minimal effect on tabanid activity (Burnett and Hays 1974) and is ruled out as a choice factor. Smaller biting flies (eg. mosquitoes and black flies) were present in August at Waterhen, but no obvious changes in their abundance were observed over the summer, and their effect on the bison was not known.

In South America, Sheppard and Wilson (1977) found that, up to 237m from the woods, female tabanid activity was greater than in the woods. Activity was greatest at the woods' edge. At Waterhen, the precise degree of tabanid activity in and away from the aspen was not known. However, activity seemed greater in the open areas. Again, one wonders why the bison did not remain in the forest. A plausible explanation is given by Duncan and Vigne (1979), who stated that herding reduces the incidence of fly attack on an ani-

mal. Bison may have found herding to be easier in the open, where they could see each other. Such behaviour is used by many gregarious ungulates for protection from carnivorous (as opposed to parasitic) predators.

The significant differences between June and July choices in all age-sex classes may have been the result of slightly decreased tabanid populations in July. Population sizes were not measured in this study, however.

Although all classes chose open habitats the most in June, spikehorns were the only ones that differed significantly from the others because of their higher use. Two explanations are put forth for this. Firstly, the spikehorns were somewhat less visible in the closed habitats due to their smaller size. This would weight observational frequencies in favour of open areas. Secondly, harassment by biting insects (bulldogs and others) may have affected them more than adults, causing them to seek the open areas for wallowing more often. Spikehorn comfort movements, such as scratching and wallowing, were used as an indication of harassment. Proportions of activity spent in comfort movements were significantly different between adults and spikehorns in June and July (Appendix K). Spikehorns exhibited comfort movements 3.1% of the time, and adults exhibited comfort movements 1.8% of the time. These results were opposite to those of Reinhardt (1985), who found that captive adult bison wallow more frequently than younger ones. He suggested

that this difference between age-classes was an effect of social status, and not insect annoyance. Only August behaviour of the Waterhen bison resembled that of Reinhardt's herd: no comfort movements by spikehorns were observed, and only 0.4% of all adult activities were comfort movements.

Cows tended to rest less than bulls in open habitats in July (93.8% of all choices), possibly due to risk of predation on their calves. This preference occurred in all months, but was significant from other classes only in July. The forest provides a hiding place from predators and Fuller (1966) thought that the trees could be used to crush attackers.

Bulls used open habitat in greater proportions in July (90.0% of all choices) than did cows (85.0%), causing these to be the only classes to differ significantly in habitat choice that month. Cows may still have chosen the thickest cover to protect calves. Spikehorns were intermediate between bulls and cows and were not significantly different from either, as in June. Lowered visibility and biting insect annoyance were possible reasons for these results.

No significant differences between any of the classes existed in August, but cows still tended to use open habitats the least of all classes (46.7% of all choices). Annoyance by biting insects (other than bulldogs) or selection for cover for calf protection were still possible explanations.

Use of open habitats by spikehorns may still have been caused by lowered visibility of the spikehorns during sampling or by insect harassment of the spikehorns

DAILY FEEDING ACTIVITY CYCLE

The daily feeding activity cycle of the Waterhen bison indicates that they were most active at dawn and dusk, and to lesser degree, at midday. As discussed in "Sample times", this cycle resembles that of moose most closely, as given by Belovsky and Jordan (1978), who suggested that thermal conditions limit feeding time. Feeding activity of the Waterhen herd appeared to be negatively related to air temperature (Appendix L). In addition, on nine occasions, rain fell at times when the bison were normally resting. In seven cases, the animals began to feed. Feeding during the hottest part of the day threatens an animal with over-heating. Wapiti and mule deer body temperatures increase with greater air temperatures (Parker and Robbins 1984), and would cause a increase in metabolism. An animal should not expend energy further by searching for food at this time.

Another factor related to air temperature and feeding was tabanid fly activity. A cessation in fly activity is associated with low temperatures (Burnett and Hays 1974), and may stimulate the bison to feed. The influence of tabanids is inferred by the large increase in the herd's feeding activity during the day in August, the month that few bulldogs

were present. S. Cantor (pers. comm.) and I observed similar behaviour by the herd during the summer of 1985. June was much cooler that year, and the bison exhibited diurnal feeding activity. Tabanid activity was also greatly reduced at that time. In July 1985, temperatures were similar to the previous year's, and both crepuscular feeding by the bison and tabanid activity increased. Howell et al. (1949) identified temperature and rainfall as the most important factors influencing tabanid activity. They also noted that wind velocities under 9 miles per hour did not affect the flies. Knorre (1959) associated an increase in summer diurnal feeding of moose with a decrease in tabanid fly and gadfly (Sephenomyia ulrichi) activity. The decrease in fly activity was concurrent with cold temperatures and increased rainfall. Collins and Urness (1982) also implicated fly activity in similar behaviour patterns of wapiti. Wapiti reduced feeding activity when tabanid numbers were high. However, Collins and Urness did not bring up the point that temperature may directly affect activity, and also stated (but did not actually prove) that their animals compensated for time lost during fly attacks by grazing more at dusk. S. Cantor (pers. comm.) stated that domestic cows do not compensate this way. Whether or not the Waterhen herd compensated is not known as evening activity could not be observed.

DISCUSSION-VEGETATION STUDY

BIOMASS

The larger biomass of burned to unburned fens during July and August were probably the result of earlier growth caused by litter removal, but not by nutrient availability. The unburned vegetation in the low-water type grew until the onset of senescence in late August. Nutrient flushes from the burns would also stimulated earlier growth, as observed by Hoffpauir (in Thompson 1982) and Thompson (1982). Significant nutrient flushes probably did not occur, as discussed in "Calcium" (below).

The biomass of vegetation from low- and high-water unburned fens differed during June, and may have been due to flooding of uplands. However, an increase in production probably did not happen, as Ca was most often lower in the high-level fen vegetation (discussed later). The water level in the high-water fen was actually lower in previous growing seasons. High-water would be expected to impede or delay solar warming, but this was probably a minor factor.

The biomass from low-water level unburned and burned transects appeared similar during June, even though the burned transect was expected to be greater because of earli-

er growth. The best explanation was that small differences in water depth may have existed between the burned and unburned transects. Such differences may affect growing conditions (nutrient availability, etc) and, in turn, affect growth. Another explanation was that the animals may have fed on the emerging shoots in the low burned fen in April. This would have caused an artificial decrease in biomass, and account for the similarity to the low unburned fen.

The preference of C. aquatilis for high-water levels has three possible explanations. Firstly, C. aquatilis may have initiated growth sooner. This would have caused its % composition to be initially high, and then relatively lower as other Carex spp. began to grow. This happened in all transects with the exception of the high-water unburned one. Secondly, small differences in water depth may favour one species over another. Jeglum (1973) and Leiffers (1984) noted the preference of C. aquatilis for deeper waters. Thirdly, sorting techniques may have been inaccurate, although every effort was made to keep sorting methods and parameters consistent. Plot size change would not have an effect on means, only on variances, as shown by Kershaw (1973).

Biomass differences between burned high- and low-water levels are influenced by the time of burning. The high-water fen was burned nine days prior to the low-water one, and, thus, would be subjected to earlier solar warming. This in

turn could cause an initially higher biomass in the high-level fen.

In August, growth was complete, and the biomass of vegetation from unburned and burned transects were similar. Unburned and burned reedgrass stands grow in a pattern like this (Thompson 1982). High- and low-water transects had dissimilar growth patterns by August. Biomass of vegetation in high-water unburned fen increased greatly up to August, whereas that from low-water unburned fen slowed by July. Both should have slowed at the same time. This brings up a factor that involves changing water levels: the drop in water level between July and August in the high level exposed more of the plants for clipping. Plants were clipped at positions relative to the water surface, rather than to the soil surface. Therefore, as water level dropped, a larger proportion of the plant was taken (than would have been at a higher water level), and biomass was inflated. Comparisons were not possible.

STATISTICAL ANALYSIS OF QUALITY PARAMETERS

Wilcoxon's paired-sample test is used for nonparametric analysis of data where one sample is correlated to another. It is differences between these correlated samples that are tested (Zar 1974). Wilcoxon's test was used to examine quality parameters of sedges in this study.

A short-coming of the Wilcoxon test is that, in one-tailed tests, the probability of getting a significant result increases when d (the difference between two samples) equals zero, even when the data obviously has no significant result. So when there are several d 's equalling zero, the test becomes invalid for these comparisons (Conover 1971). One example of this occurring is with comparisons of P between C. aquatilis and Carex spp. using unburned transects only (see "Results- Phosphorus"). A second short-coming occurs with ties in differences. Ties, or several d 's of the same absolute value, causes acceptance of the null hypothesis when it is not true (Conover 1971). An example is the comparison of TDN between high- and low-water transects for C. aquatilis samples only (see "Results- Total Digestible Nutrients").

In view of these short-comings, the discussion of quality parameters is based upon general comparisons (as opposed to statistical comparisons) between treatments.

CRUDE PROTEIN (CP)

A drop in CP of C. aquatilis occurred in all transects after growth and seed production in June. N-fractions decline because of hydrolysis and amino acid translocation. Mineralization and leaching-out also occur, but these are less important than translocation (Chapin and Kendrowski 1983). N and P were observed to decrease with age in reed

stands (Bailey and O'Neill 1972). Sedges from high-water burned fen always had the lowest CP values because they possibly matured earlier and, as a result, decreased in CP content sooner. Early maturation follows earlier growth start, as was evident by the greater biomass in the high-water burned transect in June. Nutrient flush from ash is a low probability, as discussed below in "Calcium". Another possibility is that CP is always low following a spring fire, and early maturity was not the only factor affecting CP. Samples were not taken before June, so peak CP period was not known for sure. In addition, burned transects had CP values lower than unburned transects in August, as would be expected if they matured earlier. Overall relative rank fluctuation over the months cannot be adequately explained by treatments, and may have been further affected by sample degradation during transport to Winnipeg. Quality analysis procedures were assumed to be alike for each batch and ensured by quality control.

A drop in CP was also observed with Carex spp. samples. Overall, high-water burned transect values were never greater than low-water burned transects, suggesting earlier maturation or decreased values due to water level status.

ACID DETERGENT FIBRE (ADF)

As the more digestible parts of the plant degrade after maturation, fibre would be expected to make up a larger proportion of the tissue. This pattern occurred in both C. aquatilis and Carex spp. over the summer. Relative ranks were the same between species only in August. ADF in unburned transects was generally greater, but this was related to species: C. aquatilis was less affected by fire than was Carex spp. Carex spp. unburned fen vegetation had greater ADF's, suggesting that burning caused them to mature sooner than C. aquatilis. Furthermore, ADF is affected by species-type between high- and low-water levels: low-water had larger values only with Carex spp. samples. By the same token, Carex spp. had the greatest ADF values when compared to C. aquatilis only in low-water levels in unburned situations. Carex spp. may, thus, mature sooner in low unburned transects. Sampling from before June was desired to describe entire ADF patterns over the season. This would have confirmed if ADF differences were the result of treatment or of species.

TOTAL DIGESTIBLE NUTRIENTS (TDN)

Energy content of shoots, as estimated by TDN, dropped from June to August in both C. aquatilis and Carex spp., as expected. Peak TDN was not known for sure as samples were not taken before June. Total nonstructural carbohydrate

(TNC) content of C. lacustris shoots in central Minnesota peaked in mid-August at 224.5g/m² dry matter weight. TNC is an estimate of total energy available for plant growth. Translocation of carbohydrate reserves belowground occurred after this peak (Roseff and Bernard 1979).

Treatment by burning affected TDN of Carex spp. only. This could have been the result of Carex spp. maturing after C. aquatilis. The latter would have begun to lose energy reserves first, and had no difference in values between unburned and burned after June.

Water level affected TDN of Carex spp. only, suggesting that these sedges matures later in high-water levels, or that they accumulated more energy in these levels. If they matured later than C. aquatilis, they would have greater TDN values (as they did) because C. aquatilis began translocation and degradation already.

CALCIUM:PHOSPHORUS (CA:P)

Increases in Ca:P from June to August related to gains in Ca and, primarily, losses of P. Similar situations occurred with sedges on Devon Island (Muc 1977) and with Hamamelis virginiana in Ohio (Boerner 1985). Ca is a highly immobile plant tissue element and P is a highly mobile one. P is translocated in plants (Chapin and Kendrowski 1983) and is also readily returned to the environment nutrient pool by

decomposition and leaching (Muc 1977). Church and Pond (1974) recommended a Ca:P of 2.00 for domestic cattle forage. The high values found in Waterhen sedges in June are contrary to this recommendation. No concern should be raised, however, as bison (and all other North American ungulates) have existed in P-deficient range. More research is required on the physiology of P use in bison to ascertain true needs and requirements.

Results indicated that burning had little effect on C. aquatilis Ca:P, but caused Carex spp. to have higher Ca:P values. What effect burning had directly on seasonal Ca:P ratios cannot be properly concluded as sampling was not done before June. Microhabitat differences affecting Ca and/or P of one or both sedge types would further alter the ratios. This subject is further discussed in "Calcium" and "Phosphorus".

Sampling before June would pinpoint the dates of greatest Ca and P contents and allow conclusions pertaining to maturity to be made. Thompson (1982) suggested that differences in mineral composition between unburned and burned reed stands were due to differences in phenology.

High-water had some effect on Ca:P, but most comparisons showed the same values for high- and low-water. Carex spp. had a definite dominance over C. aquatilis in Ca:P, suggesting either that time of maturing was dependent upon species,

or that Ca:P was always greater in Carex spp. The ratio was influenced by the high frequency of high Ca values and the low frequency of high P values in Carex spp. Once more, the effect of the different treatments cannot be properly ascertained because no samples were collected before June.

CALCIUM (CA)

Burn treatment of the Waterhen fens resulted in lower Ca content in sedge samples from those fens. However, these plants should have had a greater Ca content (from excess Ca released from ash) or an equal content (from maximum assimilation potential for that mineral) throughout the summer. This is explained by the fact that Ca is relatively immobile in plants (Chapin and Kendrowski 1983). The discrepancy has two possible explanations. First, the ash may have been lost to the air, as ice still covered the water, and, second, Ca from ash was bound up by organic or inorganic factors in the water.

Carex spp. accumulated Ca more when growing in a low-water fen, suggesting a preference for this habitat. Also, Carex spp. always had a greater Ca content than C. aquatilis, indicating a greater assimilation potential.

PHOSPHORUS (P)

The burning of fens had little measurable effect on overall sedge P concentration. Phosphorus, like Ca, may not have been taken up by the sedges because ash was lost to the air or bound up in the water by organic or inorganic factors. Thus, early maturation would not be caused by excess P. Treatment, however, affected P at the species level. C. aquatilis had greater values than Carex spp. in every comparison. In the case of water level, high-water levels most often had greater P values simply because C. aquatilis had greater values most often .

The P compositions of the two sedge-types indicated that Carex spp. matured sooner only when burned. Then, after senescence, its dropping P content intercepted the drop of P in C. aquatilis, causing the two types to be similar.

CONCLUSIONS

Conclusions to Hypotheses

1. The proportions of plant species grazed by the Waterhen wood bison differed between months during the summer of 1984.

As indicated by fecal analyses, sedges and grasses dominated the diet in varying proportions each month. The bison may have altered diets in response to plant quality and availability.

Diets, as indicated by observed feeding behaviour, differed between months, but also differed from the diet indicated by fecal analyses. Observed herd feeding showed forbs to dominate each month, except in August when sedges and grasses made up an equal proportion. Possible explanations for the discrepancy included the effect of sample times, amount of biomass per bite in different habitats, and the sample size. Observation of feeding bison is not a good estimator of diet.

Observed feeding behaviour of each age-sex class between months showed both bulls and cows to have similar trends - a decrease from June to August in forb use and an increase in

sedge and grass use. Spikehorns grazed forbs the most each month. Possible explanations for their forb use included increased digestibility and displacement by adults.

2. Proportions of unburned and burned sedge fen used by grazing bison differed within months, according to observed behaviour. Burned habitats never made up more than 5.3% of the choices. Habitat inaccessibility was the cause.

3. The biomass of vegetation in burned high-water fens was greater than that in unburned high-water fens in June and July, and this was attributed to earlier growth caused by litter removal and not to nutrient flush from ash.

The biomass from the burned and unburned low-water fens differed in July only, when burned fen was greater. The similarity in June was attributed to environmental differences in sampling locations. The larger biomass in the burned fen in July was probably due to early growth.

4. The biomass of vegetation from high- and low-water level fens differed in June, July, and August. High-water fens always had a greater biomass, which was attributed to a preference by C. aquatilis for high-water levels.

5. Proportions of plant species grazed did not differ between age-sex classes in June. Habitat inaccessibility was the most likely reason. All three age-sex classes had different plant species choices in July, with cows differing

from bulls and spikehorns. Cows grazed mostly on grasses and sedges (the more abundant plant species), and the bulls grazed mostly on forbs (the less abundant plant species). In this way, competition between these two classes would be reduced. Bulls and spikehorns were the only classes to differ in plant choice in August, with bulls grazing mostly sedges and grasses and spikehorns grazing mostly on forbs. Spikehorns may have been displaced from feeding sites by adults, causing the former to graze other plants.

6. Forage quality parameters (which included CP, ADF, TDN, Ca:P, Ca, and P) varied according to burn treatment, water level, and species. Conclusions on quality parameters are conditional because sampling was not done all summer, and the variability of values was not established.

CP of C. aquatilis and Carex spp. dropped from June to August, as the plants matured and senesced. Early maturity was implicated for lower values of burned fen sedges, relative to unburned fen sedges, and high-water fen sedges relative to low-water sedges.

ADF increased over the summer, and the effect of burn treatment appeared dependent upon species. Carex spp. was more affected by burning, and had higher ADF's to suggest earlier maturing. In addition, low-water levels decreased Carex spp. ADF increased only in burned fen, probably caused by early maturation.

TDN dropped each month, and the effect of burn treatment was dependent upon species: Carex spp. TDN was generally greater in burned fens, but C. aquatilis was not affected. This may have reflected an early maturing of Carex spp. Likewise, only Carex spp. had greater values in high-water fen, suggesting later maturing.

Ca:P increased from June to August. Once more, effect of burning varied by species. Burning caused Carex spp. to have higher Ca:P values, but had no effect upon C. aquatilis. Water level had little effect, however, upon either species. Most notable was an overall dominance of Carex spp. over C. aquatilis, suggesting either that maturity time was dependent upon species, or that Ca:P was always greater in Carex spp.

Burning a fen reduced Ca content of sedges. Carex spp. had greater Ca content when growing in low-water fen, and always had a greater content than C. aquatilis. For this reason, a significant nutrient flush from ash was thought not to occur. Lack of a flush was attributed to either the ash being blown away (because of ice on the fen) or the uptake of Ca by inorganic or organic factors in the water.

P content was dependent upon species, with C. aquatilis being greater most often in unburned fens and both high- and low-water levels. But when a fen was burned, C. aquatilis and Carex spp. had similar P contents. This was thought due

to Carex spp. maturing earlier, or to no nutrient flush in the burned fen.

7. The Waterhen bison herd chose resting habitats in different proportions between the three months. Open habitats were overwhelmingly dominant in June and July, but accounted for less than half of all choices in August. The high proportions in June and July were attributed to tabanid fly annoyance: to get relief, the animals probably chose areas suitable for wallowing. The bison also herded together in an attempt to reduce their incidence of fly attack.

8. Proportions of resting habitats differed between the three age-sex classes in June and July. Cows used open habitats the least each month, possibly to protect their calves. Spikehorns differed from the others because the former chose open habitats the most. This was attributed to greater tabanid annoyance upon the spikehorns. In August, habitats were used in similar proportions between the three age-sex classes.

Other Conclusions

Feeding activity of the Waterhen wood bison centred around dawn and dusk during June and July, with very little of this activity occurring during the day. Daytime feeding activity increased in August. Crepuscular feeding was attributed to threat of overheating during the day and/or to

the tabanid flies (which were inactive at dawn and dusk). The increase in diurnal feeding in August coincided with the absence of tabanids.

RECOMMENDATIONS

A program of rotated controlled spring burns in the Waterhen sedge fens is recommended. The reason is to afford the Waterhen wood bison herd a source of nutritious sedge shoots early in the spring. Burning effects are two-fold and interdependent: burning would remove the litter and promote early growth (as a result of increased solar warming); burning would remove the litter and make the emerging shoots easier to find. Burns would be beneficial to the herd only in the spring, as the bison do not have access to the open fens in summer. In April, the fens are still frozen and the herd can travel and graze through them. Rotation burning refers to burns being carried out on different fens each year, and never the same one two years in a row.

Flooding the area may increase biomass in the fen, but only when flooding is accompanied by a complete drawdown. Even after a drawdown, there is no guarantee that the fen will be accessible because of its muskeg-like nature. More study is required as to the effects of managed flooding and drawdown in the Waterhen or similar sedge fens. In view of this situation, the fens must be allowed to drain naturally over the summer after initial spring flooding. Culverts should be kept open and beaver dams cleared. Willows will

begin to move into the fen, but they can be controlled by spring burns.

The range should be large enough to provide forbs early in the spring for nutrient and mineral replenishment. In addition, preliminary calculations (Berezanski unpublished data) suggest that the bison depended upon the smaller sedge patches within the aspen. A detailed survey of vegetation communities within the aspen forest is recommended. More accurate carrying capacity estimates will be derived from such information.

Resting habitat requirements depended upon tabanid fly presence. When daytime tabanid activity was high, open, disturbed areas were used most often. More research should be done with regards to fitness of bison during the tabanid season when open or closed habitats are used for resting.

LITERATURE CITED

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227-267.
- AOAC. 1970. Official methods of analysis. Association of Official Analytical Chemists, Washington.
- Bailey, I. L. and T. A. O'Neill. 1972. Seasonal ionic fluctuations in a Phragmites communis community. *Can. J. Bot.* 50:2103-2109.
- Banfield, A. W. F. 1981. The mammals of Canada. U. of Toronto Press, Toronto. 438 pp.
- Bartmann, R. M., A. W. Alldredge, and P. H. Neil. 1982. Evaluation of winter food choices by tame mule deer. *J. Wildl. Manage.* 46:807-812.
- _____ and L. H. Carpenter. 1982. Effects of foraging experience on food selectivity of tame mule deer. *J. Wildl. Manage.* 46:813-818.
- Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.* 14:105-134.
- _____ and P. A. Jordan. 1978. The time-energy budget of a moose. *Theor. Pop. Biol.* 14:76-104.
- Boerner, R. E. J. 1985. Foliar nutrient dynamics, growth, and nutrient use efficiency of Hamamelis virginiana in three forest microsites. *Can. J. Bot.* 63:1476-1481.
- Borowski, S. and S. Kossak. 1972. The natural food preferences of bison in seasons free of snow cover. *Acta Theriol.* 17(13):151-169.
- Brink, J. Van den. 1980. The behavior of wisent and bison in larger enclosures. *Acta. Theriol.* 25(11):115-130.
- Budd, A. C. (L. Looman and K. F. Best). 1979. Budd's flora of the Canadian Prairie provinces. Minister of Supply and Services Canada, Hull. 863 pp.
- Burnett, A. M. and K. L. Hays. 1974. Some influences of meteorological factors on flight activity of female horseflies (Diptera:Tabanidae). *Environ. Entomol.* 3:515-521.

- Cabon-Raczynska, K., M. Krasinska, and Z. Krasinski. 1983. Behaviour and daily activity rhythm of European bison in winter. *Acta Theriol.* 28:273-299.
- Campbell, B. H. and M. Hinkes. 1983. Winter diets and habitat use of Alaska bison after wildfire. *Wildl. Soc. Bull.* 11:16-21.
- Chapin, F. S., III and R. A. Kendrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64:376-391.
- Church D. C. and W. G. Pond. 1974. Basic animal nutrition and feeding. D. C. Church, Corvallis. 300 pp.
- Collins, W. B. and P. J. Urness. 1982. Mule deer and elk responses to horsefly attacks. *Northw. Sci.* 56:299-302.
- Conover, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, Inc., Toronto. 462 pp.
- Considine, D. M. 1982. Foods and food production encyclopedia. Van Nostrand Reinhold, New York. 2305 pp.
- Cook, F. R. and D. O. Muir. 1984. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC): history and progress. *Can. Field-Nat.* 98:63-70.
- Dane, C. W. 1959. Succession of aquatic plants in small artificial marshes in New York State. *N. Y. Fish and Game Jour.* 6:57-76.
- Danks, H. V. 1981. Arctic arthropods: a review of systematics and ecology with particular reference to the North American fauna. Entomological Society of Canada, Ottawa.
- Daubenmire, R. 1968. Ecology of fire in the grasslands. *Adv. Ecol. Res.* 5:209-266.
- Duncan, P. and N. Vigne. 1979. The effect of group size in horses on the rates of attack by blood-sucking flies. *Anim. Behav.* 27:623-625.
- Duvall, V. L. and L. B. Whitaker. 1964. Rotation burning: a forage management system for longleaf pine-bluestem ranges. *J. Range Manage.* 17:322-326.
- Elliot, J. M. 1977. Some methods for the statistical analysis of samples of benthic invetebrates, 2nd ed. Freshwater Biological Association Sci. Publ. No. 25, The Ferry House. 160 pp.

- Environment Canada. 1982a. Canadian climate normals. 1951-1980. Vol. 2. Temperature. Canadian Climate Program. 306 pp.
- Environment Canada. 1982b. Canadian climate normals. 1951-1980. Vol. 3. Precipitation. Canadian Climate Program. 602 pp.
- Freeland, W. J. and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Nat. 108:269-289.
- Fuller, W. A. 1960. Behavior and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic 13:3-19.
- _____. 1966. The biology and management of the bison of Wood Buffalo National Park. C.W.S., National Parks Branch, Department of Northern Affairs and National Resources. Wildl. Manage. Bull. Ser.1. No. 16. 52 pp.
- Geist, V. and P. Karsten. 1977. The wood bison (Bison bison athabasca Rhoads) in relation to hypotheses on the origin of the American bison (Bison bison Linnaeus). Z. Saugetierkunde 42:119-127.
- _____. 1982. Adaptive behavioral strategies. IN Elk of North America, ecology and management. J. W. Thomas and D. E. Toweill (eds.). Stackpole Books, Harrisburg. 691 pp.
- Government of the N.W.T. 1983. Ten year wood bison management plan for the Mackenzie Wood Bison Sanctuary herd, Northwest Territories. N.W.T. Renewable Resources, Yellowknife. 24 pp.
- Hanec, W. and G. K. Bracken. 1964. Seasonal and geographical distribution of Tabanidae (Diptera) in Manitoba, based on females captured in traps. Canad. Ent. 96:1362-1369.
- Hansen, R. M., T. M. Foppe, M. B. Gilbert, R. C. Cook, and H. W. Reynolds. Undated. The microhistological analyses of feces as an estimator of herbivore dietary. Unpublished report. Composition Analysis Laboratory, Range Science Department, Colorado State University, Ft. Collins. 6 pp.
- Harris, S. W. and W. H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44:331-343.
- Haslam, S. M. 1971. Community regulation in Phragmites communis Trin. II. Mixed stands. J. Ecol. 59:75-98.

- 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, N.W.T., Canada. *J. Range Manage.* 34:126-130.
- Hobbs, N. T. and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. *J. Wildl. Manage.* 48:551-560.
- _____ and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constants. *J. Wildl. Manage.* 49:814-822.
- Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. *J. Range Manage.* 35:309-315.
- Howell, D. E., G. W. Eddy, and R. L. Cuff. 1949. Effect on horse fly population of aerial spray applications to wooded areas. *J. Econ. Entom.* 42:644-646.
- Hudson, R. J. and M. T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. *J. Range Manage.* 38:80-82.
- Jalkotzy, M. G. and J. D. Van Camp. Unpublished report. Fire and its effect on bison. Slave River Lowlands, N.W.T. N.W.T. Wildlife Service. 19 pp.
- Jeglum, J. K. 1973. Boreal forest wetlands, near Candle Lake, central Saskatchewan. *The Musk-Ox* 12:32-48.
- Kershaw, K. A. 1973. Quantitative and dynamic plant ecology, 2nd ed. American Elsevier, N.Y. 308 pp.
- Kirby, D. R. and J. W. Stuth. 1982. Seasonal diurnal variation in composition of cow diets. *J. Range Manage.* 35:7-8.
- Knorre, E. P. 1959. Ecology of elk. IN Transactions of the Pechora-Ilych State Game Preserve. Vol. VII. Komi Book Publishers, Syktyvkar. 459 pp. (Translated from the Russian)
- Krueger, W. C., W. A. Laycock, and D. A. Price. 1974. Relationship of taste, smell, sight, and touch to forage selection. *J. Range Manage.* 27:258-262.
- Leiffers, V. J. 1984. Emergent plant communities of oxbow lakes in northeastern Alberta: salinity, water-level fluctuation, and succession. *Can. J. Bot* 62:310-316.
- Leonard, R. D. 1982. Wildlife. Section 8. IN Resource description and evaluation, Wood Buffalo National Park (Draft). Unpublished Parks Canada Report.

- Looman, L. 1983. 111 range and forage plants of the Canadian Provinces. Agriculture Canada Publication 1751. Minister of Supply and Services, Ottawa. 255 pp.
- McCaffery, K. R., J. Tranetzki, and J. Piechura. 1974. Summer foods of deer in northern Wisconsin. J. Wildl. Manage. 38:215-219.
- McHugh, T. 1958. Social behavior of the American buffalo (Bison bison bison). Zoologica 43:1-40.
- Meagher, M. M. 1973. The bison of Yellowstone National Park. National Park Service Science Monograph Series. No. 1. 161 pp.
- Millar, J. B. 1973. Vegetation changes in shallow marsh wetlands under improving moisture level. Can. J. Bot. 51:1443-1457.
- Mills, G. F. and R. E. Smith. 1981. Soils of the Ste. Rose-du-Lac area. Soils report No. 21. Canada-Manitoba Soil Survey. Manitoba Department of Agriculture, Winnipeg. 183 pp.
- Mloszewski, M. J. 1983. The behavior and ecology of the African buffalo. Cambridge University Press, New York. 256 pp.
- Muc, M. 1977. Ecology and primary production of sedge-moss meadow communities, Truelove Lowland. IN Truelove Lowland, Devon Island, Canada: a high-Arctic ecosystem. L. C. Bliss (ed.). The University of Alberta Press, Edmonton. 714 pp plus maps.
- Nelson, K. L. 1965. Status and habits of the American buffalo (Bison bison) in the Henry Mountains of Utah. Utah State Dept. Fish and Game Publ. No. 65-2. 142 pp.
- Neu, E. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.
- Novakowski, N. S. 1979. Wood bison. Bison bison athabasca. Endangered Canadian wildlife series. Committee on the Status of Endangered Wildlife in Canada.
- Parker, K. L. and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. Can. J. Zool. 62:1409-1422.
- _____, _____, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474-488.

- Peden, D. G., G. M. van Dyne, R. W. Rice, and R. M. Hansen. 1974. The trophic ecology of Bison bison L. on shortgrass plains. J. Appl. Ecol. 11:489-498.
- _____ and G. J. Kraay. 1979. Comparison of blood characteristics in plains bison, wood bison, and their hybrids. Can. J. Zool. 57:1778-1784.
- Quinton, D. A. 1985. Saskatoon serviceberry toxic to deer. J. Wildl. Manage. 49:362-364.
- Reinhardt, V. 1985. Quantitative analysis of wallowing in a confined bison herd. Acta Theriol. 30:149-156.
- Reynolds, H. W., R. M. Hansen, and D. G. Peden. 1978. Diets of the Slave River Lowland bison herd, Northwest Territories, Canada. J. Wildl. Manage. 42:581-590.
- _____, R. D. Glaholt, and A. W. L. Hawley. 1982. 49. Bison. IN Wild mammals of North America. Biology. Management. Economics. J. A. Chapman and G. A. Feldhammer (eds.). The Johns Hopkins University Press, Baltimore. 1147 pp.
- Rice, P. R. and D. C. Church. 1974. Taste responses of deer to browse extracts, organic acids, and odors. J. Wildl. Manage. 38:830-834.
- Richmond, R. J., R. J. Hudson, and R. J. Christopherson. 1977. Comparison of forage intake and digestibility by American bison, yak, and cattle. Acta. Theriol. 22(14):225-230.
- Riggs, R. A. and J. M. Peek. 1980. Mountain sheep habitat-use patterns related to post-fire succession. J. Wildl. Manage. 44:933-938.
- Roath, L. R. and W. C. Krueger. 1982. Cattle grazing and behavior on a forested range. J. Range Manage. 35:332-338.
- Roe, F. J. 1970. The North American buffalo. A critical study of the species in its wild state, 2nd edition. U. of Toronto Press, Toronto. 991 pp.
- Roseff, S. J. and J. M. Bernard. 1979. Seasonal changes in carbohydrate levels in Carex lacustris. Can. J. Bot. 57:2140-2144.
- SAS Institute Inc. 1982. User's guide: basics, 1982 edition. SAS Institute Inc. Cary, NC. 923 pp.
- Scarnechia, D. L., A. S. Nastis, and J. C. Malechek. 1985. Effects of forage availability on grazing behavior of heifers. J. Range Manage. 38:177-180.

- Scoggan, H. J. 1978. The flora of Canada. Vol. 4. National Museum of Natural Sciences Publication in Botany 7(4). National Museum of Canada. Queen's Printer, Ottawa.
- Seip, D. R. and F. L. Bunnell. 1985a. Nutrition of Stone's sheep on burned and unburned ranges. J. Wildl. Manage. 49:397-405.
- _____ and _____. 1985b. Foraging behaviour and food habits of Stone's sheep. Can. J. Zool. 63:1638-1646.
- Shaykewich, C. F. and T. R. Weir. 1965. Geography of Manitoba. IN Manitoba soils and their management. Manitoba Department of Agriculture, Winnipeg. 90 pp.
- Sheppard, C. and B. H. Wilson. 1977. Relationship of horse fly host seeking activity to the edge of wooded areas in South Louisiana. Environ. Entom. 6:781-782.
- Skogland, T. 1975. Range use and food selectivity by wild reindeer in southern Norway. Proc. Int. Reindeer Caribou Symp. 1:342-354.
- Soper, J. D. 1941. History, range and home life of the northern bison (Wood Buffalo National Park, Northern Alberta and District of Mackenzie, N.W.T., Canada). Ecol. Mono. 11:347-412.
- Stewart, R. R., R. R. MacLennan, and J. D. Kinnear. 1976. Annual variation of plant phenological events and its theoretical relationship to energy balance in moose. Proc. N. Amer. Moose Conf. and Workshop. 12:1-30.
- Stormer, F. and W. Bauer. 1980. Summer forage use by tame deer in northern Michigan. J. Wildl. Manage. 44:98-106.
- Thill, R. E. 1984. Deer and cattle diets on Louisiana pine-hardwood sites. J. Range Manage. 48:788-798.
- Thompson, D. J. 1982. Effects of fire on Phragmites australis (Cav.) Trin. ex Steudel and associated species at Delta Marsh Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg. 197 pp.
- Trudell, J. and R. G. White. 1981. The effect of forage structure and availability on food intake, biting rate, and daily eating time of reindeer. J. Appl. Ecol. 18:63-81.
- Van Vuren, D. 1984. Summer diets of bison and cattle in southern Utah. J. Range Manage. 37:620-621.

- _____ and M. P. Bray. 1983. Diets of bison and cattle on a seeded range in southern Utah. *J. Range Manage.* 36:499-500.
- van Zyll de Jong, C. G. 1985 (in press). Systematic study of recent bison with particular consideration of the wood bison (*Bison bison athabasca* Rhoads 1898). Publications in Natural Sciences. National Museum of Natural Science, Ottawa.
- Viereck, L. A. 1973. Wildfire in the taiga of Alaska. *Quat. Res.* 3:465-495.
- Wales, R., L. Milligan, and E. McEwan. 1975. Urea recycling in caribou, cattle and sheep. *Proc. Int. Reindeer Caribou Symp.* 1:297-307.
- Walker, B. H. and R. T. Coupland. 1968. An analysis of vegetation environment relationships in Saskatchewan sloughs. *Can. J. Bot.* 46:509-522.
- _____ and _____. 1970. Herbaceous wetland vegetation in the aspen grove and grassland regions of Saskatchewan. *Can. J. Bot.* 48:1861-1878.
- Wasser, C. H. 1977. Bison induced stress in Colorado National Monument. Final Report (Abstract). National Parks Service Contract PX 1200606127. 120 pp.
- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *J. Wildl. Manage* 48:1285-1301.
- Willms, W. A. and A. McLean. 1978. Spring forage selection by tame mule deer on big sagebrush range, British Columbia. *J. Range Manage.* 31:192-199.
- _____, A. W. Bailey, A. McLean, and R. Tucker. 1980. The effects of fall grazing or burning bluebunch wheatgrass on forage selection by deer and cattle grazing in spring. *Can. J. Anim. Sci.* 60:113-122.
- Wright, H. A. and A. W. Bailey. 1982. Fire ecology. United States and southern Canada. J. Wiley and Sons, New York. 501 pp.
- Wydeven, A. P. and R. B. Dahlgren. 1985. Ungulate habitat relationship in Wind Cave National Park. *J. Wildl. Manage.* 49:805-813.
- Ying, K. L. and D. G. Peden. 1977. Chromosomal homology of wood bison and plains bison. *Can. J. Zool.* 55:1759-1762.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs. 620 pp.

PERSONAL COMMUNICATIONS

Blythe, C. Park warden, Elk Island National Park, Ft. Saskatchewan, Alberta. Conversation at the Western College of Veterinary Medicine, University of Saskatchewan, Saskatoon, April 1984.

Cantor, S. Graduate student, Natural Resources Institute, University of Manitoba, Winnipeg, R3T-2N2. Numerous conversations between June 1985 Febraury 1986.

Hawley, V. Biologist, Northwest Territories Wildlife Service, Fort Smith (now retired). Conversation in Fort Smith in June, 1983.

Reynolds, H. W. Biologist, Canadian Wildlife Service, Edmonton, T6B-2X3. Conversation at Waterhen, Manitoba, June 1984.

Appendix A

SEXES AND AGES OF WATERHEN WOOD BISON 1984

Males

Birthdate	Age (years)	Number	Origin
1983	calf	1	Valley Zoo (died 6/28/84)
1983	calf	2	Banff
1983	calf	1	Calgary Zoo
1982	1.5	3	Banff
1982	1.5	2	Moose Jaw Wild Animal Park
1981	2.5	1	Banff
1981	2.5	1	Moose Jaw Wild Animal Park
1980	3.5	1	Moose Jaw Wild Animal Park
1978	5.5	1	Moose Jaw Wild Animal Park
1977	6.5	1	Wildlife Reserve of Western Canada
?	6-plus	2	Moose Jaw Wild Animal Park

—
16

Females

1983	calf	1	Calgary Zoo
1983	calf	2	Banff

1983	calf	1	Wildlife Reserve of Western Canada
1982	1.5	1	Valley Zoo
1982	1.5	1	Banff
1982	1.5	2	Moose Jaw Wild Animal Park
1981	2.5	1	Wildlife Reserve of Western Canada
1981	2.5	2	Moose Jaw Wild Animal Park
1980	3.5	1	Moose Jaw Wild Animal Park
1979	4.5	1	Moose Jaw Wild Animal Park
1977	6.5	1	Wildlife Reserve of Western Canada
?	6-plus	4	Moose Jaw Wild Animal Park

Appendix B

PARTIAL VEGETATION LIST FOR WATERHEN SITE

Species indicated by (x) were found in fen vegetation plots and were included as "Other" in Table 4.

EQUISETACEAE

<u>Equisetum arvense</u> L.	COMMON HORSETAIL
<u>E. hymenale</u> L. var. <u>affine</u> (Engelm.) A.A. Eaton	COMMON
	SCOURING RUSH

PINACEAE

<u>Larix laricina</u> (DuRoi) K.Koch	TAMARACK
<u>Picea glauca</u> (Moench) Voss	WHITE SPRUCE
<u>P. mariana</u> (Mill) BSP.	BLACK SPRUCE
<u>Pinus banksiana</u> Lamb.	JACKPINE

TYPHACEAE

<u>Typha latifolia</u> L. (x)	COMMON CATTAIL
-------------------------------	----------------

JUNCAGINACEAE

<u>Triglochin maritima</u> L. (x)	SEASIDE ARROW-GRASS
<u>T. palustris</u> L. (x)	MARSH ARROW-GRASS

ALISMATACEAE

<u>Alisma plantago-aquatica</u> L.	COMMON WATER-PLANTAIN
------------------------------------	-----------------------

GRAMINEAE

<u>Beckmannia syzigachne</u> (Steud.)	COMMON REED GRASS
<u>Bromus</u> sp.	BROME
<u>Calamagrostis inexpansa</u> A	NORTHERN REED GRASS
<u>Elymus</u> sp.	WILD RYE
<u>Glyceria</u> sp.	MANNA GRASS
<u>Hordeum jubatum</u> L..	WILD BARLEY
<u>Phleum pratense</u> L.	TIMOTHY
<u>Phragmites australis</u> (Cav.) Trin. ex Steudel (x)	COMMON REED
	GRASS
<u>Scolochloa festucacea</u> (Willd.) Link (x)	SPANGLETOP

CYPERACEAE

<u>Carex aquatilis</u> Wahl (confirmed by U. of Alta. Botany Dept.)	WATER SEDGE
(x)	
<u>C. atherodes</u> Spreng. (confirmed by H. Reynolds, CWS) (x)	AWNED SEDGE
<u>C. diandra</u> Schrank (confirmed by G. Keleher, U. of Man. Botany Dept.) (x)	TWO-STAMENED SEDGE

C. lanuginosa Michx. (confirmed by G. Keleher) (x) WOOLY
SEDGE
C. rostrata Stokes (confirmed by H. Reynolds) (x) BEAKED
SEDGE
Eleocharis sp. (x) SPIKE-RUSH
Eriophorum sp. COTTON-GRASS
Scirpus validus Vahl (x) GREAT BULRUSH

LEMNACEAE

Lemna minor L. LESSER DUCKWEED

JUNCACEAE

Juncus balticus Willd. BALTIC RUSH
Juncus sp. RUSH

LILIACEAE

Lilium philadelphicum L. WOOD LILY
Maianthemum canadense Desf. var. internius Fern. WILD LILY-
OF-THE-VALLEY
Smilacina stellata L. Desf. STAR-FLOWERED SOLOMON'S SEAL
Trillium cernuum L. var. macranthum Eam.&Wieg. NODDING
WAKEROBIN
Zigadenus elegans Pursh SMOOTH CAMAS

SALICACEAE

Populus tremuloides Michx. TREMBLING ASPEN
P. balsamifera L. BALSAM POPLAR
Salix discolor Muhl. PUSSY WILLOW
S. interior Rowlee SAND WILLOW
Salix spp. (x) WILLOW

ORCHIDACEAE

Cypripedium calceolus var. parviflorum (Salisb.) Fern.
YELLOW LADY'S-SLIPPER

BETULACEAE

Betula papyrifera Marsh PAPER BIRCH
B. glandulifera (Regel) Butler (x) SWAMP BIRCH
Corylus americana Walt. AMERICAN HAZELNUT
C. cornuta Marsh. BEAKED HAZELNUT

FAGACEAE

Quercus macrocarpa Michx. BUR OAK

URTICACEAE

Urtica dioica L. var. procera (Muhl.) Wedd. STINGING
NETTLE

POLYGONACEAE

Polygonum achoreum Blake STRIATE KNOTWEED
P. convolvulus L. WILD BUCKWHEAT
Polygonum sp. SMARTWEED
Rumex sp. DOCK

CHENOPODIACEAE

<u>Atriplex patula</u> L.	ORACHE
<u>Chenopodium album</u> L.	LAMB'S-QUARTERS
<u>C. capitatum</u> (L.) Aschers.	STRAWBERRY BLITE

RANUNCULACEAE

<u>Anemone canadensis</u> L.	CANADA ANEMONE
<u>A. cylindrica</u> A.Gray	LONG-FRUITED ANEMONE
<u>Caltha palustris</u> L.	MARSH MARIGOLD
<u>Thalictrum dasycarpum</u> Fisch.&Lall.	TALL MEADOW-RUE
<u>T. venulosum</u> Trel.	VEINY MEADOW-RUE

MENISPERMACEAE

<u>Menispermum canadense</u> L.	YELLOW PARILLA
---------------------------------	----------------

CRUCIFERAE

<u>Capsella bursa-pastoris</u> (L.) Medic.	SHEPHERD'S PURSE
<u>Erysimum chieranthodes</u> L.	TREACLE MUSTARD

SAXIFRAGACEAE

<u>Parnassia palustris</u> L. var. <u>tenuis</u> Wahl.	GRASS-OF-PARNASSUS
<u>Ribes americanum</u> Mill.	WILD BLACK CURRANT

ROSACEAE

<u>Amelanchier alnifolia</u> Nutt.	SASKATOON
<u>Crataegus rotundifolia</u> Moench	ROUND-LEAVED HAWTHORNE
<u>Fragaria virginiana</u> Dcne.	SMOOTH WILD STRAWBERRY
<u>Potentilla anserina</u> L.	SILVERWEED
<u>Prunus americana</u> Marsh	AMERICAN PLUM
<u>P. pennsylvanica</u> L.f.	PIN CHERRY
<u>P. virginiana</u> L.	RED-FRUITED CHOKECHERRY
<u>Rosa acicularis</u> Lindl.	PRICKLY ROSE
<u>R. woodsii</u> Lindl.	WOOD'S ROSE
<u>Rubus idaeus</u> L. var. <u>acculeatissimus</u> Regel&Tiling	WILD RED RASPBERRY
<u>R. pubescens</u> Raf.	DEWBERRY
<u>Spiraea alba</u> DuRoi	NARROW-LEAVED MEADOWSWEET

LEGUMINOSEAE

<u>Astragalus</u> sp.	MILK-VETCH
<u>Lathyrus venosus</u> Muhl.	WILD PEAVINE
<u>Lathyrus</u> sp.	VETCHLING
<u>Medicago sativa</u> L.	ALFALFA
<u>Melilotus alba</u> Medic.	WHITE SWEET-CLOVER
<u>Trifolium</u> sp.	CLOVER
<u>Vicia americana</u> Muhl.	AMERICAN VETCH
<u>Vicia</u> sp.	VETCH

POLYGALACEAE

<u>Polygala senega</u> L.	SENECA SNAKE-ROOT
---------------------------	-------------------

ANACARDIACEAE

<u>Rhus radicans</u> L. var. <u>rydbergii</u> (Small) Rehder	POISON IVY
--	------------

ONAGRACEAE

Epilobium angustifolium L. FIREWEED
E. ciliatum Raf. NORTHERN WILLOWHERB

HALORAGACEAE

Hippuris vulgaris L. (x) MARE'S-TAIL

ARALIACEAE

Aralia nudicalis L. WILD SARSAPARILLA

UMBELLIFERAE

Cicuta maculata L. var. angustifolia Hook. (x) WATER HEM-
 LOCK

Sium suave Walt. (x) WATER PARSNIP
Osmorhiza sp. SWEET CICELY

CORNACEAE

Cornus canadensis L. BUNCHBERRY
C. alba L. RED-OSIER DOGWOOD

ERICACEAE

Arctostaphylos uva-ursi (L.) Spreng. BEARBERRY
Ledum palustre L. var. latifolium (Jacq.) Michx. LABRADOR-
 TEA

PRIMULACEAE

Primula sp. PRIMROSE

GENTIANACEAE

Gentiana andrewsii Griseb. CLOSED GENTIAN

APOCYANACEAE

Apocynum androsaemifolium L. var. incanum DC. SPREADING
 DOGBANE

CONVOLVULACEAE

Convolvulus sepium L. HEDGE BINDWEED

SCROPHULARIACEAE

Castilleja miniata Dougl. INDIAN PAINTBRUSH
Chaenorthinum minus (L.) Lange SMALL-SNAPDRAGON

PLANTAGINACEAE

Plantago major L. COMMON PLANTAIN

RUBIACEAE

Galium boreale L. NORTHERN BEDSTRAW

CAPRIFOLIACEAE

Linnea borealis L. var. americana (Forbes) Rehder TWIN-
 FLOWER
Lonicera dioica L. var. glaucescens (Rydb.) Butt. TWINING
 HONEYSUCKLE

Symphoricarpos albus (L.) Blake SNOWBERRY

S. occidentalis Hook. WESTERN SNOWBERRY

Viburnum edule (Michx.) Raf. LOW-BUSH CRANBERRY

V. lentago L.
V. rafinesquianum Schultes

NANNYBERRY
 DOWNY ARROWWOOD

CAMPANULACEAE

Campanula rotundifolia L.

HAREBELL

COMPOSITAE

Crepis runcinata (James) T.&G.

SCAPOSE HAWK'S-BEARD

Hieracium umbellatum L.

CANADA HAWKWEED

Lactuca sp.

LETTUCE

Prenanthes alba L.

WHITE LETTUCE

Taraxacum officinale Weber

DANDELION

Achillea millefolium L.

YARROW

Artemesia frigida Willd.

PASTURE SAGE

Aster laevis L.

SMOOTH ASTER

Aster sp.

ASTER

Helianthus .sp

SUNFLOWER

Petasites palmatus (Ait.) A.Gray

PALMATE-LEAVED COLT'S-FOOT

P. sagittatus (Pursh) A.Gray

ARROW-LEAVED COLT'S-FOOT

Rudbeckia hirta L.

BLACK-EYED SUSAN

Senecio sp.

GROUNDSEL

Solidago bicolor L.

PALE GOLDENROD

S. spathulata DC. var. spathulata

MOUNTAIN GOLDENROD

Solidago sp.

GOLDENROD

Appendix C
DESCRIPTION OF HABITAT TYPES

The following areas were designated as "open habitat":

- waste areas
- slash piles
- dugouts
- roads
- corral
- corral perimeter
- central sedge fen

The following areas were designated as "edge habitat":

- willow
- aspen edges

The following area was designated as "closed habitat":

- aspen forest

Appendix D

TEMPERATURES AND PRECIPITATION, CFS GYPSUMVILLE

Normals are from Environment Canada (1982a and 1982b).
Data from 1984 are from Environment Canada computer records.
July and August 1984 precipitation data were not available.

	DAILY TEMPERATURES (° C)				PRECIPITATION	
	NORMALS		1984		(mm)	
	<u>min</u>	<u>max</u>	<u>min</u>	<u>max</u>	<u>norm</u>	<u>1984</u>
MAY	3.5	16.5	2.6	13.7	34.0	60.5
JUNE	8.8	21.3	10.9	21.6	58.8	74.1
JULY	12.0	23.9	13.3	24.2	63.6	--
AUGUST	10.2	22.3	13.6	25.6	63.6	--

Appendix E

DESCRIPTION OF QUALITY PARAMETERS

Crude Protein (CP)

CP is a measurement of total nitrogen, as determined by the Kjeldahl method, multiplied by 6.25. It is expressed as % dry matter weight.

Protein is an important component of animal tissue, especially of muscle. All cells synthesize protein for all or part of their lives. In addition, all cells contain protein, which is subject to rapid turnover. Protein from the diet replaces the lost body protein as well as supplies the requirements for growth and other functions (Church and Pond 1974).

Acid Detergent Fibre (ADF)

Fibre in plant tissues is composed of complex carbohydrates such as celluloses, hemicelluloses, pentosans, uronic acids, gums, mucilages, and lignin. Most of these substances are found in the cell walls (numerous authors in Considine 1982). The IFT Panel on Food Safety and Nutrition (1979 in ibid) summarizes three physiological roles for fibre:

- a) Definite value- relieving constipation by increasing water content of feces.
- b) Probable value- treatment (or prevention) of diverticulum disease.
- c) Possible value- reduce serum cholesterol and prevent numerous disorders.

Total Digestible Nutrients (TDN)

TDN is the sum of digestible protein (nitrogen-free extract) + 2.25 times the digestible ether extract (crude fat). Fat is multiplied by 2.25 to account for its higher caloric value. Protein energy is underestimated because protein is not completely oxidized by the body (Church and Pond 1974).

TDN is a measurement of energy. Quantitatively, energy is the most important component of diet. To drive all biochemical functions, energy is required (Church and Pond 1974).

Calcium:Phosphorus (Ca:P)

Skeletal ossification uses hydroxyapatite crystals, formed from calcium and phosphate ions. A critical minimum level of these two ions is required for ossification. If one or both of these components falls below the concentration required to precipitate calcium phosphate into the crystal structure, ossification does not occur. To avoid osteomala-

cia (rickets), a Ca:P ratio of 2:1 is recommended for livestock (Church and Pond 1974).

Calcium (Ca)

Ca is a structural component of bones, and is continuously turned over as animals grow and mature. Ca also controls nerve and muscle functions., and is required for blood coagulation (Church and Pond 1974).

Phosphorus (P)

Phosphorus is another component of the skeleton (as phosphate), and is present in soft tissue in organic form. It exists in phospholipids (for lipid transport and metabolism and membrane structure) and functions in energy metabolism as part of AMP, ADP, ATP, and creatinine phosphate (Church and Pond 1974). RNA, DNA, and several enzyme systems all utilize P.

Appendix F

DIETS OF WOOD BISON PRIOR TO MANITOBA TRANSFER

This list was compiled by Hal Reynolds, CWS Edmonton.

CALGARY ZOO

- mixed hay (brome/timothy) }
- alfalfa (50%) } free
- herbivore pellets (16% CP) } choice
- blue salt lick (cobalt, iodine) }
- salt
- poplar and willow browse- when available

BANFF

- alfalfa/timothy hay (40%:60%) free choice
- water
- salt

ALBERTA WILDLIFE PARK

- brome hay
- daily ration pellets (13% CP)
- salt
- water

MOOSE JAW WILD ANIMAL PARK

- free grazing prior to corralling (primarily grass; little browsing)
- brome hay } in the corral
- salt block (blue) } prior to transport
- water

VALLEY ZOO

- grazed in pasture (crested wheat)
- pellets (high roughage content- poplar sawdust)
- alfalfa/timothy hay (>60% timothy)
- bush trimmings and tree trimmings from time to time

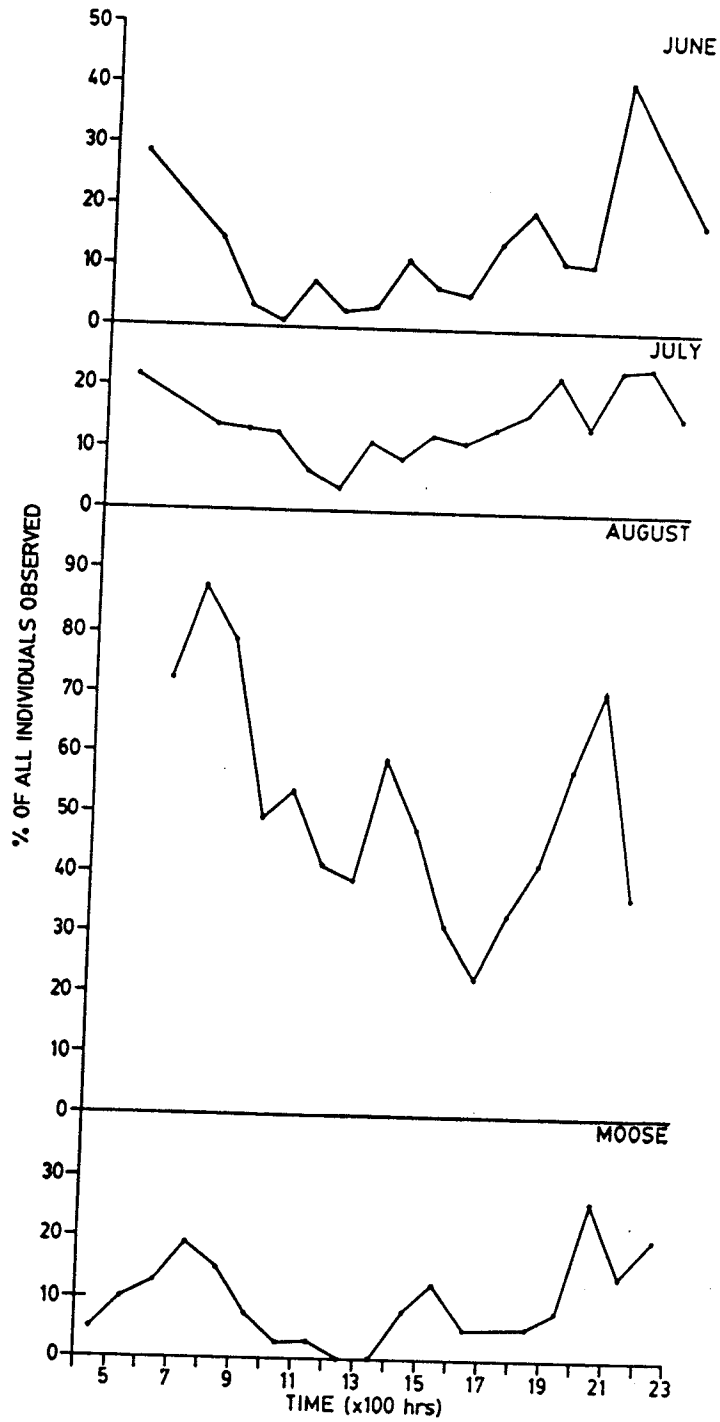
WILDLIFE RESERVE OF WESTERN CANADA

- free ranging predominantly
- brome/timothy hay (small amounts periodically)

Appendix G

DAILY FEEDING TIMES OF WOOD BISON

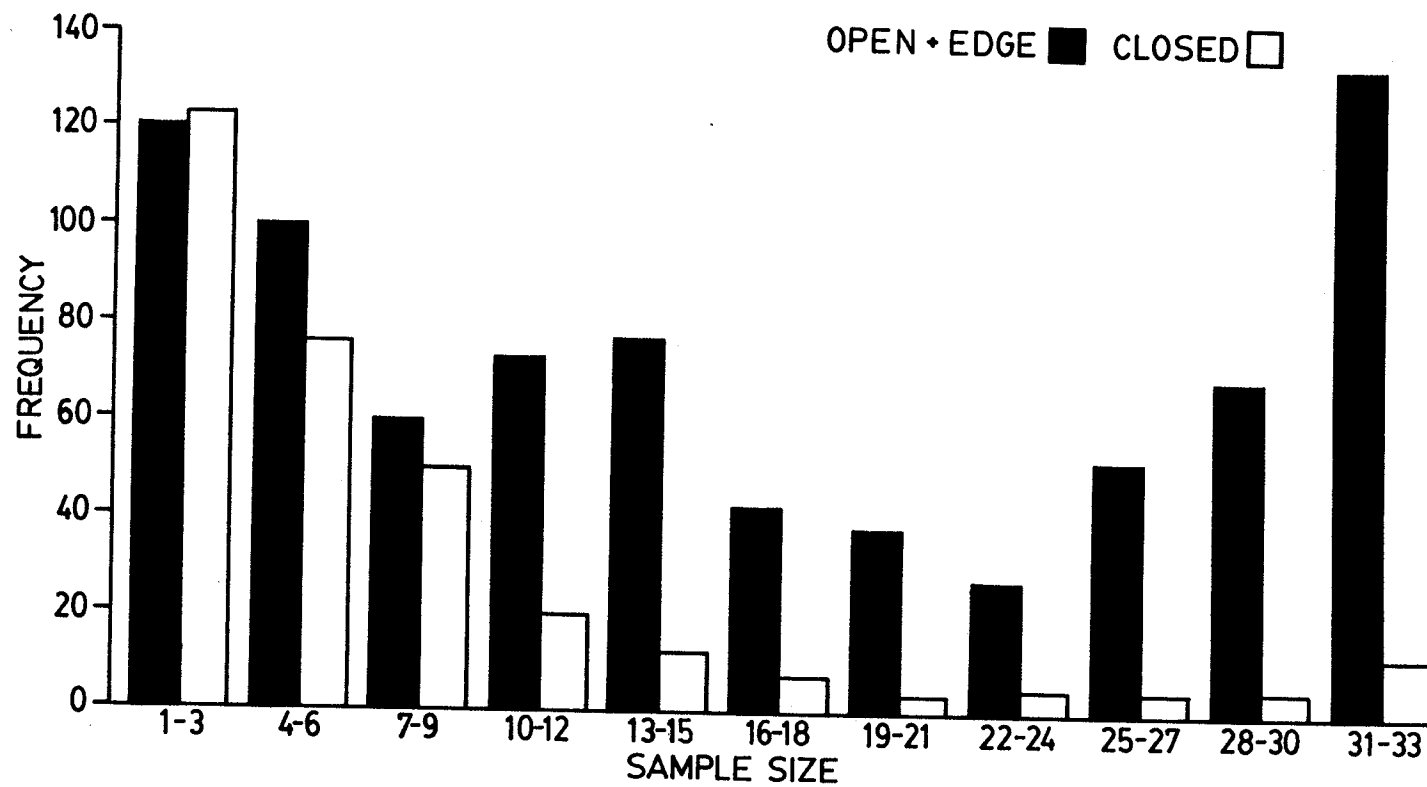
For this plot of feeding times, calves are not included with bison. Observations during rain are not included. Moose data are from Belovsky and Jordan (1978).



Appendix H

SAMPLE SIZE FREQUENCY DISTRIBUTION BY HABITAT TYPES

For this plot, calves are not included. Open+edge types
N=803. Closed (aspen) type N=310.



Appendix I

FREQUENCY OF SPIKEHORNS OBSERVED FEEDING BY HABITAT

Figures in brackets are %frequency of that month.

MONTH	CLOSED	EDGE	OPEN	SUM
June	39 (40.6%)	22 (23.0%)	35 (36.5%)	96
July	43 (16.2%)	39 (14.7%)	184 (69.2%)	266
August	<u>109</u> (23.5%)	<u>160</u> (34.6%)	<u>194</u> (41.9%)	<u>463</u>
	191 (23.2%)	221 (26.8%)	413 (50.1%)	825

Appendix J

FREQUENCY OF OBSERVED FEEDING OF EACH CLASS BY HABITAT

Data are from August only. Figures in brackets are
%frequency of that class.

CLASS	CLOSED	EDGE	OPEN	SUM
Bulls	174 (31.8%)	215 (39.2%)	159 (29.0%)	548
Cows	249 (30.2%)	322 (39.0%)	255 (30.9%)	826
Spike-				
horns	<u>109</u> (23.5%)	<u>160</u> (34.6%)	<u>194</u> (41.9%)	<u>463</u>
	191 (23.2%)	221 (26.8%)	413 (50.1%)	825

Appendix K

FREQUENCY OF OBSERVED COMFORT AND OTHER BEHAVIOURS

Figures in brackets are % frequency of that class. χ^2
=14.1, df=1, $P<0.001$.

AGE-SEX CLASS	COMFORT BEHAVIOUR	OTHER	SUM
Spikehorns	67 (3.14%)	2068 (96.8%)	2135
Adults	<u>161</u> (1.82%)	<u>8692</u> (98.2%)	<u>8853</u>
	228	10760	10988

Appendix L

RELATIONSHIP OF TEMPERATURE AND BISON FEEDING
ACTIVITY

For this plot, calves are not included.

