

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

University of Alberta

Management, growth and performance of bison
(*Bison bison*) on seasonal pastures

by

Bruce David Rutley



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Doctor of Philosophy

in

Wildlife Ecology and Management

Department of Renewable Resources

Edmonton, Alberta

Fall 1998



National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-34828-8

University of Alberta

Library Release Form

Name of Author: Bruce David Rutley

Title of Thesis: Management, growth and performance of bison (*Bison bison*) on seasonal pastures


Short Title: Seasonal performance of farmed bison

Degree: Doctor of Philosophy

Year this Degree Granted: Fall 1998

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly, or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.


Bruce David Rutley
Box 74
Fairview, AB T0H 1L0

Submitted to the Faculty of Graduate Studies and Research: 2 October 1998


The buffalo has returned




University of Alberta

Faculty of Graduate Studies and Research

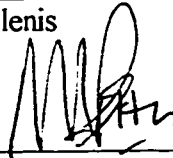
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Management, growth and performance of bison (*Bison bison*) on seasonal pastures" submitted by Bruce David Rutley in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Wildlife Ecology and Management.



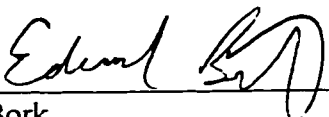
Dr. R. J. Hudson



Dr. P. V. Blenis




Dr. M. A. Price



Dr. E. Bork



Dr. M. Macharechian


for _____
Dr. D. Christensen



Dr. A. L. Schaefer

Oct 1, 1998
Date approved by committee

Abstract

Sixteen commercial bison herds, within the Peace River Region of British Columbia and Alberta, were surveyed to determine which management practices affected herd productivity. Management factors of herd health, weigh date and length of grazing season affected measures of body weight. Body weights collected from 3329 bison (November 1992 to October 1994) were used to develop the following profile. A typical Peace Country bison is born May 15 weighing 30 kg. It is weaned 240 days later at 187 kg. It gains 0.21 kg d^{-1} post weaning. At one year it weighs 209 kg. During the subsequent summer through winter period, it gains 0.41 kg d^{-1} and weighs 310 kg by January 15 as a long yearling. Catch-up growth was evident in a significant negative relationship between winter gain (X) and subsequent summer gain (Y) on pasture ($Y = -0.50X + 0.71$, $SE_b = 0.03$, $n = 339$, $R^2 = 0.39$, $P < 0.0001$).

The performance of bison on seasonal pasture was also studied. Bison grazed selectively; exhibited seasonal variation in bite rate, grazed throughout the year, altered foraging behaviour when supplemental feed was provided, exhibited distinctly polyphasic activity patterns and altered their activity budgets seasonally.

Two field methods used to estimate seasonal intake and energy requirements were compared with actual intake during companion pen trials. Although estimates of dry matter intake were highly variable, seasonal variation in appetite was clear. Bison were

estimated to consume $11.6 \pm 0.5 \text{ kg d}^{-1}$ (bite count method), $2.4 \pm 0.2 \text{ kg d}^{-1}$ (single marker method) or $4.9 \pm 0.5 \text{ kg d}^{-1}$ (actual intake) during summer. The single dose marker method was considered less useful for bison than wapiti, where estimates are considered quite reliable.

Metabolizable energy requirements of penned bison for maintenance rose from $532 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in winter to $956 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in summer. Although absolute values were highly variable, both the marker and bite count methods clearly indicated seasonal variation up to 200% for bison on pasture. Current data would indicate that highly expressed seasonal cycles are not exclusive to cervids.

Bison production characteristics, including growth and maturity, seasonal cycles of activity, appetite and energy requirements, are unique. Development of management strategies specifically for bison is recommended.

Dedication

This thesis is dedicated to the
Bison Industry

Acknowledgments

With respect and pleasure, I acknowledge the support, guidance and friendship of my supervisor, Dr. Robert J. Hudson. I acknowledge and appreciate the support I received from Dr. A. L. Schaefer as a committee member and an enthusiast for the development of the bison industry. The academic support of Dr. A. W. Bailey while serving as a committee member, prior to his retirement, is gratefully appreciated. The guidance and critical review of the defense committee is greatly appreciated. Thanks to Dr. P. Blenis for the assistance provided during the statistical revisions.

The Peace Country Bison Association (PCBA) provided financial support for the survey. Alberta Agriculture Research Institute (Farming for the Future) financed the seasonal pasture studies. Norwest Laboratories (Edmonton, AB), Kasper Laboratories (Edmonton, AB) and Northern Lights College (Dawson Creek, BC) are gratefully acknowledged for additional financial support.

The contributions of the PCBA research committee and participating producers are appreciated. I acknowledge the assistance of the following Center for Agricultural Diversification staff: C. Jahn, Dr. D. Klassen, M. Fritsche, A. Hogberg, J. Riddle, J. Church, L. Papp, C. Rasmussen and J. Kemp (data collection); and P. Garnham, F. Burton and R. Carlson (animal handling). I acknowledge R. Begg, C. Rasmussen, S. Melnyk, P. Hanson and J. Galbraith for their assistance with feeding and handling of the Ministik bison. For laboratory analyses, I acknowledge T. Ree, C. Rasmussen (chromium) and M. Fenton (lignin) at the University of Alberta; K. Mrazek and staff of Norwest Laboratories, Lethbridge; and Dr. T. Higgins and staff of Kasper Laboratories, Edmonton.

I would like to thank Mr. Bill Bickford for kindling my interest in bison; Mr. Ross Carlson, former President of the PCBA, for directing me to the research needs of this developing industry, Northern Lights College for the development of the Center for Agricultural Diversification and to Dr. A. W. Bailey for precipitating my interest in a Doctoral program.

I wish to acknowledge my fellow graduate students for their interest, academic stimulation, advice and camaraderie: J. Church, S. Kathnelson, R. Nixdorf and T. Ree. To my sister and brother in-law, Dawn and Erwin Friesen, thanks for letting me crash!

Finally, without the support and patience of my family, Lois, Ryan and Trevor, there would be nothing to report.

TABLE OF CONTENTS

CHAPTER 1. History and Changing Role of the Bison	1
1.1 INTRODUCTION.....	1
1.2 KEY IMPACTORS ON CONTEMPORARY <i>BISON</i>	5
1.2.1 Taxonomy and Interbreeding	5
1.2.2 Decimation and Recovery	6
1.2.2.1 Genetic Bottleneck	6
1.2.2.2 Genetic Contamination with <i>Bos</i>	7
1.2.3 Canadian Bison Industry	8
1.2.4 Bison - a naturally adapted species good for sustainable development	9
1.3 BISON RESEARCH	9
1.3.1 Early Research	9
1.3.2 Growth	9
1.3.3 Weight, Factors Affecting Weight and Gain in Juvenile Bison	10
1.3.4 Seasonality	11
1.3.5 Daily Intake	12
1.3.6 Digestibility and Rate of Passage	12
1.3.7 Tame Pasture Grazing	13
1.3.8 Winter Grazing	13
1.3.9 Activity Budgets	13
1.3.10 Park and Free-Ranging Wild Bison	14
1.4 REFERENCES	20
CHAPTER 2. Management, gain and productivity of bison (<i>Bison bison</i>) in the Peace Country	31
2.1 INTRODUCTION	31
2.2 METHODS.....	32
2.2.1 Classification, Calculations and Data	32
2.2.2 Statistical Methods.....	34
2.3 RESULTS.....	35
2.3.1 Management Survey.....	35
2.3.2 Weight.....	37
2.3.3 Effect of Management Factors on Weight	38

2.3.4 Gain.....	39
2.4 DISCUSSION.....	40
2.4.1 Typical Peace Country Bison and Bison Operation.....	40
2.4.2 Management, Gain and Productivity.....	41
2.5 CONCLUSIONS.....	43
2.6 REFERENCES.....	50
CHAPTER 3. Activity budgets and foraging behaviour of bison on seasonal pastures	53
3.1 INTRODUCTION.....	53
3.2 METHODS.....	56
3.2.1 Location and Climate.....	56
3.2.2 Vegetation and Phenology.....	56
3.2.3 Study Animals	57
3.2.4 Activity Budgets.....	57
3.2.5 Forage Biomass and Quality.....	59
3.2.6 Statistics and Calculations.....	61
3.3 RESULTS.....	63
3.3.1 Seasonal Activity Budgets.....	63
3.3.2 Seasonal Foraging and Resting Bouts.....	63
3.3.3 Resting Behaviour.....	64
3.3.4 Daily Activity.....	65
3.3.5 Sward Structure, Forage Quality and Diet Selection.....	66
3.3.6 Winter Grazing.....	68
3.4 DISCUSSION	69
3.4.1 Activity Patterns	69
3.4.2 Foraging Activity	71
3.4.3 Temperature and Thermoregulation	72
3.4.4 Winter Grazing	74
3.4.5 Bite Rate, Consumption Rate and Dry Matter Intake	74
3.4.6 Grazing Behaviour and Diet Selection	76
3.4.7 Bison and Cattle	77
3.4.8 Scanning Frequency and 24 h Observation Scans	78
3.4.9 Summary	79
3.5 REFERENCES	90

CHAPTER 4. Energy requirements of free-grazing bison on seasonal pasture	95
4.1 INTRODUCTION	95
4.2 METHODS	96
4.2.1 Location and Pasture Characteristics	96
4.2.2 Field Trials	96
4.2.3 Pen Trials	98
4.2.4 Single Marker Method	99
4.2.5 Calculation of Feed Intake Using the Marker Method	99
4.2.6 Feed Intake by the Bite Count Method	100
4.2.7 Chemical Analyses	101
4.2.8 Statistics	101
4.3 RESULTS	102
4.3.1 Growth	102
4.3.2 Dry Matter and Metabolizable Energy Intake	103
4.3.3 Metabolizable Energy Requirements	104
4.3.4 Excretion Parameters	105
4.4 DISCUSSION	106
4.4.1 Marker Method	106
4.4.2 Bite Count Method	109
4.4.3 Energy Requirements	110
4.4.4 Instantaneous Growth Rate	112
4.5 CONCLUSIONS	113
4.5 REFERENCES	123
CHAPTER 5. Synthesis and Discussion.....	126
5.1 SUMMARY.....	127
5.2 GROWTH: MATURITY RATE and GAIN	129
5.3 SEASONALITY.....	131
5.3.1 Energy	131
5.3.2 Activity Budgets	133
5.4 IMPLICATIONS AND RECOMMENDATIONS.....	135
5.4.1 The Bison Advantage	135

5.4.2 Managing with Seasonal Cycles	136
5.4.3 Managing while Ignoring Seasonal Cycles	137
5.4.4 The Advantage - Use It or Lose It	137
5.4.5 Manage like Cattle or Wild Ruminant?	139
5.4.6 Sequitor	140
5.5 REFERENCES.....	144
APPENDICES	148
I.a Initial Survey for Peace Country Bison Producers	149
I.b Follow-up Survey for Peace Country Bison Producers.....	151
I.c Description of Herd Management Survey Codes Summarized in Appendices I.a and I.b	152
I.d Pasture Assessment Survey	154
II. Pasture Survey Results Summary - 1993.....	155
CURRICULUM VITAE	156

LIST OF TABLES

Table 1.1. Prices obtained from selected Western Canadian public bison auctions conducted by Moore's Auctioneering Ltd.	15
Table 1.2. Hornaday's 1888 census of the genus <i>Bison</i>	16
Table 1.3. Recent estimates of the population of the genus <i>Bison</i>	17
Table 1.4. Membership by region within the Canadian Bison Association (CBA) as at annual convention - November prior to calendar year	18
Table 1.5. Prices obtained for breeding stock sold at the Canadian Bison Association annual show and sale	19
Table 2.1. Number of Peace Country bison weighed during each weigh period	44
Table 2.2. Summary of herd health treatments routinely applied by Peace Country bison managers	45
Table 2.3. Winter weights (kg \pm SE) of Peace Country bison calves.	46
Table 2.4. Profile of typical Peace Country bison.	47
Table 3.1. Differences (\pm SE) in 24 h activity budget for yearling bison during indicated trial period	80
Table 3.2. Differences (\pm SE) in 24 h activity budget for yearling bison by season-feed group	80
Table 3.3. Foraging and bedding activity of yearling bison summarized by season-feed group	81
Table 3.4. Composition of forage within sward sites and grazed patches – summer and autumn pasture data pooled	82
Table 3.5. Composition of forage within grazed patches during June and September trial periods	82
Table 3.6. Chemical composition of forage within feeding station (emulated bites), grazed patches and sward sites for yearling bison grazing seasonal pasture	83
Table 3.7. Biomass (g m ⁻²) within sward and grazing patches	84

Table 3.8. Chemical composition of forage grazed by yearling bison during indicated grazing period (mean \pm SE)	85
Table 3.9. Bite rate, bite size and foraging intensity of free-grazing yearling bison on pasture summarized by trial period	86
Table 3.10. Influence of snow depth and condition on grazing behaviour of yearling bison	87
Table 4.1. Body weight (kg \pm SE) of yearling bison summarized by trial period	114
Table 4.2. Instantaneous growth rate (r) of yearling bison during 21day field trials	114
Table 4.3. Daily intake of ten 1994 cohort bison females during December 1994 and June 1995 pen trials	115
Table 4.4. Bite count method estimated measures of intake (\pm SE) for six free-grazing yearling bison summarized by trial period	116
Table 4.5. Marker method estimated measures of intake (\pm SE) for six free-grazing yearling bison summarized trial period	117
Table 4.6. Seasonal estimates associated with dry matter intake (\pm SE) for six free-grazing yearling bison summarized by grazing period	118
Table 4.7. Seasonal estimates associated with metabolizable energy intake (\pm SE) of six free-grazing yearling bison summarized by season-feed group	118
Table 4.8 Mean trial estimates of turnover time (h) by free-grazing and penned bison, based on fecal chromium excretion curves	119
Table 4.9 Mean season-feed group estimates (\pm SE) of turnover time (h) for six free-grazing bison based on fecal chromium curves	119
Table 4.10. Individual seasonal estimates of total turnover time (h) by free-grazing and penned bison, based on fecal chromium excretion curves.....	120
Table 5.1. Yearling weight expressed as a percentage of mature body weight	141
Table 5.2. Seasonal contrasts in metabolizable energy requirements (kJ BW ^{0.75}) of <i>B. bison</i> and <i>C. elaphus</i>	142
Table 5.3. Reproductive contrasts among bison, cattle and cervids	143

LIST OF FIGURES

Figure 2.1. Frequency distribution of weaning month for 14 bison herds in 1992 and 10 herds in 1993	48
Figure 2.2. Number of bison herds in 1992 and 1993 for which grazing season was 5-6, 7-8, 9-10, and 11-12 months long	48
Figure 2.3. Females out gained males during winter (W2SADG) but not during summer (S2WADG), nor overall (W2WADG)	48
Figure 2.4. The effect of winter weight gain (X) on subsequent summer gain (Y) in yearling bison. (Equation (dark bars): $Y = -0.50X + 0.71$, $SE_b = 0.03$, $n = 339$, $r^2 = 0.39$, $P < 0.001$)	49
Figure. 3.1. Averaged seasonal daily foraging patterns (solid bars) and the foraging pattern for a single day (line) expressed as a percentage of bison active within each 1 h interval. Top: summer grazing. Bottom: Autumn grazing. Sunrise-sunset indicated by solid arrow. Daylight-dark indicated by broken arrow.	88
Figure. 3.2. Averaged seasonal daily foraging patterns (solid bars) and the foraging pattern of a single day (line) expressed as a percentage of bison active within each 1 h interval. Top: winter grazing. Bottom: supplemented. Sunrise-sunset indicated by solid arrow. Daylight-dark indicated by broken arrow	88
Figure. 3.3. Daily activity pattern of yearling bison during winter grazing (top) and while feeding on supplemental hay (bottom). Sunrise-sunset indicated by solid arrows. Daylight-dark indicated by broken arrows	89
Figure 4.1. Dry matter intake (DMI) of pen-fed bison determined by the marker method (X) compared with actual DMI (Y) - winter ration (solid circles), summer ration (open circles). (Equation: $Y = 107X + 0.95$, $SE_b = 0.85$, $r^2 = 0.18$, $P = 0.25$)	121

Figure 4.2. Dry matter intake (DMI) of free-grazing yearling bison determined by the bite-count (Y) and marker methods (X). (Equation: $Y = 1.74X + 7.62$, $SE_b = 0.54$, $r^2 = 0.28$, $P < 0.01$)	121
Figure 4.3. Metabolizable energy (ME) intake of free-grazing (estimated via marker (MM) and bite count (BC) methods) and penned (actual intake) yearling bison. Each method confirms seasonal variation in ME intake for bison	122

Management, growth and performance of bison
(*Bison bison*) on seasonal pastures

CHAPTER 1. History and Changing Role of the Bison

1.1 INTRODUCTION

The plains bison (*Bison bison*) has been farmed, ranched or managed since the late 1800's when the species was rescued from extinction (Hornaday 1890; Roe 1970; Dary 1974; Meagher 1978; Ogilvie 1979; Gates and Reynolds 1989). Previous bison production has been primarily for personal enjoyment or restoration of the species (Rorabacher 1970), but a recent wave of expansion has been fueled by 1) the demand for lean red meat, 2) a new level of maturity associated with bison management, 3) a threshold level of breeding stock and 4) the resulting positive economic outlook for the industry. Attempts to hybridize bison with cattle have all but been abandoned (Peters 1984).

Although bison have been raised as semi-domesticates for the last century, are managed similar to domestic livestock, and are considered similar enough to cattle that some researchers have recently suggested reclassification as *Bos* (Jones et al. 1992), *bison* still retain many of the characteristics attributed to wild ruminants. They exhibit severe stress when confined, they rut (McHugh 1958; Rutley and Rajamahendran 1995), they are adapted annual grazers, and apparently exhibit seasonal cycles for growth and metabolism (Richmond et al. 1977; Christopherson et al. 1979b).

Application of production techniques developed for cattle have been successful (American Bison Association 1993; National Buffalo Association 1993). Furthermore, an increasing proportion of the industry is applying these intensive production techniques. For example, there is an increase in the number of bison producers who feed bison calves grain-based rations from weaning to slaughter. In general, the industry is rapidly changing to one that parallels the cow-calf, specialized

feeder/feedlot, commercial vs. breeder types of enterprise distinctions common to the livestock industry.

Despite significant developments in the commercial bison industry, it is still in its infancy. Therefore, it is appropriate to consider this global question: are bison to be managed as a wild ruminant or like its closest analog, domestic cattle? One could pose the question more philosophically as - do we (humans) adapt to them (bison) or do we expect them to adapt to us (and our modern livestock management practices)?

We have the opportunity to take advantage of the perceived evolutionary advantage of this ruminant, thereby developing new or applying suitable existing management practices that will facilitate economical extensive production systems without compromising the integrity of the species. Alternatively, we could continue to apply existing livestock production practices, like grain-based growing and finishing rations, high protein pregnancy rations, and continue to be influenced by axioms like 'bigger is better' when planning selection programs. Ultimately, the production techniques and (or) production practices that dominate will be based upon how bison respond to the techniques applied to them.

By continuing to develop the industry without evaluating the nature of the species prior to the application of livestock management techniques or selection procedures, we not only 'expect bison to adapt to us', but we fail to provide a benchmark that will contribute to meaningful future comparisons. Undertaking a more complete evaluation of the nature and biology of bison now, will not only benefit future comparisons, but will provide managers who wish to adapt to bison, with insights into 1) the evolutionary advantages of bison, 2) which existing practices are appropriate for application, and 3) where the need for the development of new techniques exists.

This dissertation is in support of the latter approach. We must first develop a more complete understanding of the nature and biology of *Bison*. This will also enable us to gain insights into the global question - what is the bison advantage?

Although industry literature provides good insights on commercial production practices (American Bison Association 1993; National Buffalo Association 1993) and the scientific literature is extensive (Arthur 1985), neither are complete with respect to providing answers to the global question. Research areas considered most lacking were related to bison growth and gain, their response to changes in seasonal forage conditions (seasonal activity budgets, winter grazing) and the determination of seasonal cycles for metabolizable energy requirements under free-grazing conditions.

It was also considered desirable to select study groups that would be complementary to industry development, providing that decision did not compromise the intent of the research. As primary research questions were related to growth, gain, activity and energy requirements, and as current production systems for adult bison were considered to be of lesser importance, juvenile bison were selected for study. In addition, current industry expansion depended on a steady supply of juvenile bison - males primarily for the red meat market and females for breeding markets. Other considerations for selecting juveniles over adults include 1) juveniles were considered easier to handle than adults, 2) activity budgets and seasonal energy requirements from juveniles or adults were considered to be equally beneficial for industry development, and 3) because there are few serious health issues associated with bison calves, growth becomes the single most important factor affecting juveniles.

The growth of the juvenile depends primarily on its success at obtaining nutrients. This is most critical following weaning when the juvenile bison is directly responsible for its nutrient intake. In a commercial setting, it must source nutrients from feedstuffs

within the environment provided by the manager. A more complete understanding of bison growth and energy requirements is thus pre-requisite to adapting production techniques to bison. Therefore, the initial period of growth, when the bison calf must forage independently of its dam (between 8 and 20 months of age) was selected for study.

The research strategy employed was to first address general questions about growth as it is impacted by the environment within commercial herds (that is, how do current production practices affect measures of growth in juvenile bison?). A controlled survey research format addressed the general questions. The survey format provided data associated with varying management practices, while collection of on-farm empirical data enhanced the quality of the data.

To answer the more specific questions regarding seasonal variation in energy requirements for maintenance and gain, activities of a separate study group were documented. This also enabled exploration of seasonal activity budgets and foraging behaviour in free-grazing bison. Companion field and pen trials were used to address the set of specific objectives.

Surveys and experiments were designed and conducted to provide insights into the global question and to meet the following specific objectives:

1. Develop a profile of the bison industry, based on a survey of Peace Country bison, and obtain insights on the effect of management practice on measures of growth (weight and gain) in juvenile bison.
2. Evaluate the seasonal activity budgets and foraging strategies of bison, including selectivity and feeding efficiencies in relation to pasture biomass and structure.

3. Determine the extent that juvenile bison exhibit seasonal variation in metabolic energy requirements ($ME_{\text{maintenance}}$ and ME_{gain}), i.e. dry matter intake, passage rate and estimates of digestibility.

The dissertation is presented in research paper format and is composed of five chapters. Chapter 1 includes a summary of the events and factors that impact the current industry and a review of the literature. Chapter 2 reports the survey research. Chapter 3 focuses on activity budgets and foraging behaviour. Chapter 4 addresses the specific questions associated with seasonal variation in metabolizable energy requirements for maintenance and gain. Finally, Chapter 5 contains discussion, synthesis, and implications for bison management.

1.2 KEY IMPACTORS on CONTEMPORARY *BISON*

1.2.1 Taxonomy and Interbreeding

Evolution and dispersal of Bison has been described (Geist 1971; Geist and Karsten 1977). Based on historic range and phenotypic characteristics American bison have been considered to be two distinct sub-species - the northern wood bison (*Bison bison athabascae*, Rhoads) and central plains bison (*Bison bison bison* Linnaeus). Other accounts often referred to the Mountain bison, however they were “for all intents and purposes” the same as wood bison (Rorabacher 1970; Geist 1991).

The distinction between wood and plains bison is based primarily on seven phenotypic characteristics (van Zyll de Jong 1986; Stelfox 1993). This distinction is supported by Canada’s Wood Bison Recovery Team who have aided the recovery of the wood bison from Endangered to Threatened by the Convention on International Trade in Endangered Species (CITES) (Gates and Reynolds 1989, van Zyll de Jong et al. 1993).

Genetic studies, however, do not support this distinction (Bork et al. 1991; Geist 1991; Polziehn et al. 1996). Restriction fragment length polymorphism (RFLP) substitutions indicated that divergence of the species has been recent (Bork et al. 1991) and comparisons of mitochondrial DNA haplotypes led Polziehn et al. (1996) to conclude that neither are a well defined taxon.

Whether or not wood bison remain a “special genetic breed” (as defined by the Canadian Bison Association) separate from plains bison, is not a concern of many commercial bison producers because recent commercial practice has been to introduce “wood bison” bulls into “plains bison” herds. Producers following this practice see an economical advantage because bison displaying the wood bison pelage characteristics receive premium prices (Table 1.1).

Mixing of “wood” and “plains” bison will continue within the commercial bison industry to the consternation of those interested in bison conservation.

1.2.2 Decimation and Recovery

1.2.2.1 Genetic Bottleneck

Estimates of the number of bison at the arrival of Europeans to North America in the early 1500's range from 40 to 80 million for plains bison (Roe 1970; Dary 1974) and 150-200,000 for wood bison (Gates and Reynolds 1989).

The rapid demise of the bison began in 1840 and by the late 1880's less than 300 plains bison (Hornaday, 1890; Rorabacher, 1970) and 300 wood bison (Reynolds 1991) remained. Hornaday (1890) accounted for seventy-seven (77) bison within 19 non-breeding captive establishments and 184 within 5 foundation herds (Table 1.2).

Significant aspects of the plains bison recovery include 1) 80% of all plains bison in 1902 had descended from the 8 head which became the Pablo-Allard herd, which became the Elk Island National Park (EINP) and Buffalo National Park (BNP) herds, 2) BNP bison contracted brucellosis and tuberculosis while at the Park and when transported to Wood Buffalo National Park spread the disease and “hybridized” with wood bison (Ogilvie 1979), and 3) surplus EINP animals contributed significantly to the growth of the western Canadian commercial bison industry.

Elk Island National Park wood bison are descendants of 42 Nyarling River bison translocates (Polziehn et al. 1996). The 2200 bison in the Mackenzie Bison Sanctuary descended from 18 translocates from EINP. Disease and hybridization with plains bison (Ogilvie 1979; Gates and Reynolds 1989; Reynolds and Gates 1991) exacerbated the recovery of the wood bison. The disease issue continues to negatively impact the commercial bison industry.

The total contemporary bison population (over 18,000 within public herds and 250,000 commercial head) has descended from these few small, potentially inbred populations. This resulting genetic bottleneck (Falconer 1981; Gilpin and Soule 1986) could have had a devastating effect on the bison population due to inbreeding depression (Shaw 1993).

Shaw (1993) concludes that the reason bison are not considerably inbred today is due to the survival of a wild herd in Yellowstone National Park and the parallel growth within the commercial population.

1.2.2.2 Genetic Contamination with Bos

The nucleus of many commercial bison herds within the United States were derived from the Buffalo Jones herd (one of the 5 foundation herds) which was a collection of

pure and (cattle) hybrid bison (Ogilvie 1979). Concurrently, most of the U.S. public herds developed from multiple translocations, although some herds developed in isolation (National Buffalo Association 1993). However, all public herds were subject to translocations of animals that probably contained some cattle genes (Ogilvie 1979; Peters 1984). Recently, Ward and Derr (1997) confirmed the presence of cattle mitochondrial DNA in bison within 4 of 14 public and private U.S. bison herds.

Repopulation of *Bison* continues through expansion of public and some private commercial herds (Table 1.3) with animals that have survived a severe genetic bottleneck and some hybridization with cattle.

1.2.3 Canadian Bison Industry

Recent industry expansion has coincided with the change in structure of the Canadian Bison Association (CBA) to national based producer organization with 8 strong regional organizations (Table 1.4). The CBA has successfully represented the maturing industry on disease issues within Wood Buffalo National Park and the implementation of the Federal Government Captive Ungulate Policy. Recent developments impacting on the bison industry include 1) development and approval of the Canadian Bison Grading system and the Industry-Government Liaison Committee, 2) development of a sustained export market (Europe and U.S.), 3) industry driven bison research and demonstration initiatives, 4) development of market infrastructure supporting red meat and breeding stock sales (Tables 1.1, 1.5), and 5) a climate in which shared bison management practices are market driven.

Market forces associated with the commercial industry will remain a dominant influence on species developments.

1.2.4 Bison - a naturally adapted species good for sustainable development

Bison are hardy, naturally adapted to the prairies, and were once dominant within the prairie ecosystem (Roe 1970; Dary 1974). What makes them suitable candidates for northern sustainable agricultural systems is their ability to 1) respond to cold stress by lowering their metabolic rate (Christopherson et al. 1979a, 1979b), 2) winter graze (even with snow depths up to four feet, McHugh 1958), and 3) exhibit efficient utilization of low quality forages (Peden et al. 1974; Richmond et al. 1977; Schaefer et al. 1978; Reynolds and Hawley 1987a).

1.3 BISON RESEARCH

1.3.1 Early Research

Many early bison studies focused on hybridization with cattle (Boyd 1914; Goodnight 1914; Peters 1984) in an attempt to improve the hardiness of domestic cattle. Cattalo, beefalo and the American breed were the results of these crosses (Peters 1984). Generally, first generation crosses were plagued with hydramnios, reduced ratio of male calves and infertile male F1 crosses (Boyd 1914; Peters 1984). Although cattalo outgrazed beef cattle during winter grazing trials (Smoliak and Peters 1955), they did not become accepted livestock. However, a few producers of beefalo and cattalo still exist.

1.3.2 Growth

Growth is the only bioenergetic category (above maintenance) of importance to subadults. Growth is ultimately described by mature size, which is generally considered fixed and genetically determined (Berg and Butterfield 1976; Price and White 1985; Tolkamp and Ketelaars 1992). Growth curves have been developed for park bison, from annual winter body weight measures (Renecker et al. 1989). These curves have limited value to commercial producers because 1) producers are more

concerned about subadult growth (early and rapid growth is a desirable production practice), and 2) older males, which comprise a large component of park herds, are generally not part of commercial herds.

The gap between actual and theoretical growth rate can result in reduced farm revenues, and coupled with concern over permanent stunting associated with under-nutrition, encourages production practices that promote rapid growth at a young age (that is, feeding grain-based supplemental winter rations high in protein and (or) energy). Impact of feeding practices on growth and ultimate mature body size has not been determined in bison. However, feeding higher quality winter rations resulted in significantly lower subsequent summer gain (0.15 kg d^{-1} vs 0.30 kg d^{-1}) in yearling wapiti (*Cervus elaphus*) stags (Wairimu et al. 1992).

1.3.3 Weight, Factors Affecting Weight and Gain in Juvenile Bison

Measures of body weight for bison are sparse. Peters (1958) started bison males (156 and 171 kg, year 1 and 2, respectively) and females (150 and 166 kg, year 1 and 2, respectively) onto a feedlot ration January 7 (year 1) and December 30 (year 2), respectively. Ten, 8-month bison bulls weighing 185 kg were compared with Hereford and Brahman cattle for feedlot gain and carcass characteristics (Koch et al. 1988). Renecker et al. (1989) reported growth curves for Elk Island National Park wood and plains bison herds, however factors affecting these weights were not reported. In contrast, factors affecting growth and measures of weight have been well established in domestic livestock (Newman 1977; Kruesi 1985; Taylor and Bogart 1988). Feedlot gain for bison calves ranged between 0.40 and 0.63 kg d^{-1} (males), 0.22 and 0.50 kg d^{-1} (females; Peters 1958) and averaged 0.77 kg d^{-1} (Koch et al. 1988).

1.3.4 Seasonality

Northern wild ruminants exhibit strong seasonal cycles of growth, appetite and energy metabolism (Bandy et al. 1970; Christopherson et al. 1979b; Hudson and White 1985; Hudson et al. 1985; Jiang and Hudson 1994). In wapiti and red deer (*Cervus elaphus*), these cycles are associated with seasonal endocrinological changes and are photoperiodically entrained (Barry et al. 1991; Shi and Barrell 1992). Early work assumed that energy expenditure was the driving mechanism and that metabolic cycles represented a form of winter dormancy with reduced requirements (Jiang and Hudson 1994). However, seasonal cycles are expressed even in a stable environment (Kay 1979; Adam et al. 1986). Recent studies question whether fasting metabolic rates are seasonal (Jiang and Hudson 1993) and indicate that wapiti have unusually high spring and summer values rather than low winter values (Jiang and Hudson 1993, 1994).

Previous research (Hudson et al. 1994) suggests that game farmers should work with the seasonal cycle rather than against it. The extent to which bison (*Bison bison*) express seasonal cycles, however, has not been completely documented. Seasonal energy expenditure for bison does vary by month (Christopherson et al. 1978), with an increase in spring over winter, however energy expenditure in that study was not determined throughout the year nor conducted with free-grazing animals. Other limitations of this early work were that energy expenditure, rather than energy requirement was measured (Jiang and Hudson 1994). A more direct measure of maintenance requirements can be obtained by determining the amount of feed needed to maintain the body energy throughout the year (Blaxter 1989). A regression analysis of metabolizable energy (ME) on liveweight gain provides a simultaneous estimate of seasonal energy requirement for maintenance and liveweight gain (Jiang and Hudson 1994).

1.3.5 Daily Intake

The most important factor affecting growth is metabolizable energy intake (MEI). MEI is a direct function of feed intake dynamics and feed quality (Hudson and White 1985; McDonald et al. 1988; Ketelaars and Tolcamp 1992a, 1992b; Tolcamp and Ketelaars 1992). Forage intake is related to cropping rate (Jiang and Hudson 1992), season (Hudson and Watkins 1986) and forage depletion (Hudson and Nietfeld 1985). Variation in seasonal forage quality is well established (Tainton 1984; Holochek et al. 1989). However, seasonal variation in MEI for bison has not been documented.

1.3.6 Digestibility and Rate of Passage

Digestibility studies of forages grazed by bison have been conducted within prairie ecosystems (Peden et al. 1974; Hudson and Frank 1987; Plumb and Dodd 1993). Peden et al. (1974) confirmed that bison were primarily grass eaters while grazing shortgrass prairie dominated with blue grama (*Bouteloua gracilis*). Bison had a slower rate of passage than cattle (Schaefer et al. 1978) and greater utilization of sedge hay than cattle (Hawley et al. 1981). Keith et al. (1981) suggest that urea metabolism in bison may respond to dietary N-levels, indicating urea conservation in bison. Specifically, “bison fed one-half as much N in their diet excreted about one-half as much urea in their urine, and had ruminal ammonia concentrations approximately one-half as large as bison in the high-N diet group. However, BUN and salivary urea levels in the bison on the low-N diet were ... only reduced to about two-thirds the levels of bison receiving the high-N diet”. Varel and Dehority (1989) determined that bison differed from cattle-bison hybrids and cattle in percentages of bacteria species and protozoa genera within the rumen, suggesting metabolic differences exist among these animal groups.

1.3.7 Tame Pasture Grazing

Utilization of forages, by wood bison grazing in the Slave River low-lands (Hawley 1987, Reynolds and Hawley 1987a; Reynolds and Peden 1987; Larter and Gates 1991) and plains bison grazing native range (Peden et al. 1974; Hudson and Frank 1987; Plumb and Dodd 1993) have been described. Commercial production would benefit from assessment of utilization of tame mixed grass-legume pastures by bison.

1.3.8 Winter Grazing

The rich resources of the prairie ecosystem that used to sustain livestock during winter were well described by Latham (1871). This resource, however, was eventually fenced, plowed and largely replaced with European cultivars with cattle and sheep becoming the predominant grazers in the region. As a result, most forage-related research was directed at these European species - species that do not tolerate winter graze well. Therefore, data on winter sward biomass, structure, quality and utilization is limited (Miner and Peterson 1989; Miner et al. 1990). Winter grazing of native range has received some attention (Grimm 1939; Coughenour 1991) but studies relating to winter grazing by bison are limited to range condition assessment (DelGuidice et al. 1994). Understanding how bison compensate for reduced forage quality in winter (increasing bite rate, bite size, grazing time, and selectivity) would benefit the commercial bison industry as it attempts to include winter grazing within grazing plans.

1.3.9 Activity Budgets

Social behaviour of wild bison (McHugh 1958), cow-calf relationships (Egerton 1962; Green 1986; Green et al. 1989), activity budgets for penned bison (Robitaille and Prescott 1993), time budgets for free ranging bison (Belovsky 1986; Belovsky and Slade 1986) and relationships between wild bison and wolves (Carbyn and Trottier

1987) have been described, however activity budgets of bison grazing tame pasture in the absence of predators have not.

1.3.10 Park and Free-Ranging Wild Bison

A considerable volume of research has been collected on park and free-ranging wild bison (McHugh 1958; Meagher 1978; Reynolds et al. 1982; Reynolds and Hawley 1987b; Hawley 1989; Meagher 1989; Renecker et al. 1989; Gates and Larter, 1990; Walker 1993; Kirkpatrick et al. 1991, 1992, 1993; Berger and Cunningham 1994). However, this research may have limited application to commercial herds for three main reasons. Parks and free ranging herds are managed respecting policies of 1) limited manipulation of stocking rates, 2) no supplemental feeding, and 3) male:female ratios near 1:1.

Table 1.1. Prices obtained from selected Western Canadian public bison auctions conducted by Moore's Auctioneering Ltd.

Year	Location	Class of Animal	n	Average	High	Low
April 1998	Alder Flats	1996 Males (Semen Tested)	16	\$2,211	\$6,500	\$1,460
		1996 Males (Not Semen Tested)	36	\$1,506	\$925	\$5,000
		1997 Males	44	\$1,094	\$3,500	\$700
October 1997	Alder Flats	1997 Females	30	\$4,980	\$6,000	\$4,000
		1995 Bred Females	34	\$7,504	\$8,100	\$7,000
		1996 Females	9	\$4,872	\$5,300	\$4,600
April 1996	Alder Flats	1997 Females	19	\$3,876	\$4,250	\$3,700
		1994 Males (Semen Tested)	38	\$6,753	\$13,200	\$2,300
		1994 Males (Not Semen Tested)	5	\$1,780	\$2,150	\$1,500
November 1995	Alder Flats	1995 Males	4	\$981	\$1,075	\$700
		1994 Females	26	\$4,696	\$5,800	\$2,500
		1995 Females	44	\$3,770	\$4,200	\$2,500
November 1995	Alder Flats	1995 Wood Bison Females	3	\$7,067	\$7,500	\$6,200
		1994 Males (Not Semen Tested)	2	na	\$1,600	\$1,370
		1995 Males	82	na	\$1,115	\$670
March 1995	Alder Flats	Bred Cows	5	na	\$6,500	\$6,000
		1994 Females	25	na	\$4,700	\$2,850
		1995 Females	87	na	\$4,700	\$2,550
March 1995	Alder Flats	1993 Males	na	na	\$1,500	\$1,325
		1994 Males	na	na	\$1,050	\$1,000
		Bred Cows	na	na	\$5,100	\$3,100
March 1994	Alder Flats	1993 Females	na	na	\$3,700	\$2,100
		1994 Females	na	na	\$2,700	\$2,000
		Wood Bison Cows	na	na	\$9,500	\$6,500
March 1993 ^z	Alder Flats	1993 Wood Bison Males	na	na	\$4,400	\$4,000
		1993 Wood Bison Females	na	na	\$4,600	\$4,500
		1991 Males	na	\$1,108	\$1,575	\$810
December 1991	Edson	1992 Males	na	\$750	\$925	\$450
		1992 Females	na	\$1,072	\$1,250	\$775
		1991 Males	na	\$510	na	na
November 1990	Dawson Creek	Cows exposed to Bulls	na	\$1,700	na	na
		1989 & 1990 Females	na	na	\$1,025	\$900
		1991 Females	na	na	\$875	\$730
		Bred Cows	65	na	\$2,700	\$1,400

^z Number of animals sold totalled 139, however number per class is unavailable.

Table 1.2. Hornaday's 1888 census of the genus *Bison*^z

Owner	Location	Males	Females	Total
<u>Buffalo in captivity:</u>				
"Buffalo Bill" Wild West Show		--	--	18
Philadelphia Zoological Society	Philadelphia, Penn.	4	6	10
Atchison, Topeka and Santa Fe RR	Bismark Grove, Kan.	3	7	10
Lincoln Park Zoo	Chicago, Ill.	2	5	7
Dr. V. T. McGillicuddy	Rapid City, S. D.	2	2	4
Central Park Menagerie	New York City	--	--	4
US National Museum	Washington, DC	1	1	2
John H Starin	Glen Island, NY	--	--	4
B.C. Winston	Hamline, Minn.	1	1	2
Jesse Huston	Miles City, Mont.	1	--	1 ^y
L.F. Gardner	Bellwood, Ore.	1	--	1 ^y
Riverside Ranch Co.	Mandan, Dakota Ter.	1	1	2
Unknown Private Parties	Dakota Ter.	--	--	4
James R. Hitch	Ptima, Indian Ter.	1	1	2
Joseph A. Hudson	Estell, Nebr.	1	--	1 ^y
London Zoological Gardens	London, England	--	--	1 ^y
Liverpool, England	Liverpool, England	--	--	1 ^x
Dresden Zoological Gardens	Dresden, Germany	--	--	2 ^y
Calcutta Zoological Gardens	Calcutta, India	--	--	1 ^y
			Total	77
<u>Foundation herds:</u>				
Col. Samuel L. Bedson	Stony Mountain, Man.	23	35	70 ^w
Charles Goodnight	Goodnight, Tex.	6	7	13
Michel Pablo and Charles Allard	Ronan, Mont.	--	--	35
Frederick Dupree	Stanley Co., S.D.	4	5	9
Charles J. Jones	Garden City, Kan.	24	33	57
			Total	184
			Grand Total	261

^z Source, G. D. Coder, 1975 after W. T. Hornaday, 1888; reprinted from Ogilvie, 1979.

^y Not considered to be in a breeding situation.

^x This was a lone animal but in the year the census was taken it was purchased by the "Buffalo Bill" Wild West Show and Hornaday evidently included it with the animals in a breeding situation.

^w This figure includes 12 calves of unknown sex.

Table 1.3. Recent estimates of the population of the genus *Bison*

	Canada	United States
Plains Bison		
Commercial Herds ^z	18,000	200,000
Free-Ranging ^y	800	none
Captive Public ^x	500	9280
Wood Bison		
Captive Breeding ^w	300	unknown
Captive Public ^x	400	none
Free-Ranging ^w	2200	none
Wood/Plains Cross		
Commercial Herds	unknown	unknown
Free Ranging ^y	3500	none

^z Rutley unpublished data (1993) - the Canadian Bison Association 1996 Census indicates 45,437 bison on 745 bison farms as at May 1996 - an annual growth rate of 1.36 (growth rate above 1.22 indicates net importation).

^y Based on 1990 census (National Buffalo Association 1993).

^x Based on 1993 data (North American Public Bison Herd Symposium).

^w Personal communication (Gates 1997).

Table 1.4. Membership by region within the Canadian Bison Association (CBA) as at annual convention - November prior to calendar year^z

Year ^y	Interior				Peace				USA ^v	Foreign ^u
	BC	Country	Alberta ^w	Saskatchewan	Manitoba	Ontario	Quebec	Maritimes		
1998	1029	138	381	227	110	52	46	2	50	na
1997	769	103	252	157	90	52	47	4	40	2
1996	668	98	203	136	79	47	50	4	29	4
1995	499	70	133	96	59	44	37	4	27	7
1994	357	52	95	78	43	33	10	3	22	5
1993	203/257	51	57	54	27	28	7	2	11	4
1992	189	41	43	42	16	22	8	2	13	2
1991	103	--	--	--	--	--	--	--	--	--
1990	87	--	--	--	--	--	--	--	--	--

^z Source: derived from figures published within Smoke Signals - the official publication of the CBA.

^y 1998 data as at April 1998 (source: The Tracker). Prior to 1992, the CBA did not have regional organizations.

^x Annual convention was held in February until 1993 when held twice to accommodate change to late November/December conventions.

^w Southern Alberta Bison Association became Alberta Bison Association - November 1996.

^v U.S. producers with membership in the CBA.

^u Members located outside North America (data combined with United States for 1998).

Year		n	Average	High	Low
November 1996	Bred Cows	na	na	\$15,000	\$7,000
	Yearling Heifers	na	na	\$21,000	\$5,900
	Heifer Calves	na	na	\$17,000	\$3,700
December 1995	Yearling Bulls (Semen Tested)	9	\$7,221	\$18,200	\$2,600
	Yearling Bulls (No Semen Test)	7	\$3,557	\$4,600	\$2,600
	Bull Calves	18	\$3,850	\$11,000	\$1,500
	2 Yr. Old Bred Heifers	8	\$6,725	\$8,700	\$3,700
	Yearling Heifers	13	\$4,615	\$5,700	\$3,700
	Heifer Calves	23	\$4,300	\$7,500	\$2,800
February 1992	Yearling Bulls (No Semen Test)	4	\$1,790	na	na
	Bull Calves	5	\$900	na	na
	Yearling Heifers	7	\$1,520	na	na
	Heifer Calves	3	\$1,300	na	na
	Exposed Cows with heifer cows	2	\$2,500	na	na
	Cows exposed to bull	8	\$2,350	na	na

1.4 REFERENCES

Adam, C. L., Moir, C. E. and Atkinson, T. 1986. Induction of early breeding in red deer (*Cervus elaphus*) by melatonin. *J. Reprod. Fertil.* 76: 569-573.

American Bison Association. 1993. Bison breeders handbook. 3rd ed. American Bison Association, Denver, CO.

Arthur, G. W. 1985. A buffalo round up: a selected bibliography. Canadian Plains Research Center. University of Regina. SK.

Bandy, P. J., Cowan, I. McT. and Wood, J. A. 1970. Comparative growth in four races of black-tailed deer (*Odocoileus hemionus*). Part I. Growth in body weight. *Can. J. Zool.* 48: 1401-1410.

Barry, T. N., Suttie, J. M., Milne, J. A. and Kay, R. N. B. 1991. Control of food intake in domesticated deer. Pages 385-401 *in* Physiological aspects of digestion and metabolism in ruminants: Proceedings of the Seventh International Symposium on Ruminant Physiology. Academic Press.

Belovksy, G. E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia (Berlin)*: 70: 35-52.

Belovsky, G. E. and Slade, J. B. 1986. Time budgets of grassland herbivores: body size similarities. *Oecologia (Berlin)*: 70: 53-62.

Berg, R. T. and Butterfield, R. M. 1976. New concepts in cattle growth. Sydney University Press, Sydney, Australia.

Berger, J. and Cunningham, C. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York, NY.

- Blaxter, K. L. 1989.** Energy metabolism in animals and man. Cambridge University Press, New York, NY. 335 pp.
- Bork, A. M., Strobeck, C. M., Yeh, F. C., Hudson, R. J., and Salmon, R. K. 1991.** Genetic relationship of wood and plains bison based on restriction fragment length polymorphisms. *Can. J. Zool.* **69**: 43-48.
- Boyd, M. M. 1914.** Crossing bison and cattle. *J. Heredity* **5**: 189-197.
- Carbyn, L. N. and Trottier, T. 1987.** Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Can. J. Zool.* **65**: 2072-2078.
- Christopherson, R. J., Gonyou, H. W. and Thompson, J. R. 1979a.** Effects of temperature and feed intake on plasma concentration of thyroid hormones in beef cattle. *Can. J. Anim. Sci.* **59**: 655-661.
- Christopherson, R. J., Hudson, R. J. and Christophersen, M. K. 1979b.** Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Can. J. Anim. Sci.* **59**: 611-617.
- Christopherson, R. J., Hudson, R. J. and Richmond, R. J. 1978.** Comparative winter bioenergetics of American bison, yak, Scottish Highland and Hereford calves. *Acta Theriol.* **23**(2): 49-54.
- Coughenour, M. B. 1991.** Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *J. Appl. Ecol.* **28**: 71-82.
- Dary, D. 1974.** The buffalo book: the final saga of the American animal. Sage Books.
- DelGuidice, G. D., Singer, F. J., Ulysees, S. S., and Bowser, G. 1994.** Physiological responses of Yellowstone bison to winter nutritional deprivation. *J. Wildl. Manage.* **58**(1): 24-34.

Egerton, P. J. M. 1962. The cow-calf relationship and rutting behaviour in American bison. M.Sc. Thesis. University of Alberta. Edmonton, AB.

Falconer, D. S. 1981. Introduction to quantitative genetics, 2nd ed. Longman, London and New York. 340 pp.

Gates, C. and Reynolds, H. 1989. The recovery of wood bison in Canada. Government of Northwest Territories, Department of Renewable Resources Publication, September 1989.

Gates, C. C. and Larter, N. C. 1990. Growth and dispersal of an erupting large herbivore population in Northern Canada: the Mackenzie Wood Bison (*Bison bison athabascae*). *Arctic* **43**: 231-238.

Geist, V. 1971. The relation of social evolution and dispersal in ungulates during the Peistocene, with emphasis on the Old World deer and the genus *Bison*. *Quaternary Research* **1**: 282-315.

Geist, V. 1991. Phantom subspecies: the wood bison *Bison bison "athabascae"* Rhoads 1897 is not a valid taxon, but an ecotype. *Arctic* **44**(4): 283-300.

Geist, V. and Karsten, P. 1977. The wood bison (*Bison bison athabascae* Rhoads) in relation to the hypothesis on the origin of the American bison (*Bison bison* Linnaeus). Pages 119-127 in Sonderdruck aus Z. f. Säugetierkunde Bd. 42 (1977) H. 2. Verlag Paul Pary, Hamburg and Berlin.

Gilpin, M. E. and Soule, M. E. 1986. Minimum viable populations: processes of species extinction. Pages 19-34 in M. E. Soule. ed. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc. MA.

Goodnight, C. 1914. My experience with bison hybrids. *J. Heredity*. **5**: 197-199.

Green, W. C. H. 1986. Age-related differences in nursing behaviour among American bison cows (*Bison bison*). *J. Mamm.* **67**: 739-741.

Green, W. C. H., Griswold, J. G., and Rothstein, A. 1989. Postweaning associations among bison mothers and daughters. *Anim. Beh.* **38**: 847-58.

Grimm, R. L. 1939. Northern Yellowstone winter range studies. *J. of Wildl. Manage.* **3**: 295-306.

Hawley, A. W. L. 1987. Bison and cattle use of forages. Pages 49-52 *in* H. W. Reynolds and A. W. L. Hawley eds. *Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT.* Occasional Paper, No. 63. Canadian Wildlife Service, Edmonton, AB. 74 pp.

Hawley, A. W. L. 1989. Bison Farming in North America. Pages 346-361 *in* R. J. Hudson, K. R. Drew and L. M. Baskin, eds. *Wildlife production systems: economic utilization of wild ungulates.* Cambridge University Press, Cambridge, UK.

Hawley, A. W. L., Peden, D. G. and Stricklin, W. R. 1981. Bison and Hereford steer digestion of sedge hay. *Can. J. Anim. Sci.* **61**: 165-174.

Holocek, J. L., Pieper, R. D. and Herbel, C. H. 1989. *Range management: principles and practices.* Prentice Hall.

Hornaday, W. T. 1890. The extermination of the American Bison. Report of the United States National Museum for 1887, 1890, pp. 367-548.

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

Hudson, R. J. and Nietfeld, M. T. 1985. Effect of forage depletion on the feeding rate of wapiti. *J. Range Manage.* **38**(1): 80-82.

Hudson, R. J. and Watkins, W. G. 1986. Foraging rates of wapiti on green and cured pastures. *Can. J. Zool.* **64**: 1705-1708.

Hudson, R. J. and White, R. G. 1985. Computer simulation of energy budgets. Pages 261-290 *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, FL.

Hudson, R. J., Nixdorf, R., Kathnelson, S., Kam, M., and Jiang, Z. 1994. Management implications of seasonal bioenergetic cycles of wapiti (*Cervus elaphus*). Farming for the Future Project # FFF 92-0194. August 1994.

Hudson, R. J., Watkins, W. G., and Pauls, R. W. 1985. Seasonal bioenergetics of wapiti in western Canada. Pages 447-452 *in* P. F. Fennesey and K. R. Drew, eds. Biology of deer production. Royal Soc. New Zealand Bull. Vol. 22.

Jiang, Z. and Hudson, R. J. 1992. Estimating forage intake and energy requirements of free-ranging wapiti (*Cervus elaphus*). *Can. J. Zool.* 70: 675-679.

Jiang, Z. and Hudson, R. J. 1993. Fasting heat production and energy requirements of wapiti (*Cervus elaphus*) for maintenance and growth. *Proc. VII World Conf. Anim. Prod.* 3: 154-155.

Jiang, Z. and Hudson, R. J. 1994. Seasonal energy requirements of wapiti (*Cervus elaphus*) for maintenance and growth. *Can. J. Anim. Sci.* 74: 97-102.

Jones, J. K., Hoffman, R. S., Rice, D. W., Jones, C., Baker, R. J. and Engstrom, M. D. 1992. Revised checklist of North American mammals north of Mexico, 1991. Occasional Papers, The Museum, Texas Tech University No. 46. Lubbock, TX.

Kay, R. N. B. 1979. Seasonal changes in appetite in deer and sheep. *Agriculture Research Council Research Review.* 5: 130-157.

Keith, E. O., Ellis, J. E., Phillips, R. W., Dyer, M. I., and Ward, G. E. 1981. Some aspects of urea metabolism in North American bison. *Acta. Theriol.* 14: 257-268.

Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992a. Toward a new theory of feed intake regulation in ruminants. 1. Causes of differences in voluntary feed intake: critique of current views. *Live. Prod. Sci.* **30**: 269-296.

Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992b. Toward a new theory of feed intake regulation in ruminants. 3. Optimum feed intake: in search of physiological background. *Live. Prod. Sci.* **31**: 235-258.

Kirkpatrick, J. F., Bancroft, K. and Kincy, V. 1992. Pregnancy and ovulation detection in bison (*Bison bison*) assessed by means of urinary and fecal steroids. *J. Wildl. Dis.* **28**: 590-597.

Kirkpatrick, J. F., Gudermuth, D. F., Flagan, R. L. , McCarthy, J. C. and Lasley, B. L. 1993. Remote monitoring of ovulation and pregnancy of Yellowstone bison. *J. Wildl. Manage.* **57**: 407-412.

Kirkpatrick, J. F., Kincy, V., Bancroft, K., Shideler, S. E. and Lasley, B. L. 1991. Estrous cycle of the North American bison (*Bison bison*) characterized by urinary pregnanediol-3-glucuronide. *J. Reprod. Fert.* **92**: 541-547.

Krusei, W. K. 1985. The sheep raiser's manual. Williamson Publishing, Charlotte, VT. pp. 288.

Larter, N. C. and Gates, C. C. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Can. J. Zool.* **69**: 2677-2685.

Latham, H. 1871. Trans-Missouri stock raising - the pasture lands of North America: winter grazing. Reprinted by The Old West Publishing Company, Denver CO. 1962.

McDonald, P., Edwards, R. A. and Greenhalph, J. F. D. 1988. Animal nutrition - 4th ed. Longman Scientific and Technical, Longman Group Ltd.

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

Meagher, M. 1978. Bison. Pages 123-133 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America: ecology and management*. Stackpole Books, Harrisburg PA.

Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. *J. Mamm.*, **70(3)**: 670-675.

Miner, J. L. and Petersen, M. K. 1989. The effects of ruminal escape protein or fat on ruminal characteristics of pregnant winter grazing beef cows. *J. Anim. Sci.* **67**: 2782-2791.

Miner, J. L., Petersen, M. K., Havstad, K. M., McInerney, M. J. and Bellows, R. A. 1990. The effects of ruminal escape protein or fat on nutritional status of pregnant winter grazing beef cows. *J. Anim. Sci.* **68**: 1743-1750.

National Buffalo Association. 1993. Buffalo producer's guide to management and marketing. K. Dowling, ed. R. R. Donnelley & Sons Company, Chicago, IL.

Newman, A. L. 1977. *Beef Cattle*, 7th Edition. John Wiley & Sons. New York, NY.

Ogilvie, S. C. 1979. The park buffalo. Calgary-Banff Chapter, National and Provincial Parks Association of Canada. Sub. P. O. 91, The University of Calgary, Calgary, AB.

Peden, D. G., Van Dyne, G. M., Rice, R. W. and Hansen, R. M. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. *J. Appl. Ecol.* **11**: 489-498.

Peters, H. F. 1958. A feedlot study of bison, cattalo and Hereford calves. *Can. J. Anim. Sci.* **38**: 87-90.

Peters, H. F. 1984. American bison, and bison-cattle hybrids. Pages 46-49 *in* I. L. Mason, ed. *Evolution of Domesticated Animals*. Longman, London.

Plumb, G. E. and Dodd, J. L. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecol. Appl.* **3**(4): 631-643.

Polziehn, R. O., Beech, R., Sheraton, J. and Strobeck, C. 1996. Genetic relationships among North American bison populations. *Can. J. Zool.* **74**: 738-749.

Price, M. A. and White, R. G. 1985. Growth and development. Pages 183-213 *in* R. J. Hudson and R. G. White eds. *Bioenergetics of wild herbivores*. CRC Press. Boca Raton, FL.

Renecker, L. A., Blyth, C. A and Gates, C. C. 1989. Game production in western Canada. Pages 248-267 *in* R. J. Hudson, K. R. Drew and L. M. Baskin, eds. *Wildlife production systems: economic utilization of wild ungulates*. Cambridge University Press, Cambridge, UK.

Reynolds, H. W. 1991. Plains bison conservation in Canada. Pages 256-266 *in* G. Holroyd, G. Burns and H. Smith, eds. *Proceedings of the second endangered species and prairie conservation workshop*. January 1989. Regina, Saskatchewan. *Natural History Occasional Paper No. 15*. Provincial Museum of Alberta, Edmonton, AB. 284 pp.

Reynolds, H. W. and Gates, C. C. 1991. Managing wood bison: a once endangered species. Pages 363-371 *in* L. A. Renecker and R. J. Hudson, eds. *Wildlife production: conservation and sustainable development*. AFES Misc. Pub. 91-6. University of Alaska-Fairbanks. Fairbanks, AL.

Reynolds, H. W. and Hawley, A. W. L. 1987. Seasonal variation in forage quality. Pages 45-48 *in* H. W. Reynolds and A. W. L. Hawley, eds. *Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT Occasional Paper, No. 63*.

Reynolds, H. W. and Peden, D. G. 1987. Vegetation, bison diets, and snow cover. Pages 39-44 *in* H. W. Reynolds and A. W. L. Hawley eds. *Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT*. Occasional Paper, No. 63.

Reynolds, H. W., Glaholt, R. D. and Hawley, A. W. L. 1982. Bison. Pages 972-1007 *in* J. A. Chapman and G. A. Feldhamer, eds. *Wild mammals of North America, biology, management, economics*. The John Hopkins University Press, Baltimore, MD.

Richmond, R. J., Hudson, R. J. and Christopherson, R. J. 1977. Comparison of forage intake and digestibility by American bison, yak and cattle. *Acta. Theriol.* 22: 225-230.

Robitaille, J-F. and Prescott, J. 1993. Use of space and activity budgets in relation to age and social status in a captive herd of American bison, *Bison bison*. *Zoo Biology* 12: 367-379.

Roe, F. G. 1970. *The North American buffalo: a critical study of the species in its wild state*. 2nd ed. University of Toronto Press, Toronto, ON. 957 pp.

Rorabacher, J. A. 1970. *The American Buffalo in transition: an historical and economic survey of the bison in North America*. North Star Press. Saint Cloud, MN.

Rutley, B. D. and Rajamahendran, R. 1995. Circannual reproductive performance of female bison (*Bison bison*). Pages 242-245 *in* Proceedings Vol. 46 - Western Section, American Society of Animal Science and Western Branch Canadian Society of Animal Science, July 6-8, 1995.

Schaefer, A. L, Young, B. A. and Chimwano, A. M. 1978. Ration digestion and retention times of digesta in domestic cattle (*Bos taurus*), American bison (*Bison bison*), and Tibetan yak (*Bos grunniens*). *Can. J. Zool.* 56: 2355-2358.

Shaw, J. H. 1993. American bison: a case study in conservation genetics. Pages 3-14 *in* R. E. Walker, ed. *Proceedings: North American Public Bison Herds Symposium*, July 27-29, 1993, Lacrosse, WI.

Shi, Z. D. and Barrell, G. K. 1992. Effects of thyroidectomy on seasonal patterns of live weight, testicular function, antler development, and molting in red deer. Pages 443-449 in R. D. Brown, ed. *The biology of deer*. Springer-Verlag, New York, NY.

Smoliak, S. and Peters, H. F. 1955. Climatic effects on foraging performance of beef cows on winter range. *Can. J. of Agric. Sci.* **35**: 213-216.

Stelfox, J. B. 1993. Introduction to Alberta's hoofed mammals. Pages 1-4 in J. B. Stelfox, ed. *Hoofed Mammals of Alberta*, Lone Pine Publishing, Edmonton, AB.

Tainton, N. M. 1984. Veld and pasture management in South Africa. N. M. Tainton, ed. Shuter and Shooter (Pty) Ltd.

Taylor, R. E. and Bogart, R. 1988. Scientific farm animal production - an introduction to animal science. Macmillan Publishing Company, New York, NY. 618 pp.

Tolkamp, B. J. and Ketelaars, J. J. M. H. 1992. Toward a new theory of feed intake regulation in ruminants. 2. Costs and benefits of feed consumption: an optimization approach. *Live. Prod. Sci.* **30**: 297-317.

van Zyll de Jong, C. G. 1986. A systematic study of recent bison, with particular consideration of the wood bison (*Bison bison athabascae*, Rhoads 1898). Publications in Natural Sciences No. 6, National Museums of Canada, Ottawa, ON.

van Zyll de Jong, C. G., Gates, C., Reynolds, H. and Olsen, W. 1993. External variation in bison (*Bos bison* L). Pages 228-241 in R. E. Walker ed. *Proceedings: North American public bison herds symposium*, July 27-29, 1993, Lacrosse, WI.

Varel., V. H. and Dehority, B. A. 1989. Ruminal cellulolytic bacteria and protozoa from bison, cattle-bison hybrids, and cattle fed three alfalfa-corn diets. *Appl. Environ. Microbiol.* **55**: 148-153.

Wairimu, S., Hudson, R. J. and Price, M. A. 1992. Catch-up growth of yearling wapiti stags (*Cervus elaphus*). *Can. J. Anim. Sci.* 72: 619-631.

Walker, R. E. 1993. Editor, Proceedings: North American public herds symposium, July 27-29, 1993, Lacrosse, WI. pp. 444.

Ward, T. J. and Derr, J. N. 1997 (Abstr). Development and application for a genetic test for the identification of domestic cattle mtDNA haplotypes in related wild species. Proceedings: International Symposium of Bison Ecology and Management in North America. July 4-7, 1997, Bozeman, MO.

CHAPTER 2. Management, gain and productivity of bison (*Bison bison*) in the Peace Country¹

2.1 INTRODUCTION

With the increase in bison ranching came an identified need for research to improve productivity and management of commercial bison herds. Previous research, obtained from free-ranging and park herds (McHugh 1958; Meagher 1978; Reynolds et al. 1982; Hawley 1987; Reynolds and Hawley 1987; Hawley 1989; Meagher 1989; Renecker et al. 1989), has limited application to commercial herds for three main reasons. Park and free ranging herds are managed respecting policies of 1) limited manipulation of stocking densities, 2) no supplemental feeding, and 3) male:female ratios near 1:1.

Growth and production research is limited (Richmond et al. 1977; Schaefer et al. 1978; Hudson and Frank 1987; Koch et al. 1988) or dated (Peters 1958). Individual bison producers have developed the techniques that have enabled industry expansion (Dowling 1990; Anonymous 1993), but these techniques have not been confirmed scientifically.

Benchmarks for weight and growth rate of bison are not available and little is known about factors that affect growth. An understanding of growth has been the basis for the development of other livestock industries (Berg and Butterfield 1976).

The goals of this research were to 1) provide industry benchmarks for measures of growth (weight, average daily gain) of young bison (calves and yearlings), 2) obtain insights into which management factors affect these measures, and 3) establish quantitative relationships between management and growth measures.

A version of this chapter has been published by the Canadian Journal of Animal Science as Rutley, B. D., Jahn, C. M. and Hudson, R. J. 1997. Management, gain and productivity of Peace Country bison (*Bison bison*). Can. J. Anim. Sci. 77: 347-353.

2.2 METHODS

Members of the Peace Country Bison Association (northwestern Alberta and northeastern British Columbia) were recruited based upon the following criteria: 1) functional handling systems (a portable squeeze/scale unit was purchased for use at facilities that did not have reliable scales), 2) willingness to complete questionnaires regarding management practices and 3) sufficiently interested to commit to the research protocol.

The project required each producer to weigh calves during the normal winter handling periods (November to March) for the two winters following 1992 and 1993 calvings. An additional weighing of the 1992 calves was required during the spring of 1993 just before the calves were turned out to pasture (May 1993) (Table 2.1). All other management practices were left to the producer's discretion.

Producers completed surveys probing both general and specific management practices associated with 1992 and 1993 calving periods. Additional requirements included: 1) maintenance of feed records during the winter feeding period, i.e. between weaning and spring weighing (May 1993) and 2) participation in a pasture survey during the summer 1993. Feed designated for the winter 1992-93 feeding period was sampled during the winter 1992 handling, then forwarded for nutrient analysis by a certified laboratory (Griffin Laboratories, Kelowna, BC).

2.2.1 Classification, Calculations and Data

Management and herd data were collected and classified for the purposes of reporting survey data. Herd measures considered were 1) herd size, which describes the total number of animals within the herd (1, <30; 2, 31-60; 3, 61-100; 4, >100), and 2) herd management style, which was coded 1 when herd was kept as one group, 2 when herd split by gender, 3 when herd split by age, 4 when herd split for breeding purposes and 5

when more than one of the above were practiced. The number of years farming bison was classified 1 (< 5 yr.), 2 (5-9 yr.) and 3 (≥ 10). Producers with reported calving related problems were coded 1 while no reported problems were coded 2. Producers who reported herd health problems were coded 1 and 2 otherwise. Producers whose management practice included a routine program of vaccinations and anthelmintic treatments in the fall/winter period were classified as 1 while producers that did not have these procedures as a part of their routine animal health program were classified 2. Herds that were vaccinated were coded 1 and 2 otherwise. Herds that provided creep feed for the calves were coded 1 and 2 otherwise. Herds that were provided grain during the breeding season were classified as 1 while herds that were not were classified as 2. Provision of salt to the herd was coded 1 and 2 otherwise. Length of grazing season was rounded to the nearest month (range 5 to 12).

Weight data were collected from all animals during routine handling (unless otherwise stated). Average daily gains (ADG) were calculated on three intervals. Winter gain represents the change in body weight from the date weighed during the 1992 winter weigh period (calf, ~8-10 months of age) until the date weighed during the spring (1993) weigh period (~12 months of age). Subsequent gain represents the change in weight from spring weigh date until subsequent winter (1993) weigh date (yearling, ~18-20 months of age). Yeargain is the change of body weight from calf winter weigh date until the subsequent winter weigh date. Separate data collected from yearlings (1991 cohort), two-year olds (1990 cohort), cows and bulls supplements data from calves born in 1992 and 1993.

Three thousand three hundred twenty-nine (3329) bison were weighed. Following editing for completeness and accuracy, records from three thousand two hundred eighteen (3218) remained. One thousand three hundred twenty-four (1324) of 5057 head within 14 herds were weighed between November 16, 1992, and March 7, 1993 - the winter 1992 weigh period. Nine hundred forty four (944) of 1128 bison, within 8 herds weighed in May

1993 (spring 1993 weigh period), were calves. Two thousand two hundred seventy-three (2273) head within 10 herds were weighed between October 15, 1993 and March 8, 1994 during winter 1993. Of the 10 herds, eight had participated during the previous year. One hundred forty five (145) calves (born 1993) within two herds were also weighed in April 1994 (spring weight) and 36 from one herd were weighed again in October 1994 (winter weight).

2.2.2 Statistical Methods

Least square means and standard errors for measures of body weight were determined using the PROC GLM procedure (SAS ver 6.10, 1990). The model included the fixed effects of herd, gender and year (when applicable).

Data were summarized and analyzed on a herd-year basis. To determine the effect of management factors on measures of body weight (calf winter weight, calf spring weight, yearling winter weight, yearling spring weight, two-year old winter weight, adult winter weight, cow winter weight) the PROC REG procedure selection STEPWISE (SAS ver 6.21 for MS Windows) was used with the significance level for entry set at $P=0.15$.

The following factors were considered for inclusion within the model. Herd size describes the total number of animals within the herd. Bison years describes the number of years that the manager was farming bison. Gender describes the ratio of females (coded 0) to males (coded 1). As animals were not all weighed in the same month during winter, weigh date was included. Calving problems describes incidence of calving related problems as reported by the manager - presence of problems were coded 0 while herds reporting no problems were coded 1. Herdhealth describes the health status of the herd - managers reporting herd health problems were coded 0 and 1 otherwise. Producers whose management practice included a routine program of vaccinations and anthelmintic treatments in the fall were classified as 0 while producers that did not have these

procedures as a part of their routine animal health program were classified 1. Herds that were vaccinated were coded 0 and 1 otherwise. Herds providing creep feed for the calves were coded 0 and 1 otherwise. Herds that provided grain during the breeding season (flushing) were classified as 0 while producers that did not were classified as 1. Provision of salt to the herd was coded 0 and 1 otherwise. Grazing describes the number of months bison were foraging on pasture.

To determine the effect of management practice on measures of gain (winter gain, subsequent gain, yeargain), the PROC REG procedure selection STEPWISE (SAS ver 6.21 for MS Windows) was used with the significance level for entry set at $P=0.15$. Factors included in the analysis were herd size, bison years, gender, herdhealth, vaccinated, flushing, creep, salt and grazing. Winter weight (the initial weight for these periods) was also considered for inclusion within the model to represent the effect that initial weight would have on gain. It was expected that younger and or lighter animals could be on a steeper portion of the growth curve. The relationship between winter gain on subsequent gain was determined by PROC REG (SAS ver 6.21 for MS Windows).

2.3 RESULTS

2.3.1 Management Survey

Management survey data were combined for both years because it was possible for the management associated with the second year and the number of animals within the herd to differ (herd-year class). Fourteen (14) producers farming 5057 head participated in 1992. Ten producers (8 repeated) farming 2273 head participated in 1993. Half of the operations had 30 breeding females or less. The largest herds had over 450 breeding females and between 964 and 2420 total head. Land base and herd size were closely related, as 12 herds with 30 or fewer breeding females all farmed less than 130 ha.

Producers had farmed bison from 1 to 15 years, with the majority farming less than ten years. Most producers (83.3%) managed the herd as one group but grouping varied with herd size. Producers recorded births by date of occurrence during 13 of 23 possible herd calving periods. Weaning of 1992 calves occurred most often in January with equal occurrence among the late fall and winter months for 1993 calves (Figure 2.1).

In 1992, four herds reported some herd health problems but only one herd reported problems in 1993. Seven herds reported some calving problems in 1992 and 4 in 1993. Twelve of fourteen herds (1992) included administration of anthelmintics and/or vaccinations as a routine component of their herd management program. All twelve used an anthelmintic but only 5 herds vaccinated with multivalent vaccine. In 1993, 7 of 10 used anthelmintics while 4 of 7 administered a multivalent vaccine (Table 2.2). Only one producer administered vitamins to the herd.

Pasture season ranged from 5 to 12 months in 1992-93 and 5 to 10 months in 1993-94 (Figure 2.2). Providing extra grain for the breeding herd before and during the breeding season (flushing) was practiced by 6 of 8 herds in 1992 and 4 of 10 herds in 1993. Two of 12 herds in 1992 and 0 of 10 in 1993 provided additional grain to the suckling calves. Three of 11 herds in 1992 and 3 of 7 herds practiced feeding oats as a taming agent in 1993. No other form of special feeding practice was reported. The number of producers not providing supplements, providing mineral supplements, and providing salt with minerals combined were 3, 6, 5 (1992); and 3, 6, 1 (1993), respectively.

Winter feeding programs varied with herd and were characterized as minimal (winter grazing and/or poor quality roughage), supplemented (good quality roughage and some grain supplementation) or planned (specific ration for each component of the herd, feed analysis conducted). Only one producer analyzed winter feedstuffs.

During the winter feeding period for 1992-93, three herds received feedstuffs containing <8% CP, five herds received feeds at ~10% CP, while three herds received high protein supplements (\geq 12% CP). Eight herds had access to some winter graze.

A pasture survey conducted during the summer 1993 provided an estimate of the forage available to the breeding herd. Pasture management practices included: use of fertilizers, harrowing, rotation practice, whether or not browse was available and evidence of overgrazing. Fertilizer was applied by 6 of 13 producers, 7 harrowed pastures, all 13 herds had access to browse, 9 rotated pastures as needed (two did not rotate pastures while two had a strictly enforced rotational grazing program). Overgrazing, a somewhat subjective measurement, was evident in 5 of 12 farms with 4 farms having adequate forage throughout the grazing season. Some overgrazing was evident in three farms while one was not assessed. Producers consistently reported that bison consumed willow and new aspen growth - especially in the spring.

2.3.2 Weight

Mean winter weight (\pm SE) for 1486 bison calves was 187 ± 1 kg. Males (196 ± 2 kg) were heavier than females (180 ± 3 kg). Calves were heavier in 1993 than in 1992 for both genders (Table 2.3). Herd mean calf winter weight ranged from 164 ± 10 kg to 236 ± 3 kg.

Mean spring weight (\pm SE) for 944 bison calves (1992 cohort) was 209 ± 1 kg with females (197 ± 2 kg) lighter than males (217 ± 1 kg). Herd means ranged from 187 ± 1 kg to 234 ± 4 kg. Mean spring 1994 weight (\pm SE) (1993 cohort; n=145) was 216 ± 4 kg. Means were 238 ± 4 kg and 193 ± 4 kg for the two herds sampled while females (197 ± 4 kg) were lighter than males (234 ± 3 kg).

Mean yearling winter weight (\pm SE) was 310 ± 2 kg for 905 yearlings from 8 herds. Females weighed 290 ± 3 kg while males weighed 336 ± 3 kg. Mean herd yearling winter weight ranged from 296 ± 2 kg to 350 ± 10 kg. Spring weight for 134 yearlings (345 ± 8 kg) was analyzed ignoring yearling winter weight. Means were 279 ± 11 kg and 377 ± 8 kg for females and males, respectively.

Mean winter weight (\pm SE) of two year old bison was 418 ± 6 kg for 47 head from five herds. Females weighed 413 ± 6 kg while males weighed 467 ± 18 kg. Mean winter weight ranged from 304 ± 22 kg to 497 ± 4 kg.

Mean adult winter weight was 456 ± 3 kg for 458 head within 5 herds. Mean winter weight was 448 ± 2 kg and 594 ± 11 kg for females and males, respectively. Winter weight for females ranged from 294 to 573 kg with 50% heavier than 509 kg. Males ranged from 416 to 887 kg.

2.3.3 Effect of Management Factors on Weight

Calf winter weight (\pm SD) was affected only by herdhealth ($P = 0.08$). Calves within herds free of herd health problems averaged 198 ± 32 kg compared with 175 ± 30 kg for herds reporting problems. For analysis of calf spring weight, data from both years were combined. Only flushing ($P=0.13$) was associated with calf spring weight. Calf spring weight (\pm SD) was 191 ± 26 kg in herds that flushed compared with 227 ± 37 kg in those that did not.

Herdhealth ($P=0.05$) affected yearling winter weight. Yearling winter weight (\pm SD) in herds free of health problems was 331 ± 49 kg compared with 297 ± 39 kg for herds reporting problems. None of the factors were identified as having an effect on yearling spring weight.

No factors affected two year old winter weight. For adults, the stepwise regression analysis was determined only on females. Both length of grazing season ($P=0.08$) and weigh date ($P=0.01$) remained in the model. Female weight (\pm SD) was 461 ± 50 , 419 ± 49 , 460 ± 45 and 440 ± 44 kg for grazing length of 5, 6, 9 and 12 months, respectively.

2.3.4 Gain

Herd mean calf winter gain ranged from 0.17 to 0.59 kg d⁻¹ for the 339 calves within four herds. Both herdhealth ($P=0.055$) and salt ($P=0.048$) affected winter gain. Managers of herds reported free from herd health problems had mean (\pm SD) winter gain of 0.40 ± 0.17 kg d⁻¹ compared with 0.17 for the herd reporting health problems. Managers that provided salt to the herd had mean (\pm SD) winter gain of 0.26 ± 0.7 kg d⁻¹ compared with 0.60 kg d⁻¹ for the herd that did not receive salt. Subsequent gain was affected only by bison years ($P=0.067$). Means ranged from 0.28 to 0.70 kg d⁻¹. Yeargain was only affected by creep feeding. Calves within herds that had been provided creep feed prior to weaning had a lower yeargain (0.42 ± 0.04 kg d⁻¹) than calves in the herd that did not (0.60 kg d⁻¹).

Animals within herds did not consistently gain more in the subsequent summer through winter period than they did during the winter period. To determine the relationship between winter gain and subsequent gain, linear regression analysis was conducted using the same data set as above. Winter gain (X) significantly ($P < 0.0001$) affected subsequent gain (Y) (Figure 2.4). The equation,

$$Y = -0.50X + 0.71 \quad [3]$$

predicts that an animal that maintains weight stasis during the winter period will have a subsequent gain of 0.71 kg d⁻¹ under conditions equivalent to those from which the data

were obtained. Further analyses using scatter plots, revealed that the largest herd had an overwhelming effect on this relationship and that 3 of the 4 herds showed no correlation. The relationship between winter gain and subsequent gain was then analyzed on a herd mean basis. A similar equation was derived:

$$Y = -0.71X + 0.74 \quad [4]$$

To provide insights into whether or not the relationship (Model 3) was unique to this data set or could be used as a prediction equation, a small independent data set was available using records from 36 male bison from one herd (1993 cohort). Average winter weight was 253 kg on February 5, 1994. They weighed 259 kg on May 1, 1994 (winter gain = 0.07 kg d⁻¹) and 404 kg October 28, 1994 (yearling gain = 0.57 kg d⁻¹). Actual subsequent gain (0.80 kg d⁻¹) was higher than the predicted gain (0.68 kg d⁻¹) [$Y=0.71-(0.50*0.07)$]. However, as the test data were limited to males while the prediction equation was derived with data for males and females, this fit tends to validate the equation.

2.4 DISCUSSION

2.4.1 Typical Peace Country Bison and Bison Operation

A typical Peace Country bison profile was developed from mean values for each weight and gain data set. Caution is advised because this profile uses means from different data sets and does not represent a cohort of animals that were studied from birth to maturity.

The typical Peace Country bison (Table 2.4) is born May 15, is weaned at 240 days of age on January 15 weighing 184 kg. It gains 0.21 kg d⁻¹ until May 15 when it weighs 209 kg at 12 months of age. During the subsequent summer to winter period it gains 0.41 kg d⁻¹.

It weighs 310 kg by January 15 as a long yearling. Over the winter, males gain 0.42 kg d^{-1} while female weight does not change. During the second summer, bison females gain 0.54 kg d^{-1} (males gain 0.35 kg d^{-1}) to weigh 413 kg (467 kg male). Females gain slightly the following year (0.10 kg d^{-1}) while males gain 0.35 kg d^{-1} . As an adult, a female will average 447 kg. The profile weight for adult males (594 kg) is not completely valid because it has not been corrected for age. Breeding males do not remain in Peace Country herds until full maturity and Renecker et al. (1989), using records from Elk Island National Park bison, have shown that male bison were still increasing in body weight at 10 years of age.

Three profiles were derived for typical Peace Country bison operations. Small herds represent producers that have approximately 30 cows, designate up to 130 ha for the bison operation and have significant off-farm responsibilities. The second designation refers to producers that farm full time and average 110 breeding females with up to 1040 ha dedicated to bison. The final designation refers to large ranches with over 450 breeding females and 2080 ha of land allocated to bison. There was only one participating herd that farmed between 150 and 450 breeding females, however the exact number of animals within the herd was unknown.

2.4.2 Management, Gain and Productivity

Calf and yearling weight was quite variable. Determination of the effects of management factors on measures of weight was limited by the size of the data set. However, weigh date, herd health, grain flushing during breeding season and length of grazing season were identified through stepwise regression analyses as affecting measures of body weight. Maintaining a healthy herd is important to herd productivity. Herds that reported some health problems had lower calf winter weight and yearling winter weight than herds reporting no herd health problems.

Wild ungulates tend to gain rapidly when conditions are favourable (Price and White 1985). Growth patterns are such that they grow more slowly during the winter and more rapidly during the summer. This pattern is in contrast to cattle that more closely follow the logistic curve (Goonwardene et al. 1981) without seasonal rhythms. Based on observations by Christopherson et al. (1977, 1978, 1979 a and b) of seasonal variation in metabolic rate and lower winter feed intake of feedlot finished bulls (unpublished data, Rutley 1995), lower winter gain followed by summer compensatory gain is expected.

There is evidence from the current research, and similar research with wapiti stags (Wairimu et al. 1992), that producers wishing to obtain maximum yearling gain during the grazing season should not target for maximum winter gain in calves. Bison calves that gained the least during the winter feeding program tended to gain in a compensatory manner during the subsequent summer to winter period. Producers are advised to reconsider winter feeding programs, because the cost of winter gain is usually greater than summer gain. However, as this relationship was greatly influenced by one herd, further study is recommended prior to implementation as a management practice.

Although minimum winter gain corresponded to compensatory gain for Peace Country bison, summer pasture may not be the best way to maximize overall gain. Stanton et al. (unpublished data 1995) reported heavier yearling winter weight (393 kg) after feeding a 12% CP ration in the feedlot compared to yearling Peace Country bulls (337 kg) after summer grazing (spring beginning weight was 235 kg and 217 kg, respectively). Although there was considerable advantage for the bulls fed the concentrate rations, and because bison respond to high concentrate rations to finish at a younger age (under 24 months), cost of gain comparisons and designation of optimum age to place bison bulls on a finishing ration need to be determined.

2.5 CONCLUSIONS

Measures of body weight and gain for bison were reported. Herd health, grain flushing, weigh date, length of grazing season were identified as affecting measures of weight and gain in Peace Country bison. Further study using a within herd design is needed to determine the effect of factors like creep feeding, flushing, multivalent vaccines, anthelmintics, and winter gain on measures of productivity. Maintaining optimum herd health is important. Bison herds that reported herd health problems had lower calf winter weight and yearling winter weight than herds reporting no herd health problems.

Bison calves that had the highest average daily gain during winter tended to have the lowest average daily gain on summer pasture and lower overall average daily gain from weaning to yearling weight. A prediction equation was derived. Although this equation was affected by one large herd, the relationship held when tested on an independent data set. There remains evidence that producers planning to maximize subsequent gain in yearlings should target for minimal winter gain as calves, however, further study is recommended prior to implementation as an accepted management practice. It is also recommended that producers evaluate the economics of their winter and summer feeding programs to determine the most economical method of feeding.

The results from this study of Peace Country bison are sufficient to serve as industry benchmarks to which producers can compare their herds.

Table 2.1 Number of Peace Country bison weighed during each weigh period.

Cohort	winter wt	spring wt	winter wt	spring wt	winter wt
	November 1992 to March 1993	May 1993	November 1993 to April 1994	May 1994	October 1994
1993 calves	--	--	597	145	36
1992 calves	889	799	723	na	na
1991 calves	182	136	na	na	na
1990 calves	47	na	na	na	na
before 1990	458	na	na	na	na

Table 2.2. Summary of herd health treatments routinely applied by Peace Country bison managers^z

Category	Treatment type	Animals	1992 ^y	1993
No treatments	na	na	2	3
Treatments	Vaccinations ^y	Calves only	4	2
		Whole herd	1	2
		Not administered	7	3
Anthelmintics ^y		Not administered	0	1
		Fall treatment	11	7
		Fall and Spring treatment	1	0

^z Fourteen herds surveyed in 1992, twelve in 1993.

^y Cattle vaccines and anthelmintics as defined by the producer.

Table 2.3. Winter weights (kg \pm SE) of Peace Country bison calves

Year	All		Females		Males	
	n	kg	n	kg	n	kg
1992	889	183 \pm 1	354	175 \pm 2	535	189 \pm 1
1993	597	197 \pm 1	297	181 \pm 3	300	203 \pm 3

Table 2.4. Profile of typical Peace Country bison

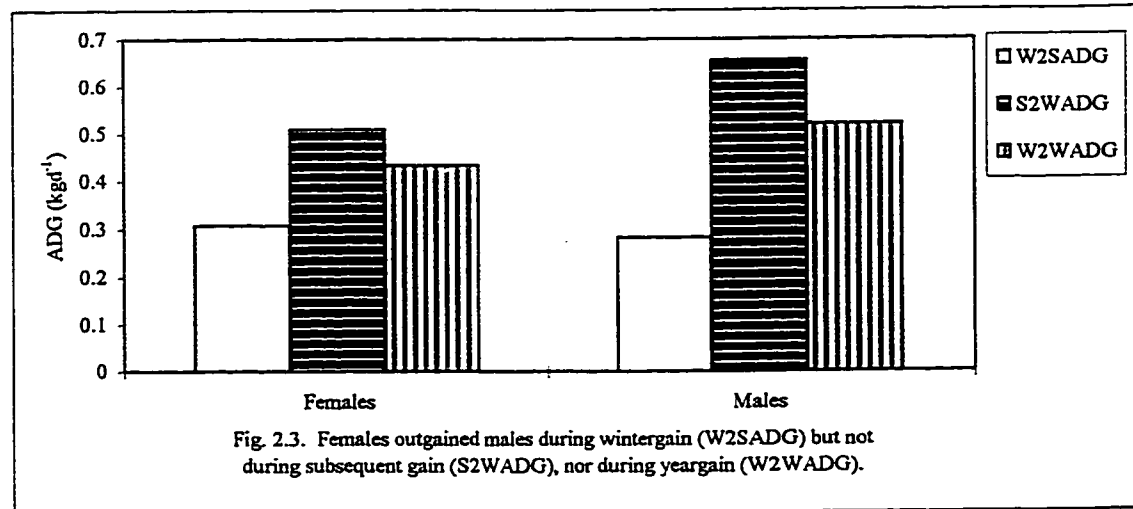
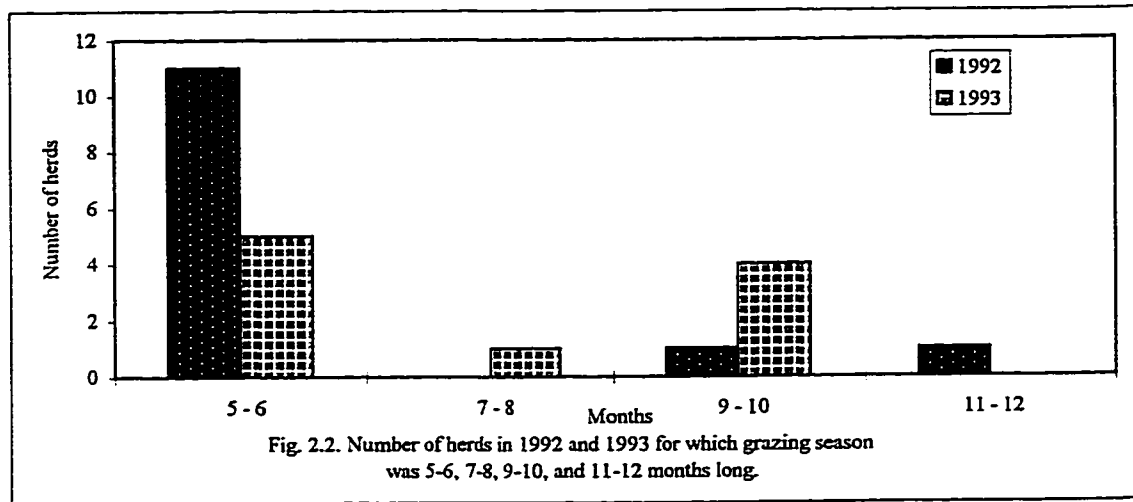
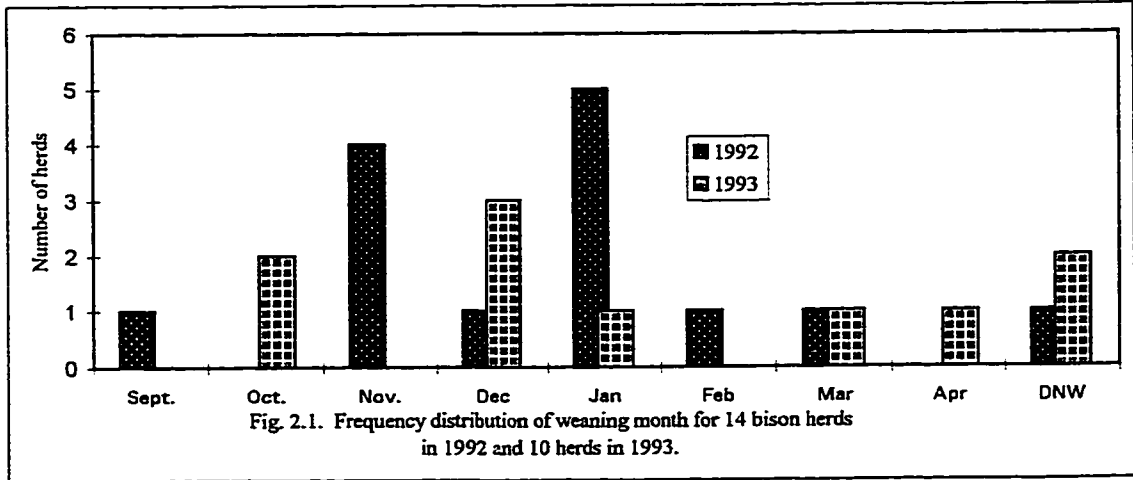
Status	Age (mon) ^z	Weigh Date ^z	Females			Males		
			n	Wt (kg)	ADG kg d ^{-1w}	n	Wt (kg)	ADG kg d ^{-1w}
Birth	--	May 15	y	25	--	y	30	--
Weaned	8	January 15	354	175 ± 2	0.61	535	189 ± 1	0.65
Yearling	12	May 15	399	197 ± 2	0.18	506	217 ± 1	0.23
Long Yearling	20	January 15	438	290 ± 3	0.38	467	336 ± 3	0.49
Two Year Old	24	May 15	45	280 ± 11	-0.08	89	378 ± 8	0.35
Long Two	32	January 15	42	413 ± 6	0.54	5 ^v	467 ± 18	0.36
Adult	>36	January 15	430	448 ± 2	0.10	28	594 ± 11	0.35

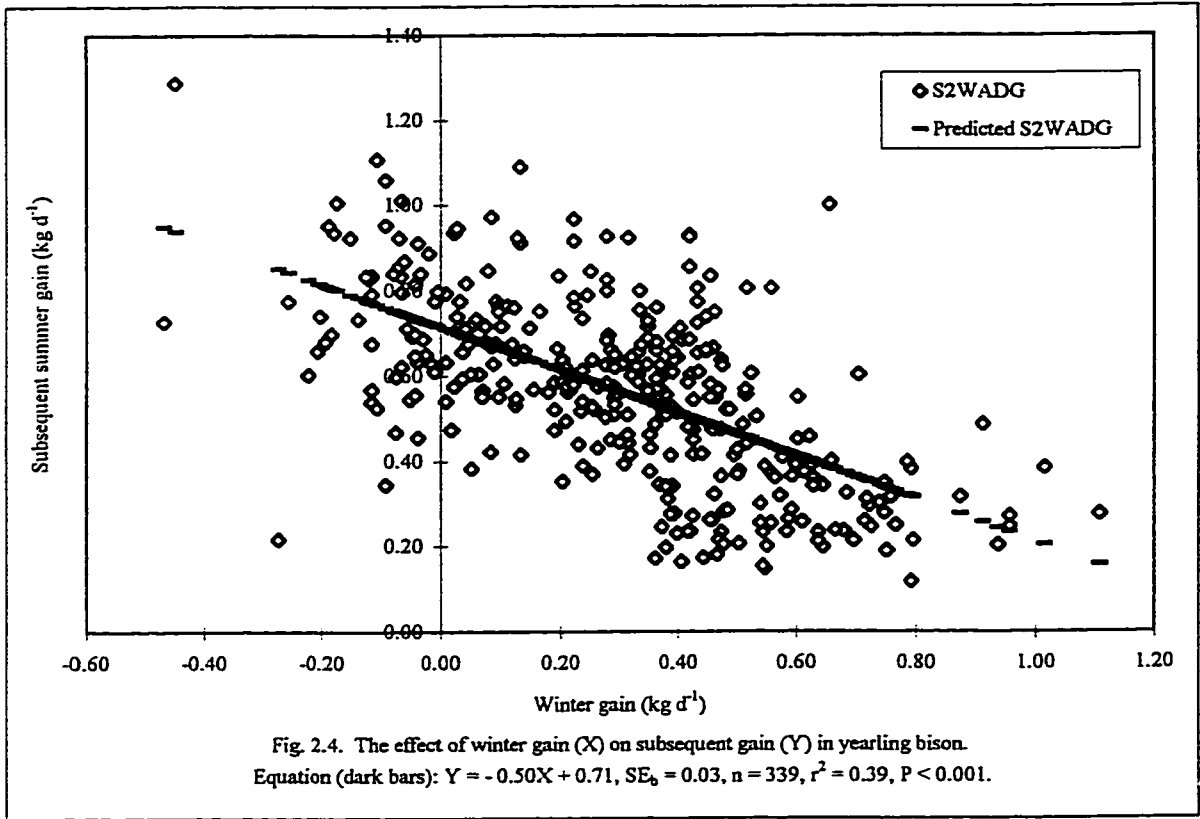
^z Theoretical ages and weigh dates based on survey data.

^y As calves (n = 62) were not sexed at weighing, birthweight represents an estimate for each gender (data provided by Herd 13).

^w Interval gain is weight change between sequential weigh periods divided by time (days).

^v Although survey data was limited, weights correspond with weights of similar aged bulls within the feedlot (Rutley, unpublished data).





2.6 REFERENCES

Anonymous. 1993. Bison breeders handbook. 3rd ed. American Bison Association, Denver, CO.

Berg, R. T. and Butterfield, R. M. 1976. New concepts in cattle growth. Sydney University Press, Sydney, Australia.

Christopherson, R. J., Gonyou, H. W. and Thompson, J. R. 1979a. Effects of temperature and feed intake on plasma concentration of thyroid hormones in beef cattle. *Can. J. Anim. Sci.* **59**: 655-661.

Christopherson, R. J., Hudson, R. J. and Christophersen, M. K. 1979b. Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Can. J. Anim. Sci.* **59**: 611-617.

Christopherson, R. J., Hudson, R. J. and Richmond, R. J. 1977. Feed intake, metabolism and thermal insulation of bison, yak, Scottish Highland and Hereford calves during winter. Pages 51-52 *in* 55th Annual Feeders Day Report. Agriculture and Forestry Bulletin, University of Alberta, Edmonton, AB.

Christopherson, R. J., Hudson, R. J. and Richmond, R. J. 1978. Comparative winter bioenergetics of American bison, yak, Scottish Highland and Hereford calves. *Acta Theriol.* **23**(2): 49-54.

Dowling, K. 1990. Buffalo producer's guide to management and marketing. National Buffalo Association. R. R. Donnelley & Sons Company, Chicago, IL.

Goonwardene, L. A., Berg, R. T. and Hardin, R. T. 1981. A growth study of beef cattle. *Can. J. Anim. Sci.* **61**: 1041-1048.

Hawley, A. W. L. 1987. Bison and cattle use of forages. Pages 49-52 *in* H. W. Reynolds and A. W. L. Hawley, eds. Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT. Occasional Paper No. 63. Canadian Wildlife Service, Edmonton, AB. 74 pp.

Hawley, A. W. L. 1989. Bison farming in North America. Pages 346-361 *in* R. J. Hudson, K. R. Drew and L. M. Baskin, eds. Wildlife production systems: economic utilization of wild ungulates. Cambridge University Press, Cambridge, UK.

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

Koch, R. M., Crouse, J. D. and Seideman, S. C. 1988. Bison, Hereford and Brahman growth and carcass characteristics. Beef Research Report, Roman L. Hruska, US Meat Animal Research Center.

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

Meagher, M. 1978. Bison. Pages 123-133 *in* J. L. Schmidt and D. L. Gilbert, eds. Big game of North America: ecology and management. Stackpole Books, Harrisburg, PA.

Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. *J. Mammal.* 70(3): 670-675.

Peters, H. F. 1958. A feedlot study of bison, cattalo and Hereford calves. *Can. J. Anim. Sci.* 38: 87-90.

Price, M. A. and White, R. G. 1985. Growth and development. Pages 183-213 *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, FL.

Renecker, L. A., Blyth, C. A and Gates, C. C. 1989. Game production in western Canada. Pages 248-267 *in* R. J. Hudson, K.R. Drew and L. M. Baskin, eds. Wildlife production systems: economic utilization of wild ungulates. Cambridge University Press, Cambridge, UK.

Reynolds, H. W., Glaholt, R. D. and Hawley, A. W. L. 1982. Bison. Pages 972-1007 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America, biology, management, economics. The John Hopkins University Press, Baltimore, MD.

Reynolds, H. W. and Hawley, A. W. L. 1987. Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT. Canadian Wildlife Service Occasional Paper No. 63.

Richmond, R. J., Hudson, R. J. and Christopherson, R. J. 1977. Comparison of forage intake and digestibility by American bison, yak and cattle. Acta. Theriologica. **22**: 225-230.

SAS Institute Inc. 1990. SAS/STAT user's guide. Version 6.10, 4th ed. SAS Institute, Inc. Cary, NC.

Schaefer, A. L., Young, B. A. and Chimwano, A. M. 1978. Ration digestion and retention times of digesta in domestic cattle (*Bos taurus*), American bison (*Bison bison*), and Tibetan yak (*Bos grunniens*). Can. J. Zool. **56**: 2355-2358.

Wairimu, S., Hudson, R. J. and Price, M. A. 1992. Catch-up growth of yearling wapiti stags (*Cervus elaphus*). Can. J. Anim. Sci. **72**: 619-631.

CHAPTER 3. Activity budgets and foraging behaviour of bison on seasonal pastures

3.1 INTRODUCTION

Free-grazing ruminants regularly alter their daily activity pattern in response to seasonal fluctuations in forage biomass. They reduce foraging time as forage quality increases and respond to declining forage biomass by increasing foraging time (Trudel and White 1981). Under severe environmental conditions, free-grazing ruminants will reach the point when energy expended to obtain forage is greater than net energy recovered from the forage (Parker et al. 1996). The benefit of reducing activity to conserve energy is offset by the increased risk of predation. Presumably, animals instinctively engage in activities that maximize fitness (McFarland 1977). Foraging strategies of grazing ruminants have been characterized as time minimizing or energy maximizing (Belovsky and Slade 1986).

Light intensity (Eriksson et al. 1981), thermal stress (Malachek and Smith 1976), disturbance (Tester and Heegan 1965), sward biomass and structure (Renecker and Hudson 1986), and physiological factors (Ketelaars and Tolkamp 1992a, 1992b; Tolkamp and Ketelaars 1992) influence changes in activity patterns. The requirements of rumination and movement of particulates through the reticulo-rumen complex (White et al. 1984; Spalinger et al. 1986; Mathison et al. 1995) restrict the amount of forage that a ruminant can ingest. Rate of passage is related to forage quality and amount (Mathison et al. 1995).

Daily activity patterns of many wild ruminants have been documented (Gates and Hudson 1983; Belovsky 1986; Collins and Smith 1989). Under commercial farm conditions (free from predators), both wapiti (*Cervus elaphus*) (Gates and Hudson

1983; Hudson and Watkins 1986) and reindeer (*Rangifer t. tarandus*) (Ericksson et al. 1981) exhibit regular polyphasic activity patterns driven by an underlying rumen depletion-repletion cycle.

Foraging behaviour (Peden et al. 1974; Hudson and Frank 1987; Plumb and Dodd 1993), activity budgets (Belovsky and Slade 1986) and activity of penned bison (Robitaille and Prescott 1993) have been studied. However, seasonal patterns under pasture conditions have not.

Wild ruminants spend most of their day alternating between foraging and resting/ruminating activity (Renecker and Hudson 1993). This activity is interrupted while walking between bedding and feeding sites, moving to alternate feeding sites, and (or) predator avoidance. Farmed ruminants are generally not exposed to disturbance from predators, therefore a full expression of activity rhythms would be expected. Furthermore, activity rhythms under game farm conditions may become a full expression of the rumen repletion-depletion cycle.

As mean plant cell wall thickness impacts on handling time (Spalinger et al 1986), it would be expected that time spent ruminating and handling would increase from summer to winter. A corresponding decrease in the number of activity cycles in winter would result. In summer, the number of cycles would be expected to increase, as lower mean cell wall thickness would enable faster clearance of particulates, thus enabling bison to return to grazing more quickly. It is expected that supplemental feeding of bison during winter would alter this relationship because the mean cell wall thickness of cured forages is generally lower than winter forage.

The goal of this study was to determine the response of bison to seasonal variations in forage quality as a contribution to the understanding of the nature of bison. The objectives were to 1) document daily foraging activity so that seasonal activity budgets

and foraging behaviour could be determined, and 2) obtain data from which seasonal metabolic energy requirements could be determined (Chapter 4).

The following hypotheses were tested in support of the goal and objectives:

1. Foraging time will increase and resting time will decrease correspondingly, while time associated with minor activities will remain constant from summer to winter.
2. Length of foraging bout will be longer in winter compared with summer; foraging bouts will be more frequent in summer compared with winter.
3. Forage consumed (feeding station) will be higher in quality (higher in crude protein, digestible energy, lower in fibre and lignin) than forage available within grazing patch and sward.
4. Bite size will be greater in summer than winter, bite rate will increase from summer to winter, and foraging intensity will be greater in winter compared to summer.
5. Dry matter intake will be greater in summer than winter.

As the bison under study were habituated to humans, the observed activity patterns provided a background to which behaviour of wild bison could be compared. It also provided a basis for comparison with commercially fed feedlot bison.

3.2 METHODS

3.2.1 Location and Climate

The field study was conducted at the Center for Agricultural Diversification, Dawson Creek, BC (55°-44'-30" N, 120°-30' W; elevation 670 m) located 600 km northwest of Edmonton, AB. The area is located entirely within the Alberta Plateau - an extension of the Great Plains. The area is in the aspen grove (wooded bluffs interspersed with open grasslands) and mixed-wood (*Populus tremuloides*, *Populus balsamifera*, *Pinus contorta*, *Picea miriana* and *Salix spp.*) sections of the boreal forest (Department of Energy, Mines and Resources 1974). Annual average rainfall is 430 mm with 330 mm falling during the growing season (April to September). Annual snow accumulations of 40 cm are common but subject to reduction due to recurring chinook winds. Mean January, July, and annual temperatures at Dawson Creek, BC are -15°C, 15°C, and 1°C, respectively, while daily temperatures of 32°C (August) and -44°C (January) are extremes.

3.2.2 Vegetation and Phenology

The study pasture was 5.4 ha in size, was fenced for bison and had a southern aspect. It was established, over 10 years earlier, to tame grasses and forbs, had not been fertilized for 5 years, yet remained relatively productive. Grasses predominated and included smooth brome (*Bromus inermis*), timothy (*Phleum pratense*), quackgrass (*Agropyron repens*) and Kentucky bluegrass (*Poa pratensis*). Predominant forbs were alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*) and dandelion (*Taraxacum officinale*). Although forages began growth in late April, they were unable to sustain grazing until late May. Dandelions emerged in mid-May and were the most visible dicot in early June. Inflorescence of grasses appeared by mid-June and alfalfa was in full bloom by July 1. First frost occurred mid-September and grasses senesced by late September.

3.2.3 Study Animals

Three male and three female bison yearlings, considered to represent commercial bison, were selected from a local commercial herd and transported to the study location in late May each year. Animals were selected from the 1993 calf crop for Year 1 trials (June 1994 to March 1995) and from the 1994 calf crop for Year 2 (June 1995 to December 1995). The source herd was checked routinely by the owner, making all animals accustomed to human activity prior to the study. Study animals were the same animals used to determine seasonal energy requirements of free-grazing bison (Chapter 4). Coloured ear tags were attached in both ears prior to release into study pasture.

3.2.4 Activity Budgets

Bison were observed for activity accommodating the protocol requirements of Chapter 4. Therefore, bison were observed for activity during the seven trial periods conducted at each equinox and solstice between June 1994 and December 1995. Two consecutive 24 h observation sessions began six days (Day -6) prior to the handling of the herd (designated as Day 0). The third 24 h observation session occurred three days (Day 3) after the herd was handled while in conjunction with the collection of fecal samples from the free-grazing bison. Disturbance attributed to the presence of the observers was considered minimal. By coincidence, full moon corresponded with at least a portion of the first five trial periods.

Animals were observed from a truck with binoculars. To determine the scan frequency required to provide an adequate estimate of forage intake, activities of individual animals were recorded at 5-minute intervals using the instantaneous scan method (Altmann 1974). Activity categories were: 1) foraging - actively engaged, 2) foraging - moderately engaged, 3) foraging - consuming hay, 4) ruminating, 5) resting - standing, 6) resting - lying (bedding), 7) resting - sleep (laying flat out), 8) minor -

water, 9) minor - walking, 10) minor - play, after Gates and Hudson (1983). Bison did not have access to browse. Interacting with other bison, grooming and 'milling' were included in the minor activity category. Rumination was recorded during daylight hours only. Location within the field by grid and weather conditions were simultaneously recorded.

Chapter 4 protocol required a high level of resolution on foraging activity to facilitate estimation of dry matter intake via the bite count method. Therefore, an evaluation was conducted to determine whether 5, 10 or 15-minute scan intervals could adequately represent foraging, resting and minor activities. This evaluation was conducted using data collected during June 1994 observation sessions. Compared to 5-minute scans (benchmark), scans at 10 and 15-minute intervals provided records of foraging activity that varied from the benchmark by -55% to 35% and -10% to 30%, respectively. Minor activities occurred infrequently. Within one 2 h segment, the 10-minute scan method overestimated minor activity by 200%, while the 15-minute scan method missed the activity completely (with a concurrent 30% overestimation of grazing activity). Therefore, 5-minute activity scans were considered necessary to adequately categorize activity in free-grazing bison at the resolution required to determine dry matter intake and elucidate whether or not seasonal changes in minor activities exist.

The analysis was based on 38,880 individual records, recorded at 5-minute intervals, obtained during 6,048 scans within twenty-one 24 h observation sessions. Because it was not always possible to identify individuals during night hours, only the number of animals participating in an activity were recorded and used for analyses. To accommodate occasional unequal group sizes and different starting times, the following method of summation was used. The total number of animals observed and the number of animals participating in a designated activity during each 5-minute

interval was recorded. The number of animals participating in each category for each 5-minute interval over the next 24 h was summed to become the category 24 h total (CT24). CT24 for each category was then expressed as a ratio of the total number of possible animal observations (CT24%). CT24% data from the two 24 h observation sessions at Day -6, combined with the Day 3 observation session CT24% data, became the data set for the trial period. For the final analyses of activity budgets, the subcategories within foraging, resting and minor activity were collapsed (Gates and Hudson 1983).

Length of foraging bout was calculated as the interval between the time when the majority (> 50%) of the group began foraging until the majority stopped foraging. Bedding bouts were defined as the interval between when the majority of the herd was laying down until the majority was standing up and moving away from the bedding site. Time foraging or bedding was calculated as the sum of 5-minute intervals associated with that activity.

3.2.5 Forage Biomass and Quality

To estimate available forage within the study pasture (sward), ten 0.5 m² quadrats were assigned in a completely random design in Year 1 and a stratified random design in Year 2. In Year 2, the study pasture was divided, by grid, into 10 equal sized areas. A location within the grid was selected at random and the corresponding site within the field was staked (station). In conjunction with each trial period, a site immediately adjacent to the station was sampled in a manner that prevented re-sampling.

To determine if bison were grazing areas within the sward that were different from the sward in general, bison were tracked for defoliation during each trial period. Once defoliation was confirmed, bison were gently disturbed and the grazed area flagged (grazed patch). Ten sites were identified during each trial period. Within each grazed

patch, the site of defoliation was identified. Immediately adjacent to each grazed patch, forage that was similar to the defoliation site, yet had escaped immediate grazing, was sampled (feeding station).

Plant height for both the sward and grazed patches was estimated as the average of twelve measures of plant height, selected at random within a 1/12 area of the 0.5 m² quadrat. An ocular estimate, taken from four feet above the quadrat, was used to estimate the ratio of bare ground:grasses:weedy forbs:cultivated forbs:litter:feces for each sward site and grazed patch. Both sward sites and grazed patches were harvested with hand shears and hand raked to simulate close grazing. Harvested forage was separated as grasses, forbs and litter, dried at 60° C, and stored until forwarded for composition analyses (Norwest Laboratories, Lethbridge, AB).

To determine the composition of forage consumed, 20 emulated bites were collected from forage immediately adjacent to the sward site (feeding station) by emulating the depth within the sward that the bison had been grazing (Hudson and Frank 1987). Identification of whether grasses or forbs had been consumed was considered to be straightforward. Emulated bites were dried and handled equivalent to procedures previously described.

Growing conditions for 1994 and 1995 were typical for the Peace Country. Because the stocking rate within the trial pasture was so low, following the June 1994 trial the six trial bison were removed to an adjacent pasture and 22 two year old bison bulls were grazed for 12 days to emulate moderately intense grazing. Trial bison were not returned until 21 days prior to trial 2 (September 1995). In Year 2, no additional grazing occurred and the trial bison remained within the pasture for the duration of the summer.

3.2.6 Statistics and Calculations

Intake and activity data for males and females were combined as gender was not considered a source of variation. A one-way analysis of variance (ANOVA, MS Excel ver 5.0) was used to determine means and standard errors (square root of variance divided by n) for measures of foraging, resting and minor activity, plant height, bite rate and foraging rate for each trial period (June 1994, September 1994, December 1994, March 1995, June 1995, September 1995, December 1995) (Model 1).

Seasonal differences in the activity budget were determined using the PROC MIXED procedure (SAS ver 6.21 for MS Windows, 1996). Three season-feed groups were created. The summer grazing group consisted of the June 1994, September 1994, June 1995 and September 1995 trials. The December 1995 trial was the winter grazing group. March 1995 and December 1995 were included in the supplementation group. Season-feed group was included in the model as a fixed effect. Trial within season-feed group (error term) was included as a random effect (Model 2). Tukey's test was used for multiple comparisons.

The number of foraging and bedding bouts, foraging and bedding bout length, and total foraging and bedding time were analyzed using the PROC MIXED procedure (SAS ver 6.21 for MS Windows, 1996). Seasonal differences were determined using the three season-feed groups described above. Season-feed group was included in the model as a fixed effect. Trial within season-feed group (error term) was included as a random effect (Model 3). Tukey's test was used for multiple comparisons.

As the dependent variables associated with quadrat structure were correlated with each other, analyses were conducted using the GLM-MANOVA (SAS ver 6.21 for MS Windows, 1996) (Model 4). Univariate ANOVA were reported for individual dependant variables.

As measures of forage composition are correlated, a multivariate analysis was used to determine differences in composition within sward sites and grazed patches. Due to the limited number of independent observations, multivariate analyses were performed on only crude protein and acid detergent fibre in the PROC GLM-MANOVA procedure (SAS ver 6.21 for MS Windows, 1996) (Model 5).

To test for differences in biomass within sward sites and grazing patches the PROC MIXED procedure (SAS ver 6.21 for MS Windows, 1996) was used. Sward sites and grazing patches were considered to be the treatments. Trial corresponded to the seven trial periods previously described. Treatment was considered fixed. Trial and trial*treatment (error term) were included as random effects (Model 6). Tukey's test was used for multiple comparisons

Mean composition of seasonal forage within feeding stations were determined using the PROC MEANS procedure (SAS ver 6.21 for MS Windows, 1996). Due to the limited number of independent observations, multivariate analyses were performed including only crude protein and acid detergent fibre in the PROC GLM-MANOVA procedure (SAS ver 6.21 for MS Windows, 1996) (Model 7). This procedure was repeated including crude protein and acid detergent lignin in the model.

Seasonal differences in bite rate and dry matter intake were determined using the PROC GLM procedure (SAS ver 6.21 for MS Windows, 1996). Grazing period was defined as June (June 1994 and 1995), September (September 1994 and 1995), December (December 1994) and March (March 1995). Grazing period was considered a treatment and was included in the model (Model 8) as a fixed effect. Trial within grazing (error term) was included as a random effect. Multiple range tests were performed with the Tukey option.

3.3 RESULTS

3.3.1 Seasonal Activity Budgets

Time allocated to foraging, resting and minor activities, as a percentage of the 24 h activity budget, varied across trial periods (Table 3.1). Resting and foraging were the most time consuming activities of yearling bison. Time foraging was always less than time resting and ranged from $40 \pm 2\%$ while grazing in December 1994 to $20 \pm 2\%$ in March 1995 during supplementation. Bison allocated significantly ($P < 0.05$) more time (means \pm SE) to foraging during winter grazing ($39.6 \pm 2.4\%$) than for summer grazing ($26.6 \pm 1.2\%$) and during supplementation ($22.0 \pm 1.7\%$) (Table 3.2).

Time resting during winter grazing ($58.5 \pm 2.6\%$) was significantly shorter than $71.1 \pm 1.9\%$ of the daily activity budget during supplementation (Table 3.2). Time resting during summer grazing was not significantly different than during supplementation. Bison often interacted with each other and with bison in an adjacent field. They also milled about, particularly after a foraging bout. These activities were categorized as resting behaviour because movement was minimal.

Minor activities comprised a low of $2 \pm 1\%$ of the activity budget during December 1995 and as much as $12 \pm 1\%$ during June 1995 (Table 3.1), however, seasonal differences were not significant (Table 3.2).

3.3.2 Seasonal Foraging and Resting Bouts

Number of daily foraging bouts and foraging bout length did not vary significantly across seasons, however, total daily foraging time (min d^{-1}) did ($P < 0.05$). During winter grazing, bison foraged $763 \pm 62 \text{ min d}^{-1}$ compared with 470 ± 32 and $418 \pm 44 \text{ min d}^{-1}$ during summer grazing and supplementation, respectively (Table 3.3).

Number of bedding bouts and total bedding time did not vary with season, however length of bedding bout did ($P < 0.05$). Length of bedding bouts was greatest during winter grazing ($276 \pm 26 \text{ min d}^{-1}$) compared with 121 ± 13 and $142 \pm 18 \text{ min d}^{-1}$ for summer grazing and supplementation, respectively (Table 3.3).

3.3.3 Resting Behaviour

In June and September, bison typically followed a foraging bout by ruminating, primarily while bedded down. In December and March, however, an extended period of standing (up to 90 minutes) usually preceded bedding down and ruminating. Lying on side occurred frequently in June, occasionally in September, infrequently in March, but never in December. Sleeping bouts rarely lasted beyond 15 minutes.

Throughout the study, bison had preferred bedding sites. The southwest corner of the study pasture, adjacent to another group of bison, was the preferred location throughout all seasons by both groups of bison. During June and September, bison would lie against the fence in shade provided by trees while during winter they frequented the hollow between the southwest corner and the knoll. This small knoll uphill from the southwest corner, was the second most frequently used bedding site and was often used during nights in December and March.

Infrequently bison bedded in the southeast corner of the field beside the water source (June and September) or supplemental feed (March 1995 and December 1995). They only bedded once along the north fence line when they bedded in deep grass during insect harassment in June 1994.

The proportion of daytime resting activity during which rumination occurred was 21%, 18% and 14% for June grazing, September grazing and during supplementation in March 1995, respectively. Rumination was detected during darkness but

quantification was not possible. Length of rumination bouts (\pm SE) during June was similar to length of rumination bouts in March (17 ± 2 min., 15 ± 3 min., respectively). However, during September, rumination bouts were frequently disrupted and were shorter in length (9 ± 1 min.). Winter grazing rumination bouts were not recorded. From random samples during March 1995 and December 1995, when hay was the forage source, it was observed that bison chewed 0.99 ± 0.01 and 1.12 ± 0.03 bites sec^{-1} , respectively.

During June and September, bison would travel to water at the conclusion of a grazing bout. Less dominant animals would interrupt foraging to join herdmates. Bison would linger or bed near water more frequently in June than September. They did not water during winter, but consumed snow.

3.3.4 Daily Activity

Bison alternated foraging and resting activity over the 24 h activity cycle. Distinct phasic activity is poorly expressed in the June grazing period due to the increased number of cycles (Fig. 3.1). In June, bison tended to bed down immediately following a foraging bout with rumination occurring half the time. Bison would frequently lie flat out during these bedding bouts. Bedding was soon followed with another foraging period. This pattern was repeated throughout the day, broken with a trip for water and an occasional run. Near sundown however, bison tended to become quite active and milled about for an extended period of time prior to an intense foraging bout as darkness fell.

During the September grazing period, a prolonged foraging bout began prior to sunrise as daylight intensified (Fig. 3.1). This was followed by a mid-morning resting period, mid-day foraging period, late afternoon resting period with foraging activity increasing in frequency in late afternoon, peaking between sundown and dusk.

Following dusk, bison tended to bed for a few hours, then graze during the early morning hours before bedding until near dawn.

Winter grazing patterns were similar to September grazing period patterns except that there were only two main grazing bouts during the day, following sunrise and prior to sunset (Fig. 3.2). Midnight grazing activity occurred regularly and rivaled early morning grazing activity. Minor activities were minimal during this period.

In March 1995 and December 1995 bison did not graze due to severe icing of pasture and heavy snow cover, respectively. As they did not venture far from the plowed roadway required for vehicle access, and in the interests of animal welfare, supplemental hay was provided (supplementation). An extended bedding period prior to sunrise, more limited nighttime foraging, and less defined foraging-resting cycles during the day, characterized this feeding period (Fig. 3.2). Similar to September and winter grazing period, activity declined sharply following sundown. In comparison to winter grazing (Fig. 3.3), bison exhibited a foraging-feeding pattern with 1) less pronounced foraging peaks following sunrise and near sunset, 2) more pronounced resting activity following sundown, and 3) more frequent nighttime foraging cycles during supplementation.

3.3.5 Sward Structure, Forage Quality and Diet Selection

There was no difference in plant height between grazed patches and sward sites. Bison grazed sites that were significantly ($P < 0.05$) different in quadrat structure from the sward, primarily lower in litter ($7.6 \pm 1.3\%$) than sward sites ($14.5 \pm 3.0\%$) (Table 3.4). Although pasture management practice was different in Year 2 than Year 1, mean plant heights were not significantly different among growing season trial periods (Table 3.5).

Bison grazed selectively. Chemical composition of forage within feeding stations (emulated bites) was significantly higher ($P < 0.05$) in crude protein (12.9 ± 0.8 vs. $10.0 \pm 0.8\%$), and digestible energy (2.70 ± 0.09 vs. 2.17 ± 0.09 Mcal kg^{-1}), while lower in acid detergent fibre (31.9 ± 0.9 vs. $38.8 \pm 0.9\%$) and acid detergent lignin (4.8 ± 0.3 vs. $6.8 \pm 0.3\%$) than forage within grazed patches (Table 3.6). Sward sites contained $8.7 \pm 0.8\%$ crude protein, $2.21 \pm 0.09\%$ digestible energy, $39.0 \pm 0.9\%$ acid detergent fibre and $6.1 \pm 0.3\%$ acid detergent fibre. Bison would frequently graze a short bout exclusively on dicots (*Medicago* spp.) or monocots (graminoids).

During the growing season, forage biomass within the sward ranged from 288 g m^{-2} to $196 \pm 23 \text{ g m}^{-2}$ (Table 3.7). In March 1995, after a series of snow, chinook and re-freezing cycles, available forage was restricted to 8 g m^{-2} within the sward. When bison attempted to graze in March 1995, they sought out sites where forage was above the snowline. However, only a very limited amount of forage was available (16 g m^{-2}).

Chemical composition of forage consumed by bison (feeding station) varied with grazing period (Table 3.8). Under multivariate analyses, level of crude protein and acid detergent fibre were significantly different ($P < 0.05$). In a separate multivariate analysis, levels of crude protein and acid detergent fibre also varied significantly with grazing period ($P < 0.05$). Crude protein was low in March ($6.6 \pm 4.4\%$) compared with June ($15.9 \pm 3.1\%$) and September ($13.1 \pm 3.1\%$). Acid detergent fibre was lowest in June ($27.2 \pm 2.9\%$) and September ($29.8 \pm 2.9\%$) and highest in March ($44.7 \pm 4.0\%$). Acid detergent lignin was lowest in June ($3.5 \pm 0.2\%$) and September ($4.4 \pm 0.2\%$) and greatest in March ($8.3 \pm 0.3\%$).

Bite rate, bite size and consumption rate varied with trial period (Table 3.9). Seasonal differences were evident for bite rate (Table 3.10). Bite rate increased significantly (P

< 0.05) from 72 ± 1 bites min^{-1} during the June grazing period to 87 ± 1 and 98 ± 2 bites min^{-1} during the September and December grazing periods, respectively. Bite rate was lowest during the March grazing period (47 ± 2 bites min^{-1}) when bison grazed on a limited basis because of snow conditions.

Consumption rates ranged from 35 to 51 g min^{-1} during the June and September trial periods. Consumption rate during winter grazing (27 g min^{-1}) was similar to the lower summer consumption rates (35 g min^{-1}) (Table 3.9). The lowest consumption rate (8 g min^{-1}) was observed during the March trial period and was associated with severe snow conditions. Mean actively engaged and moderately engaged feeding times were 5.9 ± 0.3 and $0.9 \pm 0.1 \text{ h d}^{-1}$, respectively. Overall, bison grazed at a rate of 80 ± 3 bites min^{-1} , consuming $0.42 \pm 0.03 \text{ g bite}^{-1}$ for a mean consumption rate of 33 g min^{-1} .

Dry matter intake varied significantly by grazing period ($P < 0.05$) (Table 3.10).

Intake during September grazing period ($14.7 \pm 0.8 \text{ kg d}^{-1}$) was significantly greater than during June ($10.1 \pm 0.8 \text{ kg d}^{-1}$). December intake did not vary from either June or September ($11.9 \pm 1.2 \text{ kg d}^{-1}$).

3.3.6 Winter Grazing

Yearling bison obtained all their forage while grazing during December 1994 when snow depth was between $39 \pm 1 \text{ cm}$ and $23 \pm 2 \text{ cm}$ (Table 3.11).

By the beginning of the March 1995 trial, a series of chinooks and refreezing had created a $28 \pm 4 \text{ cm}$ snow pack that was impenetrable to grazing by bison, therefore, bison consumed supplemented hay. On March 21, 1995, a chinook significantly reduced the snow pack to $17 \pm 1 \text{ cm}$. This was followed with an evening snowfall to yield total snow cover of $23 \pm 2 \text{ cm}$ on March 22, 1995. Bison voluntarily returned to grazing on a limited basis and grazed patches that had a more limited snow cover ($13 \pm 1 \text{ cm}$) than the sward ($23 \pm 2 \text{ cm}$). Grazed patches also contained significantly

greater accessible forage biomass (16 g m^{-2}) than was contained within sward sites ($8 \pm 3 \text{ g m}^{-2}$) (Table 3.7).

In December 1995, when snow depth was $47 \pm 0 \text{ cm}$, the bison refused to graze - except along a plowed roadway within the field that was used for vehicle access, therefore, supplemental hay was provided. In contrast, a group of 2-year old bison bulls, fed grain and hay in an adjacent pasture went out to graze daily.

3.4 DISCUSSION

3.4.1 Activity Patterns

Activity patterns for free-grazing bison were distinctly polyphasic and consistent with other free-grazing ruminants. Eriksson et al. (1981) reported polyphasic activity in supplemented reindeer ($63^{\circ} 49' \text{ N}$), however, bison exhibited more cycles during summer grazing with 20 h daylight than reindeer under 24 h daylight. Conversely, reindeer exhibited 4-6 cycles during winter, compared with 2-3 for bison ($55^{\circ} 44' \text{ N}$). Neither supplemented bison in March (Fig 3.2), nor free-grazing wapiti in spring (Gates and Hudson 1983) displayed the distinct triphasic cycles of free-grazing Alaskan reindeer on the Seward peninsula in late February-early March (Collins and Smith 1989) and winter grazed bison in the current study.

Although averaging circadian activity by season-feed group increases the quality of the data it tends to dampen seasonal activity patterns, particularly during summer.

Activity patterns were generally consistent day to day, however they would shift an hour or two causing bedding activities to be averaged with foraging activity. While the number of foraging and bedding cycles is adequately displayed (Fig. 3.1) the amplitude is more accurately reflected by the single day pattern. Conversely, relying on a single day's activity to describe seasonal activity patterns is unacceptable.

The number of summer foraging bouts in the current study (8.0 ± 1.0 bouts d^{-1}) are intermediate to bison on northern mixed prairie (10.5 ± 0.7 feeding bouts d^{-1} ; Plumb and Dodd 1993) and bison in boreal mixed-wood forest (4-5 feeding bouts d^{-1} ; Hudson and Frank 1987). Winter grazing activity patterns in the current study were similar to autumn (October 20) activity patterns observed by Hudson and Frank (1987).

Seasonal changes in foraging activity for bison would appear to be more related to forage quality not forage biomass. Sward biomass remained consistent throughout the year (Table 3.7), however, foraging bout length and total foraging time increased significantly from summer grazing to winter grazing period (Table 3.3). This corresponds consistently with the expected increase in foraging activity as forage quality decreases from summer to winter.

As expected (hypotheses 1) foraging time increased, resting time decreased and time in minor activities remained constant from summer to winter (Table 3.3). It is interesting to note that changes in foraging time were best described by total foraging time while corresponding changes in bedding activity were best described by a significant increase in bedding bout length. The time spent in minor activities, while not significant, was considerably shorter during winter grazing (1.8%) than during summer grazing (6.9%) and during supplementation (6.2%). Current data do not support the second hypotheses that length of foraging bout would be longer during winter grazing compared with summer grazing and that foraging bouts would be more frequent during summer grazing compared to winter grazing. Further study will be required to determine the extent that seasonal changes in bout frequencies and time spent in minor activities are present.

Consistent with other free-grazing ruminants, provision of supplemental feed during winter months alters foraging behaviour. Foraging and resting cycles in bison (Figure

3.3) and reindeer (Eriksson et al. 1981) became less distinct (i.e. transition between foraging to bedding and bedding to foraging bouts became less defined). Cattle (Krysl and Hess 1993) and bison allocated less time to grazing. For bison, time allocated to minor activities was similar to time allocated during summer grazing, even though daytime temperatures ranged between -12°C and -22°C during supplementation.

Activity patterns appear to be free from influence of pen (field) size. Bison, in a 2400 ft² pen, allocated 40% of daytime summer activity resting, 25% standing, 23% feeding and 12% engaged in social activities (Robitaille and Prescott 1993). This compares favourably with the activity budgets for free-grazing bison in the current study (Table 3.1) - when supplementally fed in March 1995 and while grazing in June 1995. Activity budget was influenced by social ranking, age and gender (Robitaille and Prescott 1993).

3.4.2 Foraging Activity

Time allocated to summer grazing (470 min d^{-1} , 45% of daylight h) was considerably greater than that of bison on the National Bison Range in Montana (178 min d^{-1} , daylight h, Belovsky and Slade 1986), however their data must be considered cautiously because of sampling methods (losing site of focal animals after a few hours). Time allocated to summer grazing was less than the 8.7 h d^{-1} reported by Hudson and Frank (1987) for bison foraging in a boreal mixed wood forest setting. However, in spite of differences in latitude, ecotype and nighttime foraging activity, time foraging (expressed as a percentage of daylight; 45% in current study) is equivalent to the 44% reported by Plumb and Dodd (1993) for bison grazing northern mixed prairie in South Dakota. Further work is required to determine the impact that day length (photoperiod) has on comparisons of foraging activity at differing latitudes. Forage type, forage quality and group dynamics may also contribute to these variations.

Bison tended to be more responsive to changes in daylight intensity than sunrise-sunset. Foraging activity often began at dawn, prior to sunrise. Foraging activity, more frequently than not, continued through sunset, ending sharply, shortly after onset of darkness. This pattern is consistent with free-grazing reindeer (Eriksson et al. 1981 63° 49'N; Collins and Smith 1989, 64° 45' N). Malachek and Smith (1976) indicated onset of morning grazing activity in cattle was related to a threshold level of light intensity. Future studies, which record changes in light intensity, could provide insights into photo cues for bison.

3.4.3 Temperature and Thermoregulation

Thermoregulation is a major factor in ungulate ecology (Parker and Robbins 1985) and is a more important influence on foraging activity than energetic considerations for many grassland herbivores (Belovsky and Slade 1986). Northern wild ruminants are well adapted to cold temperatures, however as ambient temperatures drop below the animal's lower critical temperature (LCT), additional energy is required to maintain body core temperature. This additional expenditure imposes an additional energy demand. Common thermoregulatory behaviours to reduce heat loss may include reduced activity (including grazing), shelter seeking, and gregarious huddling. Postural adjustment, to increase net heat gain through solar radiation, is an alternative energy gaining behaviour.

Smoliak and Peters (1955) determined that temperature was the most important factor affecting winter grazing behaviour in cattle and bison hybrids. In free-grazing range cattle (Malachek and Smith 1976), mean daily air temperature was negatively related to time spent standing and was positively related to time spent grazing. This reduction of time that range cattle spent grazing on cold days, resulted in an estimated 20% reduction in energy intake. However, this was also offset with a reduction of energy expenditure.

Lower critical temperature is considered to be near -30°C for bison under laboratory conditions (Christopherson et al. 1978, 1979). Under natural conditions, factors like wind velocity, humidity, hair coat and condition will impact negatively on lower critical temperature, resulting in an additional energy demand on the ruminant. Although LCT was not quantified, the daytime winter temperatures in the current study (-21°C to $+4^{\circ}\text{C}$) were considered to be above the estimated lower critical temperature for bison. As bison in the current study appeared to graze independently of ambient temperature in winter, it would appear that factors, other than ambient temperature, are of greater importance in the decision to initiate grazing activity.

Heat stress depresses feed intake immediately (Ketelaars and Tolcamp 1992a). When ambient temperatures rise above the upper critical temperature (UCT), additional energy expenditure is required to facilitate heat loss and maintenance of core body temperature. Shelter seeking in shade is a common thermoregulatory behaviour. In prairie ecosystems with an absence of shade, bison reduced summer grazing activity as ambient temperature increased (Belovsky and Slade 1986). During elevated summer temperatures in the current study (14°C to 21°C), bison frequently utilized the shade available at the southwest corner of the field, but neither consistently grazed nor avoided grazing during the midday to late afternoon period normally associated with maximum solar radiation.

The selection of a study pasture with a consistent southern aspect is considered to have standardized the influence of aspect on thermoregulation and foraging activity in the current study.

3.4.4 Winter Grazing

Condition of snow pack affects grazing behaviour. Under a thin layer of snow, bison clipped off exposed forage above the snow line whereas, in deeper snow, they cleared a trench by swinging their head side to side (McHugh 1953). Consistent with McHugh (1953), bison in the current study had difficulty foraging when the sward was covered with a hard snow pack or when icy conditions prevailed, because they only pawed infrequently. Reynolds and Peden (1987) concluded that snow hardness had the greatest impact on whether or not bison grazed a particular site, therefore, under hard snow pack conditions within the current study (March 1995), only forage above the snow pack was considered available for grazing.

During December 1994, when snow depth was 39 cm, yearling bison continued to graze. However in December 1995, unlike a group of two-year old bison bulls in an adjacent pasture (n=42) and other bison herds within the Peace Country (personal observation), yearling bison did not attempt to graze when snow depth was 47 cm. Snow conditions were considered similar to the previous year. Reynolds and Peden (1987) reported little differences in feeding and non-feeding sites for snow depth and density.

3.4.5 Bite Rate, Consumption Rate and Dry Matter Intake

Current data confirm the fourth hypotheses that bite rate would increase from summer to winter. However, it was not expected that September and December bite rates would be statistically equivalent. As bite rates for September 1994 and September 1995 were numerically similar (Table 3.9), differences may be better elucidated with additional study. Hudson and Watkins (1986) speculate that differences in bite rates may be related to moisture content (i.e. killing frost), however, current data would indicate that the influence of the killing frost in September 1995 on bite rate was minimal.

Seasonal changes in bite rate for bison were similar to moose. Seasonal bite rate in moose declined from 23 g DM min⁻¹ in summer to 18 g DM min⁻¹ in autumn and 11 g DM min⁻¹ in winter and was significantly influenced by forage type (Renecker and Hudson 1986).

As expected, bison consumed larger quantities of forage compared with wapiti (18 g min⁻¹; Hudson and Nietfeld 1985) and moose (23 g min⁻¹; Renecker and Hudson 1986). Maximum consumption rates for bison yearlings in the current experiment (51 g min⁻¹) were lower than the 68 g min⁻¹ for pooled consumption rates of sub-adult males, adult females and yearlings (Hudson and Frank 1987). Seasonal variation in consumption rates was expected. From this research, it is clear that maximum consumption rates occur during the growing season. It is not clear, however, whether June or September rates are maximal.

The decline in consumption rates from June to September (41 g min⁻¹, 35 g min⁻¹, respectively) during Year 2, is consistent with Hudson and Frank (1987; 43 g min⁻¹, 39 g min⁻¹, respectively). In contrast, the increase in bison consumption rates from June (35 g min⁻¹) to September (51 g min⁻¹) (Year 1) is consistent with wapiti (0.11 g min⁻¹; 0.22 g min⁻¹, respectively; Hudson and Watkins 1986). This difference within the current study, may be due to differences in animals between years, differences in pasture management practices between years or the impact of a recent killing frost in September 1995 (Year 2). However, based on the Hudson and Frank (1987) observation that “bison foraged more efficiently on sparse pastures than might be expected”, and Hudson and Watkins (1986) conclusion that “mean bite size [is] strongly correlated with grassland mass”, the difference in consumption rates may be best explained by differences in pasture management practice.

Bison were able to consume up to $11.9 \pm 1.2 \text{ kg d}^{-1}$ while winter grazing under adequate sward cover and in acceptable snow conditions. This intake level is intermediate to June and September grazing periods, therefore, hypotheses five cannot be accepted.

3.4.6 Grazing Behaviour and Diet Selection

The observation that bison selectively graze tame pasture supports previous research conducted on prairie ecosystems (Peden et al. 1974; Belovsky 1986; Plumb and Dodd 1993). Bison consistently consumed the upper portion of the plant. This selection enabled them to consume a diet that was significantly higher in crude protein and digestible energy (as derived from ADF), while significantly lower in lignin and ADF, compared to forage available to them from within grazed patches and the sward. This data supports the third hypotheses that forage consumed would be higher in quality than forage available within the sward and grazing patch.

In cattle and sheep, rumination and eating time are shorter when NDF of consumed forage is lower (Welsh and Smith 1969, 1970). In elk and mule deer, mean retention time increases as lignin content increases; mean cell wall thickness increases linearly as NDF increases; and mean cell wall thickness has been shown to be related to mean particle breakdown time (Spalinger et al. 1986). Therefore, selection of a diet low in fibre and lignin would ultimately decrease rumination, handling and mean retention time, thus enabling bison to consume greater quantities of high quality forage. Although bison are known for their ability to utilize poor quality forages, it would appear that when high quality forage is available, they will actively select it. In addition, when forage within the sward is of poorer quality, as it is in winter, bison continue to be selective by continuing to graze the upper portions of the plant.

It is possible, during summer grazing of low fibre and lignin forages (relative to winter forages), that diet selection would be associated with optimizing nutrient intake because fibre intake would not likely approach physical limits of handling. In winter however, diet selection could be related more to minimizing handling time associated with the high fibre and lignin winter forages, than to optimizing nutrient intake.

Grazing strategies of herbivores have been characterized as time-minimizers, digestive capacity minimizers or energy maximizers (Belovsky 1986). In a study of various herbivores grazing on the National Bison Preserve, Belovsky (1986) concluded that herbivores, including bison, were best characterized as energy maximizers. However, they also observed that bison was the only species with observed diets not significantly different from the predicted diets for time-minimizers (monocot or dicot specialists). Alternative strategies include optimizing and satisficing (Bunnell and Gillingham 1988).

Social ranking influences grazing behaviour. Higher-ranking individuals tended to initiate main foraging bouts. Lower-ranking individuals were subject to frequent disturbance during grazing bouts by higher-ranking individuals, even though higher-ranking individuals did not displace lower-ranking individuals from their summer grazing patches. During supplementation, however, lower-ranking individuals were frequently displaced. In pen-fed bison, lower-ranking individuals spent significantly more time feeding than higher-ranking individuals (Robitaille and Prescott 1993).

3.4.7 Bison and Cattle

Commercial producers often compare bison to cattle, however, there have only been a few direct comparisons related to forage utilization (Richmond et al. 1977; Hawley 1987; Koch et al. 1988). Time allocated daily to grazing increased steadily between June and October (47% to 67%) and was always less for bison than for cattle (51 to

71%, Plumb and Dodd 1993). Duration of foraging bouts was consistently shorter for bison than cattle throughout the grazing season, with bout frequency steadily declining as summer progressed into autumn (Plumb and Dodd 1993). That browse and forbs comprise a smaller component of the bison diet compared to cattle (Plumb and Dodd 1993) supports the classification (Hoffman 1989) of bison as less selective than cattle.

3.4.8 Scanning Frequency and 24 h Observation Scans

Boertje (1985) hypothesized that one could base 24 h activity patterns as an extrapolation of a single active-rest cycle, thus reducing the need for nighttime observations. Thomson (in Collins and Smith 1989) cautioned that potential errors could result if researchers failed to account for long winter nights. Collins and Smith (1989) observed free-grazing reindeer (24 h observations) on the Seward Peninsula, Alaska and observed that daytime only observations overestimated feeding by 37%. Plumb and Dodd (1993) discontinued nighttime observations of bison because they observed very little grazing activity during preliminary observations. However, current observations with free-grazing bison, would support the conclusion of Collins and Smith (1989) that “behaviour budgets based on daytime observations [only] may be significantly biased and of questionable value”.

Frequency of activity scans was evaluated during this study. Compared to 5-minute scans (benchmark), scans at 10 and 15-minute intervals provided records of foraging activity that varied from the bench mark by -55% to 35% and -10% to 30%, respectively. Minor activities occurred infrequently and in one 2 h segment, 10-minute scan overestimated minor activity by 200% and 15-minute scans missed the activity completely, with a concurrent 30% overestimation of grazing activity. Therefore, 5-minute activity scans are considered necessary to adequately categorize activity in free-grazing bison.

3.4.9 Summary

Bison alter their activity budget from summer to winter by increasing foraging time, and decreasing bedding time. Total time foraging and bedding bout length were greatest during winter grazing. Supplemental feeding of bison during the non growing season altered activity budget. Foraging and resting cycles became less distinct and time in minor activities became similar to summer, even when daytime temperatures were between -22°C and -12°C .

Activity budget is best described as polyphasic, alternating between bouts of foraging and resting activity. Activity was distinctly tri-phasic during winter grazing bouts when bison displayed two main daytime foraging bouts and significant nighttime foraging activity. Phasic activity was poorly expressed during June and September grazing periods primarily due to the increase in the number of foraging bouts.

Chemical composition of forage selected in feeding stations was compared with forage within grazing patches and representative sward sites. Bison were able to source a diet that was significantly lower in acid detergent fibre and lignin, thus higher in crude protein and digestible energy than that available from within the grazing patch and sward. This provides further evidence that bison graze selectively.

Table 3.1. Differences (\pm SE) in 24 h activity budget for yearling bison during indicated trial period

Trial Period	Activity		
	% Foraging	% Resting	% Minor
June 1994	27 \pm 1	68 \pm 1	5 \pm 1
September 1994	30 \pm 2	66 \pm 2	4 \pm 1
December 1994	40 \pm 2	58 \pm 2	2 \pm 1
March 1995	20 \pm 2	73 \pm 2	7 \pm 1
June 1995	25 \pm 1	64 \pm 1	11 \pm 1
September 1995	26 \pm 1	70 \pm 2	4 \pm 1
December 1995	25 \pm 1	69 \pm 1	6 \pm 1

Table 3.2. Differences (\pm SE) in 24 h activity budget for yearling bison by season-feed group

Season-Feed Group ^z	Activity		
	% Foraging	% Resting	% Minor
Summer grazing	26.6 \pm 1.2 ^b	67.2 \pm 1.3 ^{ab}	6.2 \pm 1.5
Winter grazing	39.6 \pm 2.4 ^a	58.5 \pm 2.6 ^b	1.8 \pm 3.1
Supplementation	22.0 \pm 1.7 ^b	71.1 \pm 1.9 ^a	6.9 \pm 2.2

^z Summer grazing = June 1994 and 1995, September 1994 and 1995;

Winter grazing = December 1995; Supplementation = March 1995, December 1995.

Means (\pm SE) within columns with different letters are significantly different at $P < 0.05$.

Table 3.3. Foraging and bedding activity of yearling bison summarized by season-feed group

Season-Feed Group ^z	Foraging			Bedding		
	Number of foraging bouts (bouts d ⁻¹)	Foraging bout length (minutes)	Total foraging time (min d ⁻¹)	Number of bedding bouts (bouts d ⁻¹)	Bedding bout length (minutes)	Total bedding time (min d ⁻¹)
Summer grazing	8.0 ± 1.0	69 ± 9	470 ± 32 ^b	6.6 ± 0.5	121 ± 13 ^b	793 ± 31
Winter grazing	6.7 ± 2.0	123 ± 17	763 ± 62 ^a	3.0 ± 1.0	276 ± 26 ^a	698 ± 61
Supplementation	5.5 ± 1.4	77 ± 12	418 ± 44 ^b	5.8 ± 0.8	142 ± 18 ^b	795 ± 43

^z Summer Grazing = June 1994 and 1995, September 1994 and 1995;

Winter Grazing = December 1995; Supplementation = March 1995, December 1995.

Means (± SE) within columns with different letters are significantly different at P < 0.05.

Table 3.4. Composition of forage within sward sites and grazed patches - June and September trial periods data pooled²

Type	Plant height cm	Quadrat structure					
		Bare ground %	Graminoids %	Weedy forbs %	Cultivated forbs %	Litter %	Feces %
Grazed patches	24.7 ± 1.9	3.8 ± 2.2	49.8 ± 4.2	14.6 ± 2.4	23.4 ± 3.4	7.6 ± 1.3 ^b	0.8 ± 0.4
Sward	26.1 ± 1.7	5.9 ± 2.2	47.0 ± 3.3	13.6 ± 2.3	18.5 ± 3.0	14.5 ± 2.5 ^a	0.5 ± 0.3

² Plant height was analyzed as a one-way ANOVA, quadrat structure was analyzed using the GLM-Multivariate procedure. Means (± SE) within columns with different letters are significantly different at P < 0.05.

Table 3.5. Composition of forage within grazed patches during June and September trial periods

Trial period	Plant height cm	Quadrat structure					
		Bare ground %	Graminoids %	Weedy forbs %	Cultivated forbs %	Litter %	Feces %
June 1994	24.7 ± 3.9	12.0 ± 4.2	36.8 ± 7.7	20.7 ± 4.3	17.7 ± 6.8	11.3 ± 2.5	1.5 ± 0.8
September 1994	21.8 ± 3.9	1.5 ± 4.2	56.0 ± 7.7	12.5 ± 4.3	18.5 ± 6.8	10.5 ± 2.5	1.0 ± 0.8
June 1995	27.3 ± 3.9	1.5 ± 4.2	40.4 ± 7.7	19.6 ± 4.3	32.5 ± 6.8	5.5 ± 2.5	0.5 ± 0.8
September 1995	25.1 ± 4.1	0.0 ± 4.4	67.8 ± 8.1	4.4 ± 4.6	25.0 ± 7.2	2.8 ± 2.6	0.0 ± 0.8

Table 3.6. Chemical composition of forage within feeding station (emulated bites), grazed patches and sward sites for yearling bison grazing seasonal pasture

	Feeding station	Grazed patches	Sward sites	SEM ^z
Crude Protein % ^y	12.9	10.0	8.7	0.8
Calcium %	0.65	0.67	0.54	0.05
Phosphorus %	0.22	0.20	0.19	0.01
Potassium %	1.8	1.5	1.3	0.1
Magnesium %	0.26	0.27	0.26	0.02
Sodium %	0.03	0.03	0.03	0.01
Acid Detergent Fibre % ^z	31.9	38.8	39.0	0.9
Digestible Energy Mcal kg ⁻¹	2.70	2.17	2.21	0.09
Acid Detergent Lignin %	4.8	6.8	6.1	0.3

^z Standard error of the mean

^y Crude protein and acid detergent fibre significantly different at $P < 0.05$ under GLM-Multivariate analysis.

Table 3.7. Biomass (g m^{-2}) within sward sites and grazed patches

Trial Period ^z	Sward site	Grazed patch
June 1994	275	263
September 1994	288	311
March 1995 ^y	8	16
June 1995	281	297
September 1995	196	231
Overall (\pm SE)	210 ± 5.6	223 ± 5.6

^z Biomass of sward site in December 1994 (not included in the analysis) was 253 g m^{-2} .

^y Only forage above the snowpack was considered available.

Table 3.8. Chemical composition of forage grazed by yearling bison during indicated grazing period (mean \pm SE)²

	Grazing period ^y		
	June	September	March
Crude Protein %	15.9 \pm 3.1	13.1 \pm 3.1	6.6 \pm 4.4
Calcium %	0.56 \pm 0.17	0.78 \pm 0.17	0.57 \pm 0.24
Phosphorus %	0.30 \pm 0.03	0.19 \pm 0.03	0.12 \pm 0.04
Potassium %	2.1 \pm 0.3	1.6 \pm 0.3	1.5 \pm 0.4
Magnesium %	0.26 \pm 0.03	0.31 \pm 0.03	0.14 \pm 0.04
Sodium %	0.02 \pm 0.02	0.04 \pm 0.02	0.02 \pm 0.02
Acid Detergent Fibre %	27.2 \pm 2.9	29.8 \pm 2.9	44.7 \pm 4.0
Digestible Energy Mcal kg ⁻¹	3.17 \pm 0.19	2.72 \pm 0.19	1.74 \pm 0.27
Acid Detergent Lignin %	3.5 \pm 0.2	4.4 \pm 0.2	8.3 \pm 0.3

² Crude protein and acid detergent fibre significantly different at $P < 0.05$ under GLM-Multivariate analysis.

² Crude protein and acid detergent lignin significantly different at $P < 0.05$ under GLM-Multivariate analysis.

^y June = June 1994 and 1995; September = September 1994 and 1995; March = March 1995.

Table 3.9. Bite rate, bite size and foraging intensity of free-grazing yearling bison on pasture summarized by trial period

	June 1994	September 1994	December 1994	March 1995 ²	June 1995	September 1995	December 1995 ²
Bite rate (b min ⁻¹)	73 ± 8	87 ± 2	98 ± 3	47 ± 9 [†]	70 ± 4	88 ± 3	na
Bite size (g bite ⁻¹) ^y	0.48	0.59	0.28	0.18 [†]	0.59	0.40	na
Consumption rates ^z (g min ⁻¹)	35	51	27	8 [†]	41	35	na
AF (h d ⁻¹) ^x	5.4	6.0	8.8	4.4	4.3	4.4	5.8
AF rate % ^x	85 ± 3	93 ± 2	82 ± 2	96 ± 1	85 ± 1	94 ± 1	96 ± 1
MF (h d ⁻¹) ^x	1.0	1.3	0.7	0.4	1.6	0.6	na
MF rate % ^x	20	20	20	80	20	60	na

² Bison were supplemented during March 1995 and December 1995.

^y Values without standard errors are based on a group observation not individual observations.

^x AF = Actively foraging; MF = Moderately foraging.

[†] Represents data obtained during limited grazing activity present in March 1995.

Table 3.10. Seasonal estimates associated with dry matter intake (± SE) for six free grazing yearling bison summarized by grazing period

	Grazing period		
	June	September	December
Bite rate (b min ⁻¹)	72 ± 1 ^b	87 ± 1 ^a	98 ± 2 ^a
Body weight change (kg d ⁻¹)	0.6 ± 0.4	0.5 ± 0.4	-0.7 ± 0.4
Est. DMI (kg d ⁻¹) bite count	10.1 ± 0.8 ^b	14.7 ± 0.8 ^a	11.9 ± 1.2 ^{ab}
			na

Grazing periods: June = June 1994 and 1995; September = September 1994 and 1995;

December = December 1994; March = March 1995.

Means (± SE) with different letters within rows indicates significant difference $P < 0.05$.

DMI is dry matter intake.

Table 3.11. Influence of snow depth and condition on grazing behaviour of yearling bison

Date	Site ^z	Depth cm	Snow Condition ^y	Behaviour ^x
12&13 December 1994	Snow station	39 ± 1.3	Powder	Graze
21 December 1994	Snow station	22 ± 0.4	Powder	Graze
22 December 1994	Sward Site	23 ± 0.7	Powder	Graze
23 December 1994	Grazed Patch	23 ± 1.7	Powder	Graze
14&15 March 1995	Snow station	28 ± 3.8	Hard Pack	No Graze
20&21 March 1995	Snow station	26 ± 0.8	New over pack	No Graze
22 March 1995	Snow station	17 ± 1.3	New over pack	No Graze
23 March 1995	Sward Site	23 ± 2.4	New over pack	No Graze
24 March 1995	Grazed Patch	13 ± 0.8	New over pack	Supple, Graze ^w
December 1995	Snow station	47 ± 0.2	Powder	No Graze

^z Combined measurements from a snow station and within sward and patch sites.

^y Powder = crystallized powder snow easily moved by grazing bison.

Hard Pack = packed snow that yearling bison were unable to penetrate.

New over pack = fresh powder over existing Hard Pack.

^x Graze = forage intake exclusively from grazing; No Graze = refused to graze - forage intake from supplemented hay.

^w Bison voluntarily grazed exposed forage, therefore forage intake March 24, 1995 was from both grazing and supplemented hay.

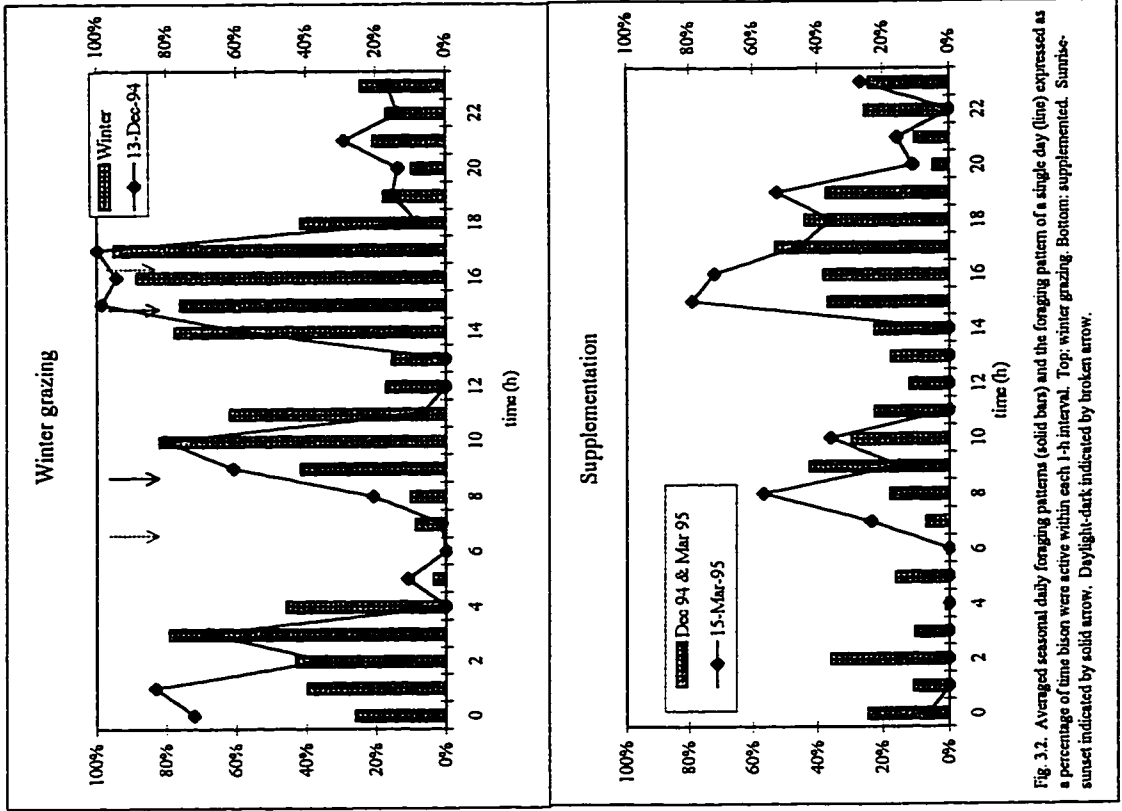


Fig. 3.1. Averaged seasonal daily foraging patterns (solid bars) and the foraging pattern for a single day (line) expressed as a percentage of time bison were active within each 1-h interval. Top: summer grazing. Bottom: autumn grazing. Sunrise-sunset indicated by solid arrow. Daylight-dark indicated by broken arrow.

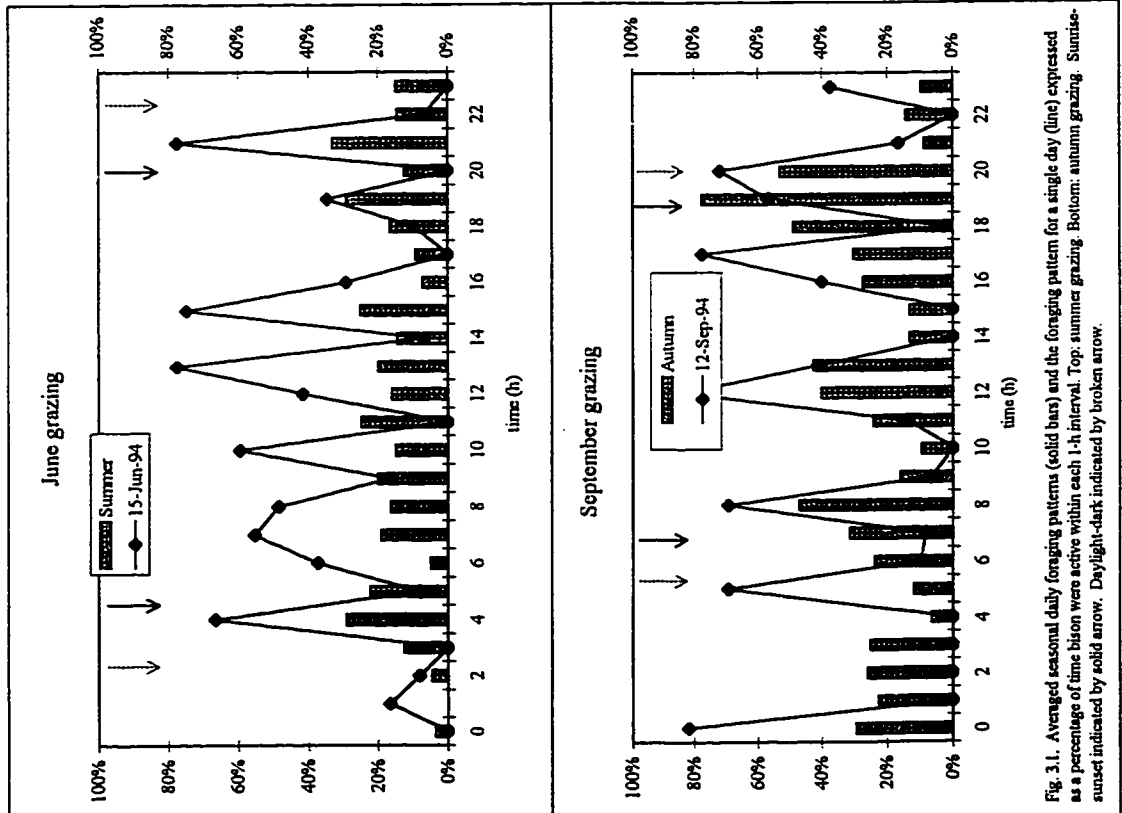
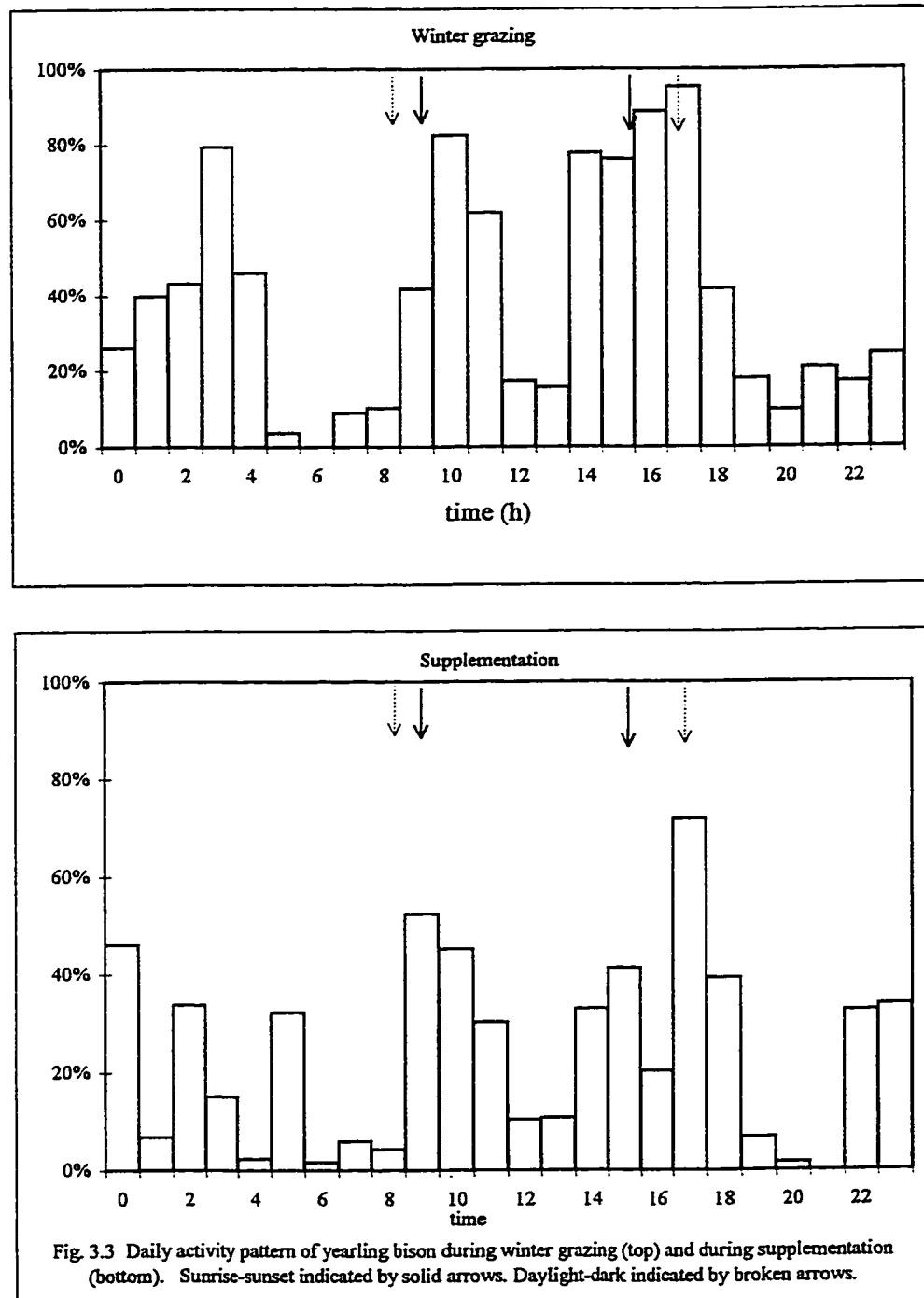


Fig. 3.2. Averaged seasonal daily foraging patterns (solid bars) and the foraging pattern of a single day (line) expressed as a percentage of time bison were active within each 1-h interval. Top: winter grazing. Bottom: supplemented. Sunrise-sunset indicated by solid arrow. Daylight-dark indicated by broken arrow.



3.5 REFERENCES

- Altmann, J. 1974.** Observational study of behaviour: sampling methods. *Behaviour*, 49: 227-267.
- Belovksy, G. E. 1986.** Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia (Berlin)*: 70: 35-52.
- Belovsky, G. E. and Slade, J. B. 1986.** Time budgets of grassland herbivores: body size similarities. *Oecologia (Berlin)*: 70: 53-62.
- Boertje, R. D. 1985.** Seasonal activity of the Denali caribou herd, Alaska. *Rangifer* 5(2): 32-42.
- Bunnell, F. L. and Gillingham, M. P. 1988.** Foraging behaviour: dynamics of dining out. Pages 53-79 in R. J. Hudson and R. G. White eds. *Bioenergetics of wild herbivores*. CRC Press. Boca Raton, FL.
- Christopherson, R. J., Hudson, R. J. and Christophersen, M. K. 1979.** Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Can. J. Anim. Sci.* 59: 611-617.
- Christopherson, R. J., Hudson, R. J. and Richmond, R. J. 1978.** Comparative winter bioenergetics of American bison, yak, Scottish Highland and Hereford calves. *Acta Theriol.* 23(2): 49-54.
- Collins, W. B. and Smith, T. S. 1989.** Twenty-four hour behaviour patterns of free-ranging reindeer in winter. *Rangifer* 9(1): 2-8.
- Eriksson, L-O., Kallqvist, M-L. and Mossing, T. 1981.** Seasonal development of circadian and short-term activity in captive reindeer, *Rangifer tarandus* L. *Oecologia (Berl)* 1981. 48: 64-70.

Gates, C. C. and Hudson, R. J. 1983. Foraging behaviour of wapiti in a boreal forest enclosure. *Naturaliste can.* **110**: 197-206.

Hawley, A. W. L. 1987. Bison and cattle use of forages. Pages 49-52 *in* H. W. Reynolds and A. W. L. Hawley eds. *Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT.* Canadian Wildlife Service Occasional Paper No. 63. Minister of Supply and Services Canada, Ottawa, ON. 1987. 74 pp.

Hoffman, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* **78**: 443-457.

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

Hudson, R. J. and M. T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. *J. Range Manage.* **38**: 80-82.

Hudson, R. J. and Watkins, W. G. 1986. Foraging rates of wapiti on green and cured pastures. *Can. J. Zool.* **64**: 1705-1708.

Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992a. Toward a new theory of feed intake regulation in ruminants. 1. Causes of differences in voluntary feed intake: critique of current views. *Live. Prod. Sci.* **30**: 269-296.

Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992b. Toward a new theory of feed intake regulation in ruminants. 3. Optimum feed intake: in search of physiological background. *Live. Prod. Sci.* **31**: 235-258.

Koch, R. M., Crouse, J. D. and Seideman, S. C. 1988. Bison, Hereford and Brahman growth and carcass characteristics. Beef Research Report, Roman L. Hruska, US Meat Animal Research Center.

Krysl, L. J. and Hess, B. W. 1993. Influence of supplementation on behaviour of grazing cattle. *J. Anim. Sci.* **71**: 2546-2555.

Malachek, J. C. and Smith, B. M. 1976. Behaviour in range cows in response to winter weather. *J. Range. Manage.* **29**: 9-12.

Mathison, G. W., Okine, E. K., Vaage, A. S., Kaske, M. and Milligan, L. P. 1995. Current understanding of the contribution of the propulsive activities in the forestomach to the flow of digesta. Pages 23 to 41 *in* W. v. Englehardt, S. Leonhard-Marek, G. Breves, and D. Giesecke, eds. Ruminant physiology: digestion, metabolism, growth and reproduction. Proceedings of the eight international symposium on ruminant physiology. Ferdinand Enke Verlag Stuttgart 1995.

McFarland, D. J. 1977. Decision making in animals. *Nature.* **269**: 15-21.

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

Parker, K. L. and Robbins, C. T. 1985. Thermoregulation in ungulates. Pages 161-182 *in* R. J. Hudson and R. G. White eds. Bioenergetics of wild herbivores. CRC Press. Boca Raton, FL.

Parker, K. L., Gillingham, M. P., Hanley, T. A. and Robbins, C. T. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Can. J. Zool.* **74**: 442-450.

Peden, D. G., Van Dyne, G. M., Rice, R. W. and Hansen, R. M. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. *J. Appl. Ecol.* **11**: 489-498.

Plumb, G. E. and Dodd, J. L. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecol. Appl.* **3(4)**: 631-643.

Renecker, A. L. and Hudson, R. J. 1986. Seasonal foraging rates of free-ranging moose. *J. Wildl. Manage.* **50(1)**: 143-147.

Renecker, A. L. and Hudson, R. J. 1993. Morphology, bioenergetics and resource use: patterns and processes. Pages 141-163 in J. B. Stelfox, ed. Hoofed mammals of Alberta. Lone Pine Publishing, Edmonton, AB.

Reynolds, H. W. and Peden, D. G. 1987. Vegetation, bison diets, and snow cover. Pages 39-44 in H. W. Reynolds and A. W. L. Hawley eds. Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT. Occasional Paper, No. 63.

Richmond, R. J., Hudson, R. J. and Christopherson, R. J. 1977. Comparison of forage intake and digestibility by American bison, yak and cattle. *Acta. Theriologica.* 22: 225-230.

Robitaille, J-F. and Prescott, J. 1993. Use of space and activity budgets in relation to age and social status in a captive herd of American Bison, *Bison bison*. *Zoo Biology* 12: 367-379.

Smoliak, S. and Peters, H. F. 1955. Climatic effects on foraging performance of beef cows on winter range. *Can. J. of Agric. Sci.* 35: 213-216.

SAS Institute Inc. 1990. SAS/STAT user's guide. Version 6.10, 4th ed. SAS Institute, Inc. Cary, NC.

Spalinger D. E., Robbins, C. A., and Hanley, T. A. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. *Can. J. Zool.* 64:312-321.

Tester, J. R., and Heegan, K. L. 1965. Deer response to a drive census determined by radio-telemetry. *Biosci.* 15:100-104.

Tolkamp, B. J. and Ketelaars, J. J. M. H. 1992. Toward a new theory of feed intake regulation in ruminants. 2. Costs and benefits of feed consumption: an optimisation approach. *Live. Prod. Sci.* 30: 297-317.

- Trudel, J. and White, R. G. 1981.** The effect of forage structure and availability on food intake, biting rate, bite size and daily eating times of reindeer. *J. Appl. Ecol.* **18**: 63-81.
- Welsh, J. G. and Smith, A. M. 1969.** Influence of forage quality on rumination time in sheep. *J. Anim. Sci.* **28**: 813-818.
- Welsh, J. G. and Smith, A. M. 1970.** Forage quality and rumination time in cattle. *J. Dairy Sci.* **53**: 797-800.
- White, R. G., Holleman, D. F., Schwartz, C. C., Regelin, W. L. and Franzman, A. W. 1984.** Control of rumen turnover in northern ruminants. *Can. J. Anim. Sci.* **64**(Suppl.): 349-350.

CHAPTER 4. Energy requirements of free-grazing bison on seasonal pasture

4.1 INTRODUCTION

Previous research suggests that game farmers should work with the seasonal cycle rather than against it (Hudson et al. 1994), however, the extent to which bison (*Bison bison*) express seasonal cycles has not been fully evaluated. Christopherson et al. (1978) have reported that energy expenditures of penned bison vary by month (higher spring than winter values), however, circannual energy expenditure conducted with free-grazing animals needs determination.

Another limitation of previous work was that energy expenditure rather than requirement was measured (Jiang and Hudson 1994). A more direct measure of maintenance requirements is obtained by determining the amount of feed needed to maintain body weight throughout the year (Blaxter 1989). Regression of metabolizable energy ($ME W^{0.75}$) on liveweight gain ($g W^{0.75}$) provides a simultaneous estimate of seasonal energy requirement for maintenance and liveweight gain (Jiang and Hudson 1992). The challenge is to develop and apply methods for conducting this analysis with animals on pasture, the only relevant setting for bison and other farmed game. However, this does ignore seasonal weight change associated with wild ruminants. Although this may seem imprecise to those accustomed to feeding standards for dairy or beef cattle, the alternative is to conduct controlled pen studies and apply an arbitrary scalar for animals on pasture.

The purpose of this study was to estimate seasonal energy requirements for maintenance and gain of free-grazing bison via the bite count and marker methods.

4.2 METHODS

The approach involved assessment of liveweight gains and digestible dry matter intake of bison on pasture summer solstice, autumn equinox, winter solstice and spring equinox (field trials). To calibrate the internal marker method, trials in metabolism crates (pen trials) were conducted in summer and winter to compare the greatest expected contrasts in metabolic requirements and appetite. The contrast of field and pen trials also provided an opportunity to quantify the incremental costs of free-grazing. In both field and pen trials, energy requirements for liveweight maintenance and liveweight change were estimated by simple linear regression of metabolizable energy intake (MEI) ($\text{kJ W}^{-0.75}$) against liveweight gain ($\text{g W}^{-0.75}$) (Jiang and Hudson 1992). Energetic values of mobilizing and depositing tissue were also determined.

4.2.1 Location and Pasture Characteristics

The field study was conducted at the Center for Agricultural Diversification, Dawson Creek, BC ($55^{\circ}44'30''$ N, $120^{\circ}30'$ W) located 600 km northwest of Edmonton, AB. Pen trials were conducted at the Ministik Wildlife Research Station located in the Cooking Lake Moraine, 50-km southeast of Edmonton, AB. The study pasture was 5.4 ha in size, fenced for bison and had a south-facing slope. Grasses predominated and included smooth brome (*Bromus inermis*), timothy (*Phleum pratense*), quackgrass (*Agropyron repens*) and Kentucky bluegrass (*Poa pratensis*). Predominant forbs were alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*) and dandelion (*Taraxacum officinale*).

4.2.2 Field Trials

Three male and three female bison yearlings, considered to represent commercial bison, were selected from a local commercial herd and transported to the study location in late May each year. Animals were selected from the 1993 calf crop for Year 1 trials (June 1994 to March 1995) and from the 1994 calf crop for Year 2 (June 1995 to December 1995). The source herd was checked routinely by the owner, making all animals accustomed to

human activity prior to the study. Study animals were the same animals used to determine activity budgets of free-grazing bison (Chapter 3).

Seven seasonal trials, encompassing each consecutive solstice and equinox, began in June 1994. Twenty-one days prior to treatment, the bison were released into the study pasture where they remained for the duration of the year. On Day -6 bison were observed for activity (Chapter 3). On Day 0, animals were moved into the handling facilities, individually sorted and held within a portable squeeze-scale. During the June trial each year, the lower incisor bar of each bison was measured to assist with emulating bites. The Day 0 treatment consisted of weighing (kg) and dosing with chromium mordanted fibre (CMF). Neither feed nor water was withheld prior to weighing. After handling, bison were returned to the study pasture. Animals were allowed to settle for 3 - 4 hours and were observed from a truck with binoculars for excretion. Fecal samples were collected during daylight hours over the next 120 h. To document liveweight change, bison were re-weighed on Day 21 or 22.

To determine quality of forage consumed, bison were tracked for defoliation on Day 3 of each trial period. Once defoliation was confirmed, bison were gently disturbed and the grazed area flagged (grazed patch). Within each grazed patch, the site of defoliation was identified (feeding station). Immediately adjacent to grazed patch, forage that was similar to the defoliation site yet had escaped immediate grazing was sampled. To determine the composition of forage consumed, 20 emulated bites were collected from forage immediately adjacent to the feeding station by emulating the depth within the sward that the bison had been grazing, and adjusting for incisor bar width (Hudson and Frank 1987). Identification of whether grasses or forbs had been consumed was considered to be straightforward. Emulated bites were dried and handled following procedures previously described in Chapter 3.

Similar to commercial bison ranches, supplemental grass-alfalfa hay was provided when snow cover was sufficient to severely restrict grazing (March 1995, December 1995). Water was provided in a cattle water tank, except in winter when snow became the major source of water. Minerals were provided free choice in a cattle mineral feeder. In June and December, animals received an anthelmintic injection at the rate recommended for cattle.

4.2.3 Pen Trials

Balance trials to determine feed intake, fecal and urinary excretion were conducted in metabolism crates at the Ministik Wildlife Research Station. Pen trials were conducted immediately following field trials (winter solstice 1994 and summer solstice 1995) to assess the expected extremes of intake, digestion and metabolism. Ten individually identified female bison, born spring 1994, were purchased from public auction in December 1994. They were held in a 0.25 ha paddock and provided with grass hay, minerals, water *ad libitum* and 3 kg hd⁻¹ d⁻¹ whole oats. However, twenty one days prior to each pen trial, all bison were fed the trial ration *ad libitum*.

On Day 0, animals were weighed and randomly assigned to either a treatment or control group. To measure daily dry matter intake and excretion, animals in the treatment group were dosed with chromium-mordanted fiber and placed in individual metabolism crates. Control animals were returned to the paddock without being dosed.

Two pen trial rations were used to approximate forages available on seasonal pasture. The feeds were pelleted to enable accurate determination of feed intake. The winter ration consisted of pelleted fescue hay. In summer, pre-inflorescence grass was swathed, field cured and pelleted.

4.2.4 Single Marker Method

In both pasture and pen trials, dry matter intakes and particle kinetics were determined using a single dose marker method (Jiang and Hudson 1992) with chromium-mordanted fiber (CMF) according to the procedures of Uden et al. (1980). Particles contained 0.67% Cr after mordanting. Chromium-mordanted fiber was suspended in two litres of water and administered as a drench.

Collection of fecal samples began four hours after dosing and continued during daylight hours for up to 5 days. Pen trial treatment group animals were observed every four hours for the first 48 hours and less frequently thereafter. A subsample of each excretion was saved for chromium analysis. Field excretions were painted to prevent re-sampling. Feces remaining on the floor of the digestion crates after each collection were removed to prevent re-sampling. The digestion crates were cleaned daily.

4.2.5 Calculation of Feed Intake Using the Marker Method

Seasonal appetite and apparent digestibility were determined from fecal chromium excretion curves using a single-dose marker method (Jiang and Hudson 1992). Marker concentrations were fit by nonlinear regression using a two-compartment time-dependent model (Hudson et al. 1994):

$$Y(t) = A(e^{-k_1(t-TT)} - e^{-k_2(t-TT)}) \quad (1)$$

where, $Y(t)$ is the fecal marker concentration at time t in hours, k_1 is the rate of ruminal emptying, k_2 is the rate of hindgut emptying, and TT is transit time. A is a fitted parameter representing the theoretical maximum initial marker concentration. The summary measure, turnover time (TO), was calculated as: $TO = TT + 1/k_1 + 1/k_2$.

Total excretion was integrated from the area under the excretion curve. Mean fecal concentration was calculated by dividing total excretion by the difference in time from first to last appearance of fecal chromium. From this value and the dose administered, the output of fecal dry matter was calculated (D_{fec}). Digestibility of the diet (Dig%) was determined by the ratio of fecal (L_{fecal}) and feed (L_{feed}) lignin as:

$$\text{Dig}(\%) = 100 * [(L_{fecal} - L_{feed}) / L_{fecal}] \quad (2)$$

Digestible dry matter intake (DDMI) was determined as:

$$\text{DDMI} = (2.4 * D_{fec}) / (100 - \text{Dig}\%) \quad (3)$$

Urinary and methane losses were not determined directly, but were approximated at 82% of digestible energy (Agricultural Research Council, 1980). As the digestible energy (DE Mcal kg^{-1}) of the ration was known from feed analysis, metabolizable energy intake (MEI kJ kg^{-1}) was thus estimated as a function of $\text{DE} * 0.82 * 4184$ to obtain MEI kJ kg^{-1} . Dividing by metabolic body weight ($\text{BW}^{0.75}$) provided MEI $\text{kJ kg}^{-0.75}$.

4.2.6 Feed Intake by the Bite Count Method

Forage intake during field trials was estimated as a function of bite rate, bite size, and feeding time (Hudson et al. 1985; Jiang and Hudson 1992), but modified by foraging rate. DMI was calculated as:

$$\text{DMI} = \text{BR} * \text{BS} * [(\text{AF} * \text{AFR}) + (\text{MF} * \text{MFR})] \quad (4)$$

where BR is bite rate (bites min^{-1}) and BS is bite size (g bite^{-1}). Bison grazed at different intensities in relation to foraging bouts, therefore forage rate was categorized as either 1) actively foraging (AF; characterized by head down and intense consumption, few

interruptions), or 2) moderately foraging (MF; characterized by frequent interruptions to grazing). Foraging intensity was measured as the time, within a five-minute span, that bison were actually consuming forage. Timings were made for AF and MF separately. Total time foraging on a daily basis became the summation of all 5-min activity observations categorized as AF or MF modified by the intensity for that 24-h period.

4.2.7 Chemical Analyses

Fecal and forage samples were dried, ground and analyzed for chromium concentration (Okine and Mathison 1991). Lignin and protein concentrations in feed, feces (in pen trials) were conducted at a commercial laboratory using Abrams (1984) adaptation of standard AOAC procedures.

Blood samples were collected via jugular venipuncture into 10-ml vacutainers, cooled, then centrifuged at 3200 rpm for 10 min to separate serum and blood clot. Serum was stored at -20°C until delivered to Kasper & Associates Medical Laboratory (Edmonton, AB) for analysis. Thyroxin analysis was conducted using a Kodak Amerlite TT4[®] competitive immunoassay technique assay kit for human serum. Prolactin analysis was conducted using a Kodak Amerlite Prolactin-30[®] enhanced luminescence immunoreactive technique assay kit for human serum.

4.2.8 Statistics

Means and standard errors for measures of weight and average daily gain during field trials were determined with the PROC GLM procedure (SAS ver 6.10, 1990). Year, gender and year*gender interaction were included in the model as fixed effects (Model 5). Differences in instantaneous growth rate and all other means and standard errors were determined as a one-way ANOVA (MS Excel ver. 5.0) with standard error calculated as the square root of variance divided by n (Model 6).

Seasonal differences in bite rate, body weight change, estimated dry matter intake from both the bite count and marker methods were determined using the PROC MIXED procedure (SAS ver 6.21 for MS Windows, 1996). Grazing period was considered a treatment and was included in the model (Model 7) as a fixed effect. Trial within season-feed group (error term) was included as a random effect. Tukey's test was used for multiple comparisons.

Seasonal differences in dry fecal output, percent digestibility, body weight change, estimated metabolic energy intake from both the bite count and marker methods, were also determined using the PROC MIXED procedure (SAS ver 6.21 for MS Windows, 1996). Season-feed group, previously described in Chapter 3, was considered a treatment for this analysis and was included in the model (Model 8) as a fixed effect. Trial within season-feed group (error term) was included as a random effect. Tukey's test was used for multiple comparisons.

Transit time, reticulo-rumen retention time, lower tract time and total turnover time were analyzed using the PROC MIXED procedure (SAS Institute, 1990). Seasonal differences were determined using the three season-feed groups previously described and were included in the model (Model 9) as a fixed effect. Trial within season-feed group (error term) was included as a random effect. Tukey's test was used for multiple comparisons.

4.3 RESULTS

4.3.1 Growth

Bison yearlings used in the field trials (218 ± 2 kg) were representative of average commercial bison (209 ± 1 kg) while the female bison calves used in the pen trials were lighter than average commercial bison (154 ± 3 kg vs. 180 ± 1 kg, Rutley et al. 1997). Yearling females were lighter than yearling males at each weigh period (Table 4.1).

Weight change during each 21-day field trial and between trial periods was consistent between years and genders. Weight change during the 21 day field trials varied significantly between field trial groups (Table 4.2).

Bison lost weight while contained in the balance crates; $-3.5 \pm 1.0 \text{ kg d}^{-1}$ in December and -2.2 ± 1.1 in June (Table 4.3). December weight loss for both treatment and control groups ($-3.0 \pm 0.3 \text{ kg d}^{-1}$) was similar, but in June, weight loss for the treatment group contrasts sharply with weight gain ($1.9 \pm 1.2 \text{ kg d}^{-1}$) for the control group.

4.3.2 Dry Matter and Metabolizable Energy Intake

Dry matter intake determined by the marker method compared reasonably well with actual DMI (Table 4.3) during pen trials. However, agreement between estimated and actual dry matter intake was less robust during summer trials (Figure 4.1). During field trials, the bite-count method always estimated dry matter intakes that were 4 to 5.5 times greater than the marker method. A significant relationship existed between the two methods, but the intercept was greater than zero and the slope deviated from unity (Figure 4.2).

Digestibility of winter feed (pelleted fescue hay, $67.1 \pm 0.9\%$) was unexpectedly greater than summer feed (pelleted pre-inflorescence grass hay, $59.9 \pm 0.6\%$). This may point to a problem with partial digestibility of the “lignin” fraction in fresh forage.

Using bite rates, bite sizes and feeding time, the dry matter intake of free-grazing yearling bison (Table 4.4) was estimated to be $11.6 \pm 0.5 \text{ kg d}^{-1}$. The comparable estimate by the marker method (Table 4.5) was only $2.4 \pm 0.2 \text{ kg d}^{-1}$. Strong seasonal differences were evident for bite rate and dry matter intake (Table 4.6).

In pen trials, actual ME intakes (\pm SE) were lower during winter ($528 \pm 51 \text{ kJ W}^{0.75} \text{ d}^{-1}$) than in summer ($917 \pm 69 \text{ kJ W}^{0.75} \text{ d}^{-1}$) (Table 4.3). Estimated ME intakes were more

variable (December 1994, $425 \pm 96 \text{ kJ W}^{-0.75} \text{ d}^{-1}$; June 1995, $1326 \pm 331 \text{ kJ W}^{-0.75} \text{ d}^{-1}$). Differences in methods, age of bison, penning and ration indicate that comparisons of estimated ME intake between pen and field trials need to be made cautiously. In field trials, both bite count and marker method estimated ME intakes (Table 4.7) considerably lower during winter grazing (819 ± 375 , $146 \pm 105 \text{ kJ W}^{-0.75} \text{ d}^{-1}$) than summer grazing (1977 ± 186 , $408 \pm 53 \text{ kJ W}^{-0.75} \text{ d}^{-1}$) (Table 4.7), respectively. Estimated ME intake during field trials were lower than pen trials for both actual and estimated ME intake.

Regardless of method used to estimate ME intake in field trials, a three-fold difference in estimated ME intake between September and December existed (Fig. 4.3). Using the bite count method (BC), maintenance requirements ranged from $2371 \pm 109 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in September 1994 to $818 \pm 57 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in December 1994 (Table 4.4). Using the single marker method (MM), estimates of ME requirements for maintenance ranged from $451 \pm 87 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in September 1994 to $146 \pm 22 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in December 1994 (Table 4.5). For the field trials, the bite count method seemed to overestimate while the marker method seemed to underestimate expected requirements.

4.3.3 Metabolizable Energy Requirements

Although a number of models could have been used to determine metabolizable energy requirements, simple regression of ME intake on gain was selected after Jiang and Hudson (1992). Regression of ME intake on gain (both expressed per unit of metabolic weight) gave variable estimates of metabolizable energy requirements for maintenance at weight stasis (intercept) and suspect estimates of the energy costs of liveweight change (slope) (data not shown). For pen trials, apparent (because animals actually lost weight) maintenance requirements (mean \pm SE) based on actual intake ranged from $532 \pm 178 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in winter to $956 \pm 107 \text{ kJ W}^{-0.75} \text{ d}^{-1}$ in summer (realistic values for penned animals). The marker method, however, gave spuriously low estimates in winter (only $282 \pm 234 \text{ kJ W}^{-0.75} \text{ d}^{-1}$) and unrealistically high estimates in summer ($1469 \pm 535 \text{ kJ W}^{-0.75} \text{ d}^{-1}$).

Variation during field trials was less severe ($510 \pm 135 \text{ kJ W}^{-0.75} \text{ d}^{-1}$, September 1994; $270 \pm 68 \text{ kJ W}^{-0.75} \text{ d}^{-1}$, December 1994; $191 \pm 9 \text{ kJ W}^{-0.75} \text{ d}^{-1}$, March 1995; $616 \pm 140 \text{ kJ W}^{-0.75} \text{ d}^{-1}$, June 1995; $412 \pm 109 \text{ kJ W}^{-0.75} \text{ d}^{-1}$, September 1995; $260 \pm 22 \text{ kJ W}^{-0.75} \text{ d}^{-1}$, December 1995).

Despite reservations about absolute values, seasonal contrasts are probably valid based on trends in seasonal variation of ME intake compared with actual intakes (Fig. 4.3).

Confirmatory evidence for seasonal metabolic cycles also appeared in blood hormone levels. Mean thyroxin levels (T_4), which are linked to metabolic rate, were lower in December 1994 ($82.5 \pm 4.9 \text{ nmol L}^{-1}$) compared to June 1995 ($103 \pm 4.5 \text{ nmol L}^{-1}$). Unlike deer, which display marked circannual cycles highly correlated with feed intake, there were no seasonal differences in prolactin ($2.0 \pm 0.0 \text{ } \mu\text{g L}^{-1}$, winter; $2.05 \pm 0.05 \text{ } \mu\text{g L}^{-1}$, summer).

Estimates of energy costs of liveweight gain obtained from both field and pen trials were not considered reliable and were in most cases negative. In the field trials, the relationship between liveweight change and ME_{gain} requirements accounted for some variation (r^2 ranged from 0.21 to 0.81) for each trial period (except September 95; $r^2 = 0.08$). However, only during December 1995, when bison were foraging exclusively on hay, was this relationship significant ($P < 0.05$).

4.3.4 Excretion Parameters

Excretion curve parameters varied with trial period (Table 4.8). Total turnover time during field trials ranged from $24.9 \pm 2.7 \text{ h}$ in June 1995 to $46.4 \pm 1.4 \text{ h}$ during December 1994. In field trials, transit time was significantly shorter ($P < 0.05$) during summer grazing ($5.3 \pm 1.2 \text{ h}$) than during winter grazing ($18.2 \pm 3.1 \text{ h}$) and non-growing season supplementation (15.2 ± 1.8) (Table 4.8). Variation in reticulo-rumen time across trial periods was greater than for lower tract turnover time (Table 4.7). The greatest variation between winter and

summer passage rates was evident in pen trials at Ministik (Table 4.7). All measures were between 2 and 3 fold greater in winter than summer. Individual total turnover time (Table 4.9) varied within and across seasons. Although not shown, variation in the components of excretion curve was also considerable.

4.4 DISCUSSION

The goal of this study was addressed, but the imprecision of the marker technique meant that the objectives were only partially met. The single dose marker method for estimating metabolizable energy requirements (maintenance and gain) was much less useful for bison than wapiti. Although differences between marker method estimates were not significantly different, they averaged 80% (range 5% to 210%) compared with 6% in wapiti (Jiang and Hudson 1992) where estimates were considered quite good. The marker method did not compare well with alternative methods (actual DMI in metabolism crates for the pen trials and the bite count method in field trials). Nevertheless, clear evidence of seasonal metabolic cycles was obtained and factors affecting the intake of bison on pasture were identified.

4.4.1 Marker Method

A single dose marker method has been used recently to determine fecal output of free-grazing wild cervids (Holleman and White 1989, Jiang and Hudson 1992) in contrast to domestic species where continuous dosing (1 or 2 times daily) is considered required to determine fecal output. Use of single or pulse doses, however, is considered appropriate for determining kinetics of digesta passage (Grovmum and Williams, 1973; Okine and Mathison, 1991; Khorasani et al. 1993). The single dose marker method provides an advantage of minimal handling, and was utilized in order to circumvent the negative impact that frequent handling has on intake (Rutley, unpublished data). Therefore, a main

objective of this study was to determine the usefulness of the single dose method with free-grazing bison.

Although not an ideal marker, chromic oxide is a purified chemical that forms stable complexes with food ingredients, lending itself to accurate dosing (Uden et al. 1980). Its use continues despite its limitations because a more suitable alternative has yet to be developed. Jiang and Hudson (1992) applied the single dose marker method to free-grazing wapiti to estimate intake within 6% of actual values. A question that remains is whether the disappointing results with bison are due to species differences in digestive physiology or to differences in methods.

One difference was associated with the chromium mordanted fibre. Chromium concentration (0.67%) was greater than that used by Jiang and Hudson (1992) with wapiti (0.404%). Mordanted fibre was provided to wapiti in a highly palatable alfalfa-barley pellet, the same pellet provided as the feed source. However, in the current study, cured grass hay was mordanted and provided as a drench. It was also different from the feed source as cured fescue hay (winter) and pre-inflorescence brome hay (summer) were provided in an attempt to emulate forage consumed by free-grazing bison in the companion field studies.

Method of determination of fecal output is another difference between the two studies. Jiang and Hudson (1992) determined the area under the curve as the summation of the area between each fecal chromium observation beginning with the first elevated observation until the curve reached an asymptote. In contrast, the curve-fitting program used in the current study allowed one to pre-set an estimate of transit time (TT) for animals that had elevated fecal chromium at first observation. This common occurrence was caused by a) shorter transit time than expected (< 4 h), b) delayed defecation (> 20 h with some animals), or c) later than preferred first fecal collection (over 4 h) because the bison had not

settled completely after handling during some trial periods. Therefore, by altering the estimate of pre-set TT to one that more closely corresponded to the data for the individual, a more accurate estimate of the area under the curve was possible because the iteration that provided the highest R-square statistic was selected. The advantage of this calculation over the discrete difference calculation of Jiang and Hudson (1992) is that the area under the curve from TT until the first elevated fecal chromium value is considered. With some bison, this difference approached 50%.

A secondary advantage of this method is that the need to be concerned about which is the larger compartment, reticulo-rumen (k_1) or lowergut (k_2), is eliminated. Irrespective of particle size or whether particulates are moving with the liquid or solid phase, the area under the curve provides a mathematically more accurate estimate of total excretion.

Neither laboratory nor computational methods should impair the performance of the method so it is reasonable to turn to differences in the digestive physiology of bison. Particularly noticeable was the variation in transit time (TT). Mean TT was highly variable across seasons, however there was little difference in TT between June and September implying that the killing frost in September had not completely cured the forage (Hudson and Frank 1987) nor impacted on passage rates. Mean total turnover time during June 1995 was unexpectedly short at 24.9 ± 2.7 h, 11 hours shorter than June 1994 (Table 4.8). No explanation for this observation was evident, other than that this group was considerably less settled than the previous year's group.

A comparison of TT during supplementation supports the hypothesis that timely feeding of supplemental forages can alter the metabolic requirements of bison. Mean TT was 18 h during winter grazing (December 1995) and during supplementation (March 1995) after an extended period of winter grazing. However, when bison were supplemented directly after

the September 1995 grazing period, subsequent TT during supplementation in December 1995 was only 12 h, a more intermediate time.

Differences in means across trial periods and during pen trials (Table 4.8) indicate sizable seasonal differences. However, this variation is related primarily to significant seasonal differences in transit time rather than either reticulo-rumen retention time or lower tract passage rates (Table 4.8). Because digesta outflow is determined solely by feed characteristics (Mathison et al. 1995), consistent trends across grazing periods could be expected. That did not occur. In addition, secondary “waves” of excretion were evident in a number of animals. The lack of consistency may be due to 1) stratification of rumen contents or some other sequestering phenomenon, 2) variation in daily intake, or 3) simply to the presence of the occasional long fibre that had passed through the sieve during the mordanting process. This phenomenon is not detectable in wapiti.

4.4.2 Bite Count Method

The bite count method offered an alternative for estimating intake on pasture. The application of the bite count method was refined from Jiang and Hudson (1992) in that a more direct accounting of foraging intensity and foraging rate was adopted. This alteration was expected to have increased accuracy. Measuring bite rate was the least robust of the measures as bison were viewed via binoculars from up to 100 metres, although bite rates were similar to those obtained at 30 metres. Closer observation of bison may provide greater distinction between cropping and chewing bites prior to application of this method in future studies. Sample bite size techniques have been proven previously (Hudson and Frank 1987). Sample bite sizes were adjusted for lower incisor bar width by hand gathering exposed tillers at the width of the incisor bar. This adjustment however, does assume that each bite would be maximal.

The bite count method included night grazing, which was considerable throughout the year. However, using group averages for foraging time in conjunction with individual values for bite rates and bite sizes can bias estimates. Bite count estimates resulted in reasonable daily DMI between 9 and 18 kg d⁻¹. However the ratio of DM to body weight (BW), up to 5.8% during summer trials, is extremely high in comparison to 1% to 2.8% for cattle and sheep grazing Western United States ranges (Cordova et al. 1978). On the other hand, the marker method estimated summer DMI at 2 to 3.5 kg d⁻¹ (0.6% to 1.6% BW), rates that appear low for bison. Trudel and White (1981) reported intake in reindeer at 3.8% and estimated maximum intake near 5.7% of BW. Despite questions of bias, both methods paralleled each other with respect to identifying seasonal differences, the pattern of differences, and were similar in describing the magnitude of the differences.

4.4.3 Energy Requirements

Estimates of ME were based on the assumption that inputs and outputs from the alimentary tract were in steady state (Jiang and Hudson 1992), an assumption that may not be completely valid based on considerable weight loss during many trials (winter grazing in December 1994; both winter and summer pen trials). Ecological energy requirements estimate the amount of energy required to maintain body weight throughout the year. As it is expected that most wild ruminants would exhibit circannual body weight cycles (Price and White 1985), a pattern that farmed reindeer maintained even during circannual supplemental feeding (Rutley, unpublished data), applying ecological estimates to bison may not be completely valid. However, they are the best estimates available, considering the alternative of measuring heat production while contained in metabolism crates.

Although little can be said about absolute values while grazing, bison clearly exhibit seasonal cycles for appetite and energy requirements. This confirms reports on penned animals by Christopherson et al. (1978), which showed modest seasonality. By analogy with deer (early spring peak), the expected peak for bison is the summer solstice.

However, our data show peak voluntary intake and maintenance requirements in June and September (both years using both methods), a pattern more similar to muskoxen (Adamczewski et al. 1994). Although thyroxin did reflect seasonal metabolic cycles, prolactin values were low (compared with wapiti) and did not vary with season (see Hudson et al. 1994).

Because animals experienced different handling stress, levels of intake and rates of gain, incremental costs of free-grazing (difference between pen and field trials) must be evaluated cautiously. If actual intakes for pen trials are paired with the bite count estimate for the field, then the cost of free existence is 1.5-2.5 times (which is similar to the 2.5 times energy harvested vs. energy expended for summer grazing black-tailed deer, Parker et al. 1996). However, pairing marker methods shows the reverse pattern with requirements of penned animals exceeding those on pasture.

Although seasonality was confirmed, estimates of ME requirements for liveweight maintenance were suspect. Values fell outside the expected range of 20-55 kJ g⁻¹ and were in some cases negative. This is probably due to the imprecision of the technique as discussed above, stress associated with penning and handling, and quality of winter graze.

Current data provides evidence that forage quality may override seasonal effects of photoperiod and ambient temperature. Peak seasonal variation (December and June) in ME intake for penned forage fed (pellets) bison was 48%, comparable to previous estimates for penned bison (Christopherson et al. 1978). When bison went directly from grazing to supplementation in field trials, their ME intake remained high compared with ME intake during winter grazing the previous winter (December 1994). Seasonal amplitude was estimated at 60% (marker method) and 76% (bite count method). Both pen supplemented and pasture supplemented bison expressed reduced amplitude of seasonal cycles compared with summer and winter grazing bison (200%).

Supplemental feeding of hay (March 1995) did not re-elevate ME intake once it had been reduced. It would appear that once their metabolism slows down with the change in season in late autumn, bison were unable to respond to supplemental feeding with an increase in metabolism. This observation is consistent with fed reindeer (R. G. White, personal communication). Conversely, it would appear that bison will respond to timely feeding of supplemental forage and maintain elevated metabolic activity into the winter. This supposition is supported by observations from the commercial industry. Weaned bison calves, provided and maintained on grain-based rations, will obtain slaughter weight and condition before 24 months of age compared to 30 to 33 months of age when bison are maintained on forage rations during winter and the subsequent summer (personal observation). Further studies comparing ME requirements of the mid solstice-equinox period would be beneficial to quantifying seasonal energy requirements.

4.4.4 Instantaneous Growth Rate

Supplemental feeding of bison during winter months will ameliorate negative instantaneous growth rate (r). The provision of supplemental feed enabled bison to alter their daily activities similar to those exhibited during June or September (Chapter 3), despite ambient temperatures ranging between -12°C and -22°C . Foraging time was significantly reduced in favour of increased resting and time spent in minor activities. This change probably contributed positively to an instantaneous growth rate (Kleiber 1975) near zero compared with a significantly negative instantaneous growth rate during winter grazing, when energy expenditure for forage acquisition was greater.

The results of this study would indicate that free-grazing yearling bison would be able to consume sufficient dry matter to meet their daily needs ($11.9 \pm 1.2 \text{ kg d}^{-1}$), however, they were unable to obtain enough energy from forage consumed to maintain body weight. Extending the grazing intake data for March 1995 (Table 4.4), indicates that bison would need to graze 22.6 h d^{-1} to obtain the same level of CP intake as they were able to obtain in

9.5 h d⁻¹ in December 1994. However, their December intake still resulted in daily weight loss at 4.2% of their body weight. As December 1994 snow conditions were less severe, without supplementation during conditions like those present in March 1995, weight loss could be catastrophic for free-grazing young bison.

4.5 CONCLUSIONS

Both the single marker and bite count methods provided clear evidence that bison exhibit seasonal cycles for appetite and maintenance energy (ME) requirements. A near three-fold variation between summer grazing and winter grazing ME intake was observed for free-grazing bison. However, supplementation significantly impacted the amplitude of seasonal cycles. Variation between summer grazing peaks and winter supplementation were 60% (marker method) and 76% (bite count method) compared with nearly 200% during free grazing.

Seasonal variation in turnover time is related to significant seasonal differences in transit time rather than differences in reticulo-rumen and lower tract turnover time. Evidence of secondary “waves” of excretion in a number of animals merits further study to determine if bison exhibit some stratification or sequestering of rumen contents. Further studies comparing ME requirements of the mid solstice-equinox period would be beneficial to quantifying seasonal energy requirements.

Table 4.1. Body weight (kg \pm SE) of yearling bison summarized by trial period

	n	June	September	December	March ^z
Year 1	6	228 \pm 17	315 \pm 19	331 \pm 25	350 \pm 27
Year 2	6	213 \pm 15	270 \pm 19	289 \pm 22	297 \pm 26
Females	3	195 \pm 11	259 \pm 14	282 \pm 18	276 \pm 16
Males	3	249 \pm 8	326 \pm 16	341 \pm 26	371 \pm 23

^z Although there were no field data collected in March 1994 (March Year 2), body weights were determined.

Table 4.2. Instantaneous growth rate (r)^z of yearling bison during 21 day field trials^y

	n	June grazing	September grazing	Winter grazing	Supplementation
All	6	2.4% \pm 0.0003% ^a	2.0% \pm 0.0004% ^a	-4.2 \pm 0.0004% ^c	-0.1% \pm 0.0004% ^b

^z $r = (\ln(w_2) - \ln(w_1)) / (t_2 - t_1)$ represents percent change in existing body weight per day.

^y t_1 = day marker administered, t_2 = weigh date 21 or 22 days later.

^y June grazing = June 1994 and June 1995; September grazing = September 1994 and September 1995; Winter grazing = December 1994
Supplementation = March 1995 and December 1995

Means (\pm SE) with different letters indicates significant difference $P < 0.0001$.

Table 4.3. Daily intake of ten 1994 cohort bison females during December 1994 and June 1995 pen trials

	December		June	
	Treatment ^z	Control	Treatment ^z	Control
n	4	5	5	5
Body weight (kg)	154 ± 8	153 ± 4	230 ± 9	207 ± 8
Dry faecal output (g h ⁻¹)	27 ± 5	--	125 ± 0.6	--
Digestibility %	67.1 ± 0.9	--	59.9 ± 0.6	--
Estimated DMI (kg d ⁻¹)	1.9 ± 0.4	--	7.4 ± 1.8	--
Actual DMI (kg d ⁻¹)	2.2 ± 0.3	3.3	4.9 ± 0.5	5.6
Body weight change (kg d ⁻¹)	-3.5 ± 1.0	-2.9 ± 0.2	-2.2 ± 1.1	1.9 ± 1.2
Estimated ME Intake (kJ W ^{-0.75} d ⁻¹)	425 ± 96	--	1326 ± 331	--
Actual ME Intake (kJ W ^{-0.75} d ⁻¹)	528 ± 51	--	917 ± 69	--
Estimated DM Intake (g W ^{-0.75} d ⁻¹)	45 ± 10	--	125 ± 31	--
Actual DM Intake (g W ^{-0.75} d ⁻¹)	52 ± 7	--	84 ± 7	--
Apparent ME _{main} (kJ W ^{-0.75} d ⁻¹)	282 ± 234	--	1469 ± 535	--
Actual ME _{main} (kJ W ^{-0.75} d ⁻¹)	532 ± 178	--	956 ± 107	--

^z Values given as mean ± standard error.

DMI is dry matter intake. ME is metabolizable energy.

Estimated DMI, estimated ME intake and apparent ME_{main} were determined by single marker method.

Actual DMI, ME intake and ME_{main} determined from actual feed consumption.

Table 4.4. Bite count method estimated measures of intake (\pm SE) for six free-grazing yearling bison summarized by trial period

	Trial period									
	June 1994	September 1994	December 1994	March 95 ^z	June 95	September 1995	December 1995 ^z	Mean		
Bite rate (b min ⁻¹)	73 \pm 8	87 \pm 2	98 \pm 3	47 \pm 9 [†]	70 \pm 4	88 \pm 3	na	80 \pm 3		
Bite size (g bite ⁻¹) ^y	0.48	0.59	0.28	0.18 [†]	0.59	0.40	na	0.42 \pm 0.03		
Consumption rates ^y (g min ⁻¹)	35	51	27	8 [†]	41	35	na	33		
AF (h d ⁻¹) ^x	5.4	6.0	8.8	4.4	4.3	4.4	5.8	5.9 \pm 0.3		
AF rate % ^x	85 \pm 3	93 \pm 2	82 \pm 2	96 \pm 1	85 \pm 1	94 \pm 1	96 \pm 1	88 \pm 1		
MF (h d ⁻¹) ^x	1.0	1.3	0.7	0.4	1.6	0.6	na	0.9 \pm 0.1		
MF rate % ^x	20	20	20	80	20	60	na	40 \pm 4		
Body weight change (kg d ⁻¹)	0.8 \pm 0.2	0.4 \pm 0.2	-1.4 \pm 0.1	0.1 \pm 0.2	0.4 \pm 0.1	0.7 \pm 0.1	-0.1 \pm 0.1	0.2 \pm 0.1		
Estimated DMI (kg d ⁻¹)	10.3 \pm 1.5	17.7 \pm 0.6	11.5 \pm 0.5	9.2 \pm 0.1	9.9 \pm 0.5	11.6 \pm 0.3	10.5 \pm 0.0	11.6 \pm 0.5		
Est. ME intake (kJ W ^{-0.75} d ⁻¹)	1757 \pm 177	2371 \pm 109	818 \pm 57	756 \pm 42	2170 \pm 194	1606 \pm 37	1347 \pm 75	1559 \pm 100		

^z Because bison were consuming hay, estimated dry matter intake (DMI) and estimated metabolizable energy (ME) intake are based on actual DM hay consumption.
^y Values without standard errors are based on a group observation not individual observations.

^x AF = Actively foraging; MF = Moderately foraging.

[†] Based upon observations of limited grazing activity.

Table 4.5. Marker method estimated measures of intake (\pm SE) for six free-grazing yearling bison summarized by trial period

	Trial period										Mean
	June 1994	September 1994	December 1994	March 1995	June 1995	September 1995	December 1995	September 1995	June 1995	March 1995	
Body weight (kg)	228 \pm 17	315 \pm 19	331 \pm 25	350 \pm 27	213 \pm 15	270 \pm 19	289 \pm 22	270 \pm 19	213 \pm 15	350 \pm 27	277 \pm 10
Dry faecal output (g h ⁻¹)	17 \pm 3	47 \pm 8	61 \pm 8	53 \pm 3	22 \pm 3	31 \pm 3	36 \pm 3	31 \pm 3	22 \pm 3	53 \pm 3	36 \pm 3
Digestibility %	na	66.3 \pm 1.1	32.3 \pm 0.2	43.3 \pm 0.8	76.8 \pm 0.3	65.0 \pm 1.1	61.8 \pm 1.8	65.0 \pm 1.1	76.8 \pm 0.3	43.3 \pm 0.8	60.4 \pm 2.5
Estimated DMI (kg d ⁻¹)	na	3.4 \pm 0.6	2.2 \pm 0.2	2.3 \pm 0.2	2.2 \pm 0.3	2.1 \pm 0.3	2.3 \pm 0.2	2.1 \pm 0.3	2.2 \pm 0.3	2.3 \pm 0.2	2.4 \pm 0.2
Body weight change (kg d ⁻¹)	0.8 \pm 0.1	0.4 \pm 0.2	-1.4 \pm 0.2	0.1 \pm 0.2	0.4 \pm 0.1	0.7 \pm 0.1	-0.1 \pm 0.1	0.7 \pm 0.1	0.4 \pm 0.1	0.1 \pm 0.2	0.21 \pm 0.1
Est. ME Intake (kJ W ^{0.75} d ⁻¹)	na	451 \pm 87	146 \pm 22	189 \pm 12	478 \pm 45	295 \pm 43	298 \pm 42	295 \pm 43	478 \pm 45	189 \pm 12	329 \pm 29

DMI is dry matter intake, ME is metabolizable energy.

Table 4.6. Seasonal estimates associated with dry matter intake (\pm SE) for six free-grazing yearling bison summarized by grazing period

	Grazing period		
	June	September	December
Bite rate (b min ⁻¹)	72 \pm 1 ^b	87 \pm 1 ^a	98 \pm 2 ^a
Body weight change (kg d ⁻¹)	0.6 \pm 0.4	0.5 \pm 0.4	-0.7 \pm 0.4
Est. DMI (kg d ⁻¹) bite count	10.1 \pm 0.8 ^b	14.7 \pm 0.8 ^a	11.9 \pm 1.2 ^{ab}
Est DMI (kg d ⁻¹) marker method	2.3 \pm 0.6	2.8 \pm 0.5	2.2 \pm 0.5

Means (\pm SE) with different letters within rows indicates significant difference $P < 0.05$.
DMI is dry matter intake.

Table 4.7. Seasonal estimates associated with metabolizable energy intake (\pm SE) of six free-grazing yearling bison summarized by season-feed group

	Season-feed group	
	Summer grazing	Winter grazing
Dry faecal output (g h ⁻¹)	29 \pm 6	61 \pm 13
Digestibility %	69.4 \pm 5.3 ^a	32.3 \pm 9.3 ^b
Body weight change (kg d ⁻¹)	0.5 \pm 0.1 ^a	-1.4 \pm 0.2 ^c
Estimated ME intake (kJ W ^{0.75} d ⁻¹) bite count	1977 \pm 186	819 \pm 375
Estimated ME intake (kJ W ^{0.75} d ⁻¹) marker method	408 \pm 53	146 \pm 105

Means (\pm SE) with different letters within rows indicates significant difference $P < 0.05$.
ME is metabolizable energy.

Supplementation

45 \pm 9

52.5 \pm 6.5^a

-0.0 \pm 0.1^b

1051 \pm 236

245 \pm 66

Table 4.8. Mean trial estimates of turnover time (h) for free-grazing^z and penned bison^y, based on fecal chromium excretion curves^x

Trial Periods (\pm SE)	n	Transit time	Reticulo-rumen	Lower tract	Total turnover time
June 1994	5	6.4 \pm 0.4	20.5 \pm 4.2	9.2 \pm 2.1	36.1 \pm 2.6
September 1994	6	6.0 \pm 0.5	12.2 \pm 0.4	9.0 \pm 1.4	27.2 \pm 1.1
December 1994	3	18.2 \pm 1.2	19.7 \pm 1.7	8.5 \pm 3.1	46.4 \pm 1.4
March 1995	5	18.7 \pm 2.0	11.9 \pm 1.6	8.8 \pm 0.4	39.4 \pm 1.7
June 1995	6	4.0 \pm 0.8	13.2 \pm 1.0	7.7 \pm 1.9	24.9 \pm 2.7
September 1995	6	4.8 \pm 0.7	24.1 \pm 1.1	5.8 \pm 1.4	34.6 \pm 2.8
December 1995	6	12.1 \pm 4.1	27.1 \pm 2.6	17.0 \pm 3.4	56.1 \pm 2.7

Pen Trials (\pm SD)	n	Transit time	Reticulo-rumen	Lower tract	Total turnover time
Winter	4	17.1 \pm 2.0	30.4 \pm 6.7	18.3 \pm 9.6	65.7 \pm 6.4
Summer	5	8.1 \pm 3.6	11.4 \pm 4.7	5.6 \pm 6.3	25.1 \pm 8.9

^z Bison in field trials, were free-grazing except in March 1995 and December 1995 when supplemental hay was provided.

^y Bison in pen trials consumed pelleted fescue hay in winter and pelleted pre-inflorescence grass hay in summer.

Table 4.9. Mean season-feed group estimates (\pm SE) of turnover time (h) for six free-grazing bison based on fecal chromium curves

Season-feed group	n	Transit time	Reticulo-rumen	Lower tract	Total turnover time
Summer grazing	23	5.3 \pm 1.2 ^b	17.5 \pm 3.7	7.9 \pm 1.6	30.7 \pm 3.8
Winter grazing	3	18.2 \pm 3.1 ^a	19.7 \pm 7.8	8.5 \pm 3.7	46.4 \pm 7.9
Supplementation	11	15.2 \pm 1.8 ^a	19.5 \pm 5.2	13.0 \pm 2.2	47.8 \pm 5.4

Means (\pm SE) with different letters within columns indicates significant difference $P < 0.05$.

Table 4.10. Individual seasonal estimates of total turnover time^z (h) by free-grazing and penned bison, based on fecal chromium excretion curves

Year 1 Field Trials	Individual bison ^y											
	Blue		Green		Purple		Red		White		Yellow	
	F	M	F	M	F	M	F	M	F	M	F	M
June 1994	30.1	32.8	36.0	45.6	na	35.8						
September 1994	22.2	27.6	26.0	29.5	29.5	28.3						
December 1994	43.6	48.2	47.3	na	na	na						
March 1995	37.2	44.3	39.0	41.5	41.5	34.9						
Year 2 Field Trials	Blue		Green		Purple		Red		White		Yellow	
	F	M	F	M	F	M	F	M	F	M	F	M
June 1995	17.0	21.0	23.2	27.3	27.3	24.5						
September 1995	27.9	29.1	30.7	45.3	45.3	34.7						
December 1995	55.3	55.4	53.8	66.7	66.7	46.9						
Pen Trials	6Y		8Y		12Y		17Y		47W			
December 1994	59.8	na	61.7	74.1	74.1	67.1						
June 1995	21.6	37.4	23.7	13.5	13.5	29.5						

^z Total turnover time = $1/k_1 + 1/k_2 + TT$, where k_1 is reticulo-rumen turnover time, k_2 is lower tract turnover time, and TT is transit time.

^y Data within year and (or) trial represents repeated measures on the same animals. M = Male, F = Female.

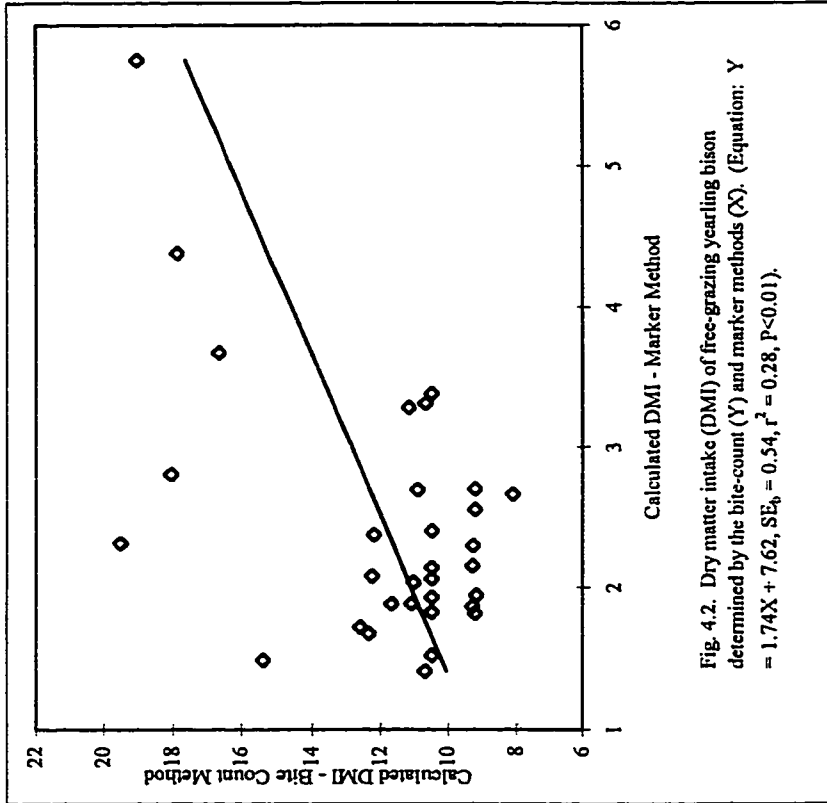


Fig. 4.2. Dry matter intake (DMI) of free-grazing yearling bison determined by the bite-count (Y) and marker methods (X). (Equation: $Y = 1.74X + 7.62$, $SE_b = 0.54$, $r^2 = 0.28$, $P < 0.01$).

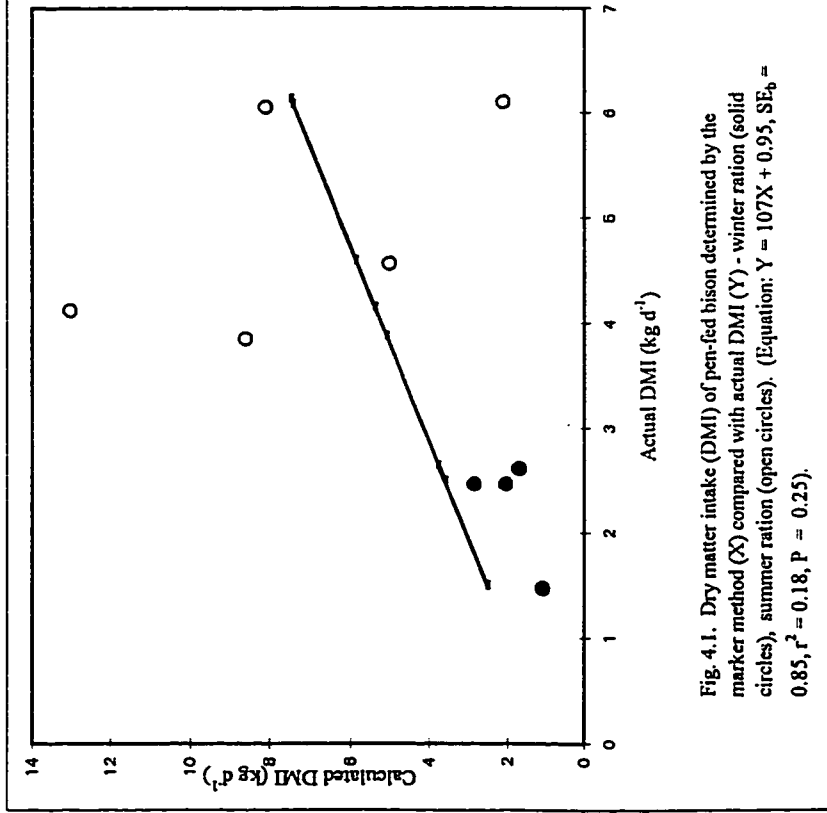
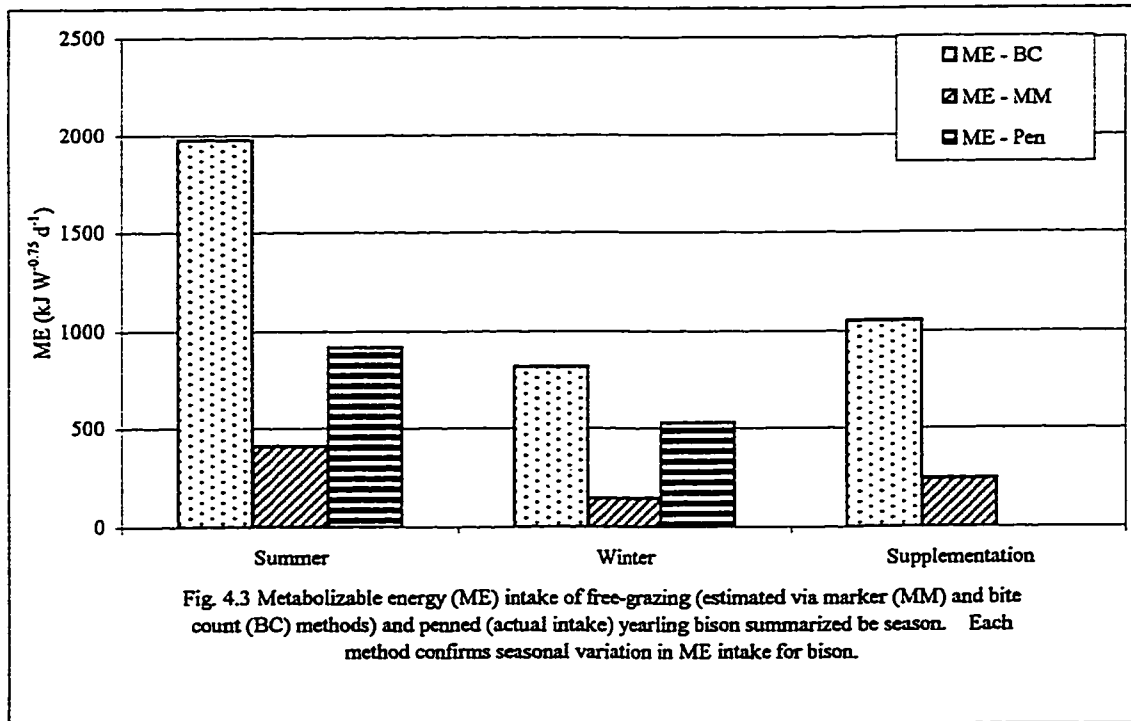
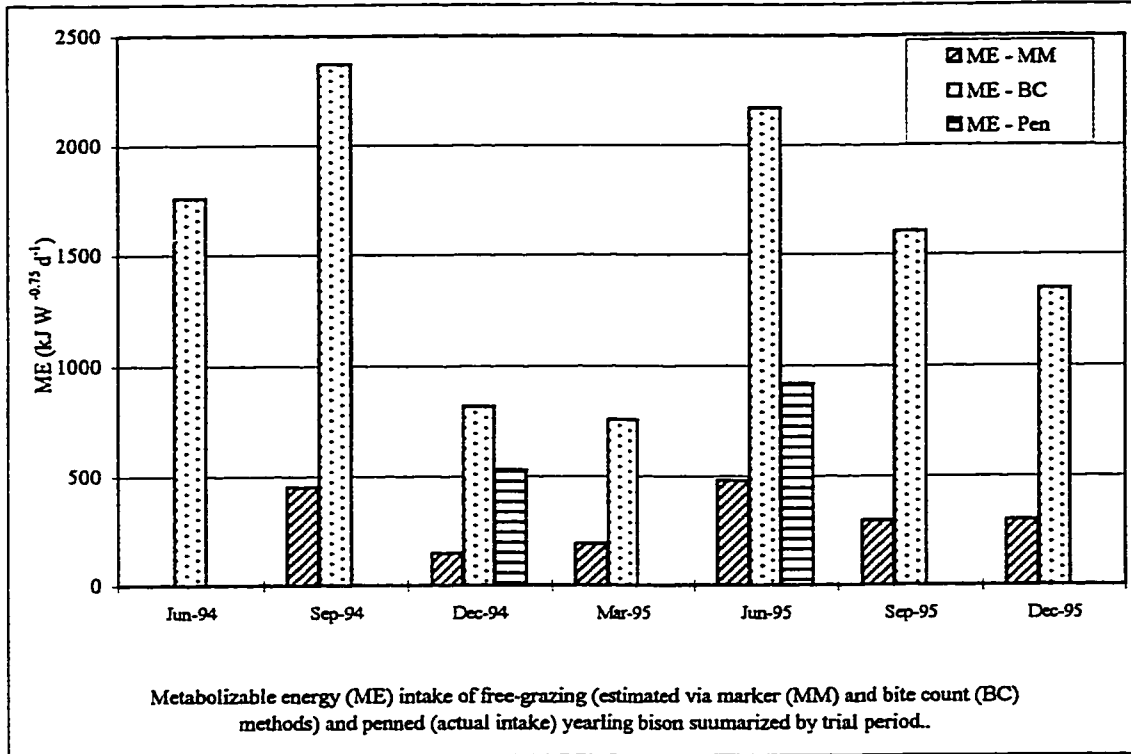


Fig. 4.1. Dry matter intake (DMI) of pen-fed bison determined by the marker method (X) compared with actual DMI (Y) - winter ration (solid circles), summer ration (open circles). (Equation: $Y = 107X + 0.95$, $SE_b = 0.85$, $r^2 = 0.18$, $P = 0.25$).



4.5 REFERENCES

Abrams, S. M. 1984. Pages 21-24 in Proceedings of the National Alfalfa Hay Quality Testing Workshop. 1984.

Adamczewski, J. Z., Chaplin, R. K., Schaefer, J. A. and Flood, P. F. 1994. Seasonal variation in intake and digestion of a high-roughage diet by muskoxen. *Can. J. Anim. Sci.* 74: 305-313.

Agricultural Research Council 1980. The nutrient requirements of ruminant livestock. Commonwealth Agricultural Bureaux, Farnham Royal, England, 1980.

Blaxter, K. L. 1989. Energy metabolism in animals and man. Cambridge University Press, New York. NY. 335 pp.

Christopherson, R. J., Hudson, R. J. and Richmond, R. J. 1978. Comparative winter bioenergetics of American bison, yak, Scottish Highland and Hereford calves. *Acta Theriologica* 23(2): 49-54.

Cordova, F. J., Wallace, J. D., and Pieper, R. D. 1978. Forage intake by grazing livestock: a review. *J. Range Manage.* 31(6): 430-438.

Gates, C. C. and Hudson, R. J. 1983. Foraging behaviour of wapiti in a boreal forest enclosure. *Naturaliste can. (Rev. Ecol. Syst.)* 110: 197-206.

Grovum, W. L. and Williams, V. J. 1973. Rate of passage of digesta in sheep. 3. Passage of a marker through the alimentary tract and the biological relevance of rate constants derived from the changes in concentration of markers in faeces. *Br. J. Nutr.* 30: 313-329.

Holleman, D. F. and White, R. G. 1989. Determination of digesta fill and passage rate from nonabsorbed particulate phase markers using the single dosing method. *Can. J. Zool.* 67: 488-494.

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

Hudson, R. J., Nixdorf, R., Kathnelson, S., Kam, M. and Jiang, Z. 1994. Management implications of seasonal bioenergetic cycles of wapiti (*Cervus elaphus*). Farming for the Future Project # FFF 92-0194. August 1994.

Hudson, R. J., Watkins, W. G. and Pauls, R. W. 1985. Seasonal bioenergetics of wapiti in western Canada. Pages 447-452 in P. F. Fennesey and K. R. Drew, eds. *Biology of deer production*. Royal Soc. New Zealand Bull. Vol. 22.

Jiang, Z. and Hudson, R. J. 1992. Estimating forage intake and energy requirements of free-ranging wapiti (*Cervus elaphus*). *Can. J. Zool.* **70**: 675-679.

Jiang, Z. and Hudson, R. J. 1993. Seasonal energy requirements of wapiti (*Cervus elaphus*) for maintenance and growth. *Can. J. Anim. Sci.* **74**: 97-102.

Khorasani, G. R., Okine, E. K., Kennelly, J. J. and Helm, J. H. 1993. Effect of whole crop cereal grain silage substituted for alfalfa silage on performance of lactating dairy cows. *J. Dairy Sci.* **76**: 3536-3546.

Kleiber, M. 1975. *The fire of life: an introduction to animal energetics*. R. E. Krieger Publishing Company, Huntington, NY. 1975. 453 pp.

Mathison, G. W., Okine, E. K., Vaage, A. S., Kaske, M., and Milligan, L. P. 1993. Current understanding of the contribution of the propulsive activities in the forestomach to the flow of digesta. Pages 23-41 in E. v. Engelhardt, S. Leonhard-Marek, G. Breves and D. Giesecke eds. *Ruminant physiology: digestion, metabolism, growth and reproduction*. Proceedings of the eighth international symposium on ruminant physiology. Ferdinand Enke Verlag Stuttgart 1995.

Parker, K. L., Gillingham, M. P., Hanley, T. A. and Robbins, C. T. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Can. J. Zool.* **74**: 442-450.

Price, M. A. and White, R. G. 1985. Growth and development. Pages 183-213 *in* R. J. Hudson and R. G. White eds. Bioenergetics of wild herbivores. CRC Press. Boca Raton, FL.

Rutley, B. D., Jahn, C. M. and Hudson, R. J. 1997. Management, gain and productivity of Peace Country bison (*Bison bison*). *Can. J. Anim. Sci.* **77**: 347-353.

SAS Institute Inc. 1990. SAS/STAT user's guide. Version 6.10, 4th ed. SAS Institute, Inc. Cary, NC.

Okine, E. K. and Mathison, G. W. 1991. Reticular contraction attributes and passage of digesta from the ruminoreticulum in cattle feed roughage diets. *J. Anim. Sci.* **69**: 2177-2186.

Uden, P., Colucci, P. E. and Van Soest, P. J. 1980. Investigation of chromium, cerium and cobalt as markers in digesta, rate of passage studies. *J. Sci. Food Agric.* **31**: 625-632.

CHAPTER 5. Synthesis and Discussion

This research was undertaken to contribute to our understanding of the nature and biology of bison, including growth, gain, response to changes in seasonal forage and determination of seasonal cycles for energy requirements. Survey data were collected and experiments were designed and conducted to determine growth and performance of bison on seasonal pastures.

This research successfully addressed the following specific research objectives as outlined in Chapter 1:

1. Develop a profile of the bison industry, based on a survey of Peace Country bison, and obtain insights on the effect of management practice on measures of growth (weight and gain) in juvenile bison.
2. Evaluate the seasonal activity budgets and foraging strategies of bison including selectivity and feeding efficiencies in relation to pasture biomass and structure.
3. Determine the extent that juvenile bison exhibit seasonal variation in metabolic energy requirements ($ME_{\text{maintenance}}$ and ME_{gain}), ie. dry matter intake, passage rate and estimates of digestibility.

Previous discussion, contained within Chapters 2-4, has focused on the specific research objectives. This chapter provides synthesis and discussion on the two areas considered most lacking - growth and gain, seasonality as well as defining 'the bison advantage'.

By developing a sound understanding of the biological characteristics of bison, we will have insights into possible impacts that newly developed or transferred existing management techniques may have on the nature of the species.

These questions are as relevant for managers of public herds as they are for managers of commercial herds because limitations in land base associated with public herds make them, in effect, merely large bison herds with a different set of management parameters.

5.1 SUMMARY

Profiles describing a typical Peace Country bison and bison enterprise are summarized in Chapter 2. Management factors affecting the weight of bison include gender, weigh date, herd health, grain flushing and length of grazing season. Managers maintaining a herd health program that included the routine use of anthelmintics and (or) vaccines were more productive. Weight data collected from on-farm surveys is sufficient to serve as a benchmark for herd comparisons.

A negative relationship exists between post weaning winter gain and subsequent gain, therefore, managers planning to maximize yearling weight gain on summer pasture are advised to target for modest winter gain. There was evidence of episodic growth in bison (a characteristic of wild ruminants), however this may be more responsive (to winter ration) than adaptive (genetic).

Circadian activity patterns for free-grazing bison were distinctly polyphasic and consistent with other free-grazing ruminants (Chapter 3). Significant seasonal variation in activity patterns was evident, primarily manifested as alterations to foraging and bedding activity. Under consistent forage biomass (DM basis), bison

responded to seasonal change by increasing foraging time and decreasing bedding time. Total time foraging and bedding bout length were greatest during winter grazing. During winter grazing, daily foraging, bedding and minor activity time allocations were 39.6%, 58.5% and 1.8%, respectively, compared with 26.6%, 67.2% and 6.2% during summer grazing. Percentage of the 24 h activity budget for foraging and resting activity did not vary significantly between summer grazing and (winter) supplementation.

Bison grazed selectively under tame pasture conditions. This observation supports previous research conducted on prairie ecosystems. Bison consistently selected forage out of proportion with availability. By consistently consuming the upper portion of the plant, they were able to consume a diet significantly higher in crude protein and digestible energy compared with a non-selective diet from the available sward.

The objectives of the pen and field studies (Chapter 4) were addressed, but the imprecision of the techniques meant that the goals were only partially met. The single dose marker method for estimating digestible dry matter intake and hence metabolizable energy requirements for maintenance and gain on pasture was much less useful for bison than wapiti where estimates were quite good (Jiang and Hudson 1992). The marker method did not compare well with actual DMI (except for winter pen trials) or the bite count method during field trials.

Bite count estimates resulted in daily DMI between 9 and 18 kg d⁻¹, however the ratio of DM to body weight (BW), up to 5.8% during summer trials, is extremely high in comparison to 1% to 2.8% for cattle and sheep grazing Western United States ranges (Cordova et al. 1978). On the other hand, the marker method estimated summer DMI at 2 to 3.5 kg d⁻¹ (0.6% to 1.6% BW), rates that appear low for bison. Despite questions of bias, both methods paralleled each other with respect to identifying

seasonal differences, as bison clearly exhibit seasonal cycles for appetite and energy requirements.

Amplitudes of seasonal energy cycles were previously estimated at 16% to 67% (Christopherson et al. 1978, 1979) but may be valid for supplemented bison only. Current data show amplitude at 48% in penned hay-fed bison while free-grazing bison exhibited highly developed seasonal cycles near 200%.

Current data also provide evidence that feed source may override seasonal effects of photoperiod and ambient temperature. Winter to summer variation in ME requirements for free-grazing bison fed hay during winter was considerably lower (60% or 76%, MM and BC methods, respectively) than the highly developed seasonal cycles (190% and 209%, MM and BC methods, respectively) exhibited by bison that winter grazed without supplementation.

Further research is needed to determine the existence of episodic growth under seasonal and consistent feed regimes. Further development of techniques to assess seasonal energy requirements of free-grazing bison is required. It would also be prudent to re-evaluate seasonal maintenance energy requirements of other wild ruminants while free-grazing versus supplementation. Further studies comparing ME requirements of the mid solstice-equinox period would be beneficial to quantifying seasonal energy requirements.

5.2 GROWTH: MATURITY RATE and GAIN

Whether bison grow more similar to wild ruminants or domestic cattle could not be answered directly with the data set obtained. However, the data enable the following

observations - observations which provide insights into how bison grow and mature, and which serve as a basis for further discussion.

Mean yearling weight, expressed as a percentage of mean adult weight (maturity rate) provides an interesting insight. Like wild and domestic ruminants, bison females obtain a greater portion of their mature body weight faster than bison males. This is probably related to their smaller mature size, as it is in other species (Bandy et al. 1970; Renecker and Samuel 1991). However, bison females obtain their mature body weight more slowly than both wild and domestic ruminants. They only obtained 65% of their mature body weight by 20 months of age compared to 72-80% in cattle and 75-90% in cervids (Table 5.1). Assuming that puberty in bison is weight dependent, as it is in some species, then a lower ratio is consistent with less than 1% of bison females calving by two years of age (Rutley and Jahn 1997). In contrast, 95% of beef cattle (Mathison 1993) and farmed reindeer (Rutley, unpublished data) calve at two years of age. Furthermore, both farmed (Rutley, unpublished data) and free-ranging reindeer (Ropstad et al. 1993) will conceive at 4-5 months of age, if they have attained 40% mature BW (45 kg body weight).

The portion of mature body weight obtained by bison yearling males (48%-55%) compares more favourably with free-ranging ruminants (near 55%) than farmed reindeer (65%) or cattle (67-78%) (Table 5.1). If passing a semen test defines sexual maturity, then bison males can be sexually mature by two years of age, depending on previous feed regime and thus body weight.

Free-ranging northern ruminants display evidence of episodic growth pulses (Bandy et al. 1970; Price and White 1985), which is contrary to beef cattle ($R^2 \sim 0.95$ for Richards function; Goonewardene et al. 1981). The mean body weight data set

(Chapter 2) is not ideal but it does provide a basis for estimating growth patterns in bison.

Rapid summer growth as a calf, slower winter growth, rapid summer growth as a yearling, slow winter growth (females) and rapid summer growth as a two year old (Table 2.3) is evidence of episodic growth similar to wild ruminants. This episodic growth is further described by the significant relationship between winter gain and subsequent gain ($Y = 0.71 - 0.50X$; Figure 2.4). However, comparing this relationship to the nearly parallel relationship in beef cattle ($Y = 1.32 - 0.69X$; Mathison 1993), that were raised in similar conditions to bison (supplemental winter-feed and subsequent summer pasture), one could conclude that bison are not different from cattle. However, because catch-up growth in wapiti yearling stags was related to winter ration (Wairimu et al. 1992), it would be more prudent to state that bison are capable of catch-up growth, which is probably dependent on both winter ration and subsequent feed source.

Frequency of weighing will impact the precision associated with describing episodic growth. Farmed reindeer continued to exhibit strong seasonal growth cycles under supplemental feeding regimes (Rutley, unpublished data) and juvenile bison did exhibit seasonal pulses (Table 4.1) based on data that were collected quarterly. Further research is needed to differentiate between genetically determined episodic growth and feed influenced episodic growth.

5.3 SEASONALITY

5.3.1 Energy

Wild ruminants express seasonal cycles for metabolizable energy expenditure (Hudson and Christopherson 1985). Northern wild ruminants (i.e. cervids) express strong

seasonal cycles (moose, 64% Brockway and Maloij 1964, 119% Renecker and Hudson 1986; white tailed deer, 73%, Silver et al. 1971; wapiti, 54%, Jiang and Hudson, 1994). Seasonal metabolic cycles are minimal (11-14%, Christopherson et al. 1993) or absent (Birkelo et al. 1991) within beef cattle. Sheep (*O. aries*) exhibit significant seasonal changes in metabolic rate (Walker 1991), however the amplitude of the oscillation is considerably lower than for most wild species.

Bison clearly have highly developed seasonal cycles. Both the marker and bite count methods estimated seasonal $ME_{(maintenance)}$ requirements in free-grazing bison between 130% and 220% (the difference between seasonal low and highs). Highly expressed seasonal cycles were thought to be exclusive to cervids (98%, free-grazing wapiti, Jiang and Hudson 1994; 119%, tethered moose, Renecker and Hudson 1986). Current data indicate otherwise. Prior to stating that bison have the most highly developed seasonal cycles of all free-grazing ruminants, one must consider that previous studies with cervids usually involved fed animals. Therefore further determination of seasonal cycles of free-grazing cervids is required. Bison exhibit strong seasonal cycles for ME like other northern wild ruminants.

Supplemental feeding dampens seasonal cycles in bison. Supplemental feeding, following a period of winter grazing, dampened the intensity of the amplitude of seasonal ME intake (the difference in maximum and minimum ME requirements between June 1994 and March 1995, 115%; between September 1994 and March 1995, 132%), but not to the extent that supplemental feeding of bison directly from late fall pasture did (June and December 1995, 61%; September and December 1995, 19%). In addition, bison in metabolism crates that were fed cured forage pellets had amplitudes dramatically lower than free-grazing bison (48% vs. 200%).

Recent studies have challenged earlier assumptions that metabolic cycles represented a form of winter dormancy. By determining energy requirements (ecological maintenance) versus energy expenditures, Jiang and Hudson (1994) concluded that winter requirements for wapiti were close to the interspecific mean, while summer requirements were unusually high. However, the questionable absolute values derived for bison from the marker and bite count methods notwithstanding, the range in oscillation between summer maximums and winter minimums support the contention that bison also have very high-energy requirements in the summer. However, it could be that bison are actually more similar to muskoxen (high late summer requirements) (Adamczewski et al. 1994) than wapiti (high spring and early summer requirements) (Jiang and Hudson 1994).

5.3.2 Activity Budgets

How the ruminant knows when its energy intake does not balance with its energy expenditure is not completely understood (Hudson and Christopherson 1985; Ketelaars and Tolkamp 1992a, 1992b; Tolkamp and Ketelaars 1992). What the ruminant does in an attempt to maintain energy balance, however, is better understood. Renecker and Hudson (1993) categorize these actions as behavioural and physiological in nature. Altering level of activity, choice of habitat, quality and quantity of forage selected, are considered behavioural, but these options are not always available to commercially raised bison. Mobilization of body reserves and altered rumen function (considered physiological in nature) are available, however.

Assuming bison, like other animals, engage in activities to maximize fitness, then variation of the activity budget (particularly time engaged in foraging) can be considered an adaptive response (Gates and Hudson 1983). Maintenance of energy balance is affected by season (Hudson and Christopherson 1985; Renecker and Hudson 1993) and wild ruminants respond by altering circadian activity patterns.

Winter activity budgets are characterized by increased foraging time and reduced minor activities (including play) compared to summer activity budgets (Gates and Hudson 1983). Current research provides evidence that bison also exhibit an adaptive seasonal response by increasing foraging activity and minimizing minor activities during winter grazing compared to summer grazing (Figure 4.1).

However, the percentage of activity budget engaged in minor activities was not linked directly to season, as bison under winter supplementation exhibited activity budgets equivalent to activity budgets for summer grazing bison. This indicates that the need for energy conservation displayed during winter grazing can be ignored when feedstuffs of sufficient quantity and quality can be sourced with minimal energy expenditure (see Figure 4.1).

What controls seasonal energy balance has yet to be established in wild ruminants, but voluntary feed intake (VFI), ambient temperature and photoperiod (or some combination) are the most probable explanations. Because voluntary feed intake varies seasonally and because feeding levels influence metabolic rate, Hudson and Christopherson (1985) questioned “whether metabolic cycles are simply a shadow of energy supply”. Subsequent work by Barry et al. (1991) with red deer indicated that metabolic cycles were not simply a shadow of energy supply, however this relationship had not been previously defined in bison.

There is sound evidence that metabolic rate is affected by ambient temperature and there is clear evidence that ambient temperature actually controls metabolic energy demand for maintenance (MED) and specifically, the seasonal variation in MED (Hoch 1971; Christopherson et al. 1993). The mechanism, however, has yet to be established.

Walker (1991) determined that seasonal photoperiod, not voluntary feed intake nor ambient temperature, was responsible for cueing changes in metabolic rate (as measured by MH_p) in sheep. That bison had dampened seasonal metabolic cycles when provided with an uninterrupted supply of good quality forage during the short daylength and -20° C temperatures of winter solstice, indicates that the mechanism that controls seasonal energy balance in bison can be overridden by altering feed energy intake. Provision of supplemental feed appropriately timed in autumn may be required to maintain elevated metabolism, because once metabolism has changed, supplemental feeding alone may not be sufficient to re-elevate ME requirements.

These suppositions are supported by information from finishers of bison for the red meat market. Bison bulls fed on a high plane of nutrition, starting as weaned calves, finish under 24 months of age vs. 33 months for bulls overwintered and grazed as yearlings.

5.4 IMPLICATIONS AND RECOMMENDATIONS

5.4.1 The Bison Advantage

Bison evolved on the prairie grasslands of North America. They are ideally suited to the climate and actively select both native and introduced grasses and forbs that are productive in contemporary North American prairie ecosystems. They are successful winter grazers and have highly developed seasonal metabolic cycles. Their rumen microflora spectrum and nitrogen recycling enable them to be efficient users of poor quality forages. While susceptible to parasites, they require minimal treatment for disease when farmed under low stocking densities. They have the ability to self regulate intake while starting onto grain diets (Rutley, unpublished data). Bison rut like cervids and are highly fecund - when adequate forage is available. Bison have a highly developed, gregarious herd structure and are capable of traveling longer

distances for water than cattle. Based on historic accounts of the prairie ecosystem, bison should be considered the North American wildebeest.

Bison have been successfully farmed for over a century. Provision of adequate forage is key (Bison Breeders Handbook, 1993). The axiom “feed for bison, fence for your neighbours” is accurate, in that few fences will contain hungry bison. Bison become stressed when confined, although the development of modern handling systems and equipment has ameliorated this problem. On adequate tame pasture, fecundity rates can exceed those of cattle (Rutley and Jahn, 1997).

Bison production is a red meat industry. Bulls will finish well, after limited feeding of grain-based rations. Their meat is high in protein, lower in fat compared to cattle and does not marble. Incidence of dark cutting is low compared to cattle. Bison have a strong social hierarchy with dominance immediately established, therefore fighting behaviour within finishing pens is minimal and castration is not required.

5.4.2 Managing with Seasonal Cycles

The ability to winter graze, high fecundity on forage-based diets, limited calving problems and an animal that ruts, are considered the bison advantage for managers preferring to ‘work with the seasonal cycles rather than against them’ within more extensive management systems. Extensive practices are generally considered less productive than intensive management practices, however, the following management strategies will contribute to high herd productivity.

The provision of fresh, good quality pasture, in conjunction with rut, will contribute to maximizing conception rates. Moving bison from good to poorer quality forage in late summer will eliminate the need to separate bulls from the herd, as estrous activity will cease (Rutley and Rajamahendran 1995). Both practices will contribute to reduced

length of calving window and will minimize late summer births. Provide the cowherd with previously ungrazed pasture for winter grazing. Overwinter calves separately from the main herd, feed for modest body weight gain and provide them with good summer forage to take advantage of catch-up growth. Select males for breeding purposes as yearlings after summer grazing. Allocate remaining bulls for feeder-fattening and limit feeding of grain-based rations at 90 to 120 days. Slaughter all grain fed animals. Selection of breeding bulls based on performance from grain-based rations would ultimately improve performance of bulls while finishing on grain-based rations prior to slaughter. However, by selecting breeding bulls based on performance with forage, selection pressure will remain on forage-based performance, which will benefit the majority of the herd (breeding bulls, young males and all females).

5.4.3 Managing while Ignoring Seasonal Cycles

Many producers have already discovered another bison advantage. When supplemental feed is provided in a timely manner, metabolism will remain at an elevated level. They wean bison calves in late fall and place the bulls directly onto high energy grain-based rations like cattle. Under this more intensive management strategy, bison bulls are ready for slaughter under 24 months of age. Other characteristics of intensive bison management include selection of breeding bulls based on performance on grain-based rations and more limited land bases with utilization of seasonal grazing vs. annual grazing systems.

5.4.4 The Advantage – Use It or Lose It

One can lose the bison advantage through management practice. Although there are definite advantages to providing supplemental feed (compensation for insufficient forage resources, reduction of winter weight loss in grazing yearlings, reduced time to slaughter), the manager needs to be careful how it is applied. Feeding for winter weight gain reduces opportunity to maximize summer weight gain, a disadvantage

within extensive management systems. Within the cow herd, winter rations high in energy or protein have contributed to calving losses similar to cattle (6%) compared to the mean (1.2%) for bison (Rutley and Jahn 1997). Provision of supplemental feeds to flush for the rut may ultimately bias the population to females that are dependent on supplemental feedstuffs for conception. New research (Deliberto, personal communication) indicates that young bison raised on high levels of protein have less highly developed digestive tracts. Deliberto cautions that as adults, bison may depend on higher quality feedstuffs. This is particularly foreboding for an industry that is altering feeding practices in response to changes in sire selection activities driven by “bigger is better”. Feeding weaned female calves primarily forage-based rations may ameliorate this concern. Also, making sire selection decisions based on performance on forage-based rations, and realizing that bigger may not necessarily be better, will reduce bias away from forage-based performance.

Maintaining cows that have had calving difficulty within the herd, for economic reasons, will contribute to endemic herd problems. Bison are susceptible to parasites, therefore keeping large numbers of bison on small land bases, for economic gain, subjects them to heavy parasite loads and continued dependence on anthelmintics and vaccines. Incidence of coccidiosis and blackleg is increasing.

Historically, decisions surrounding the development of management strategies (over and above basic husbandry practices) have been economically driven. But economic conditions in a growth industry contribute to short-term economic decisions, not developmental decisions. As man is in the unique position of developing a new industry (bison production) with relatively complete knowledge of the implications of developments in a related industry (beef cattle production), he would be well advised to more fully understand and respect the nature of the animal while applying practices

from other species. Why not develop practices that will enable man to work with this naturally adapted animal while maintaining the inherent advantages?

5.4.5 Manage like Cattle or Wild Ruminant?

Insights into the global question of ‘whether bison are best managed as a northern wild ruminant or like its closest analogue, domestic cattle’, are gained from the following comparisons.

Bison are slower to mature than both cervids and cattle (Table 5.1). Current research provided evidence of episodic growth like northern wild ruminants, but cattle raised under similar conditions also display this growth pattern.

Bison have well defined seasonal cycles like cervids (Table 5.2). Amplitudes of seasonal cycles for bison, estimated while free-grazing, were greater than for both cattle and cervids. When supplemented, amplitude of oscillation was similar to cervids and greater than cattle.

Like other wild ruminants bison alter their activity budgets seasonally, exhibit distinctly polyphasic activity patterns, graze selectively, exhibit seasonal variation in bite rate, bite size and consumption rates, winter graze, alter foraging behaviour when supplemental feed is provided, and are responsive to changes in daylight intensity. But unlike their closest analog, beef cattle, bison spend less time grazing daily, are less selective, graze less dependently on ambient temperature, are less affected by snow cover during winter grazing, and don’t graze or defecate when lying down.

Based on reproductive performance, bison are neither distinctly different from, nor similar to cattle or cervids (Table 5.3). Primiparous lactation begins at 3 years for bison, compared with 2 years for cattle (cervids are more variable at 1 to 3 years).

Calf mortality is minimal in bison (1.2%) compared with cattle (5.6%) and cervids (5.2%). Bison are seasonally polyestrous, while cattle can be characterized as circannually polyestrous and cervids characterized as seasonally monestrous.

Bison have ability to self regulate intake when starting on grain-based rations. Handling finishing bison to obtain bodyweights and mixing of animals during the final finishing period contributes to reduced intake and gain (Rutley, unpublished data). Bison utilize poor quality forages to a greater extent than cattle.

5.4.6 Sequitor

The clear evidence of highly developed seasonal cycles, once thought to be the exclusive domain of cervids, means bison are not cattle. But seasonal cycles and rut do not mean bison are cervids. Therefore, what has emerged for a preliminary answer to the global question, is that bison are unique and warrant the development of specific management strategies.

Species	Age (mon.)	Females	Males	Reference
Elk Island Bison	~20	65%	48%	Reynolds et al. 1982
Mule deer	18	80%	56%	Renecker & Samuel 1991
Free-ranging Reindeer	~14	75%	55%	Blodgett et al. 1993
Farmed Reindeer	17	90%	65%	Rutley, unpublished
Cattle	19	72-80%	67-78%	Martin et al. 1993

Table 5.2 Seasonal contrast in metabolizable energy requirements ($\text{kJ BW}^{-0.75}$) of *B. bison* and *C. elaphus*

Feed Source	Species	Estimate	Season/Month	$\text{kJ BW}^{-0.75}$	Season/Month	$\text{kJ BW}^{-0.75}$	Amplitude ^z	Reference
Supplemental	<i>B. bison</i>	resting energy	December 1994 ^y	532	June 1994	956	80%	current study
		resting energy	December 1994 ^x	282	June 1994	1469	421%	current study
			fall	499	winter	718	44%	Christopherson et al. 1979
			fall	635	spring	738	16%	Christopherson et al. 1980
	fall	685	winter	934	36%	Christopherson et al. 1981		
	fall	625	spring	938	50%	Christopherson et al. 1979		
	<i>A. alces</i>	resting energy	winter	430	late spring	940	119%	Renecker and Hudson 1986
	<i>C. elaphus</i>	resting energy	winter	473	spring	508	7%	Jiang and Hudson 1994
			winter	473	summer	728	54%	Jiang and Hudson 1994
Free-grazing	<i>B. bison</i>	ecological energy	December 1994	270	June 1995	616	128%	current study
			March 1995	191	June 1995	616	223%	current study
			December 1995	260	June 1995	616	137%	current study
	<i>C. elaphus</i>	ecological energy	winter	473	spring	900	90%	Jiang and Hudson 1994
			winter	473	summer	984	108%	Jiang and Hudson 1994

^z Amplitude of seasonal cycle expressed as percentage seasonal high greater than seasonal low.

Table 5.3 Reproductive contrasts among bison, cattle and cervids.

Measure	Bison	Cattle	Cervids
Primiparous lactation	3 yr. ^z	2 yr.	1-3 yr. ^x
Calf mortality	1.2% ^z	5.6% ^y	5.2% ^y
Breeding season	Seasonally polyestrous	Circannually polyestrous	Seasonally monestrous

^z Rutley, unpublished data.

^y Martin et al. 1993.

^x Stelfox and Stelfox 1993.

^v Church, unpublished data.

5.5 REFERENCES

- Adamczewski, J. Z., Kerr, W. M., Lammerding, E. F., and Flood, P. F. 1994.** Digestion of low-protein grass hay by muskoxen and cattle. *J. Wildl. Manage.* **58**: 679-685.
- Bandy, P. J., Cowan, I. McT. and Wood, J. A. 1970.** Comparative growth in four races of black-tailed deer (*Odocoileus hemionus*). Part I. Growth in body weight. *Can. J. Zool.* **48**: 1401-1410.
- Barry, T. N., Suttie, J. M., Milne, J. A. and Kay, R. N. B. 1991.** Control of food intake in domesticated deer. Pages 385-401 *in* Physiological aspects of digestion and metabolism in ruminants: Proceedings of the Seventh International Symposium on Ruminant Physiology. Academic Press.
- Birkelo, C. P., Johnson, D. E. and Phetteplace, H. P. 1991.** Maintenance requirements of beef cattle as affected by season on different planes of nutrition. *J. Anim. Sci.* **69**: 1214-1222.
- Brockway, J. H. and Maloiy, G. M. O. 1968.** Energy metabolism of red deer. *J. Physiol. (London)*. **194**: 22P.
- Christopherson, R. J., Hudson, R. J. and Richmond, R. J. 1978.** Comparative winter bioenergetics of American bison, yak, Scottish Highland and Hereford calves. *Acta Theriologica* Vol. 23, 2: 49-54.
- Christopherson, R. J., Hudson, R. J. and Christophersen, M. K. 1979.** Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Can. J. Anim. Sci.* **59**: 611-617.
- Christopherson, R. J., Kennedy, A. D., Feddes, J. J. R. and Young, B. A. 1993.** Overcoming climate constraints. Pages 173-190 *in* Animal production in Canada. University of Alberta Press, Edmonton, AB T6G 4G2.

Cordova, F. J., Wallace, J. D., and Pieper, R. D. 1978. Forage intake by grazing livestock: a review. *J. Range Manage.* **31(6):** 430-438.

Gates, C. C. and Hudson, R. J. 1983. Foraging behaviour of wapiti in a boreal forest enclosure. *Naturaliste Can. (Rev. Ecol. Syst.)*. **110:** 197-206.

Goonewardene, L. A., Berg, R. T. and Hardin, R. T. 1981. A growth study of beef cattle. *Can. J. Anim. Sci.* **61:** 1041-1048.

Hoch, F. L. 1971. Energy transformation in mammals: regulatory mechanisms. W. B. Saunders Company.

Hudson, R. J. and Christopherson, R. J. 1985. Maintenance metabolism. Pages 121-142 *in* R. J. Hudson and R. G. White, eds. *Bioenergetics of wild herbivores*. CRC Press Inc., Boca Raton, FL.

Jiang, Z. and Hudson, R. J. 1992. Estimating forage intake and energy requirements of free-ranging wapiti (*Cervus elaphus*). *Can. J. Zool.* **70:** 675-679.

Jiang, Z. and Hudson, R. J. 1994. Seasonal maintenance and growth energy requirements of wapiti (*Cervus elaphus*). *Can. J. Anim. Sci.* **74:** 97-192.

Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992a. Toward a new theory of feed intake regulation in ruminants. 1. Causes of differences in voluntary feed intake: critique of current views. *Live. Prod. Sci.* **30:** 269-296.

Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992b. Toward a new theory of feed intake regulation in ruminants. 3. Optimum feed intake: in search of physiological background. *Live. Prod. Sci.* **31:** 235-258.

Mathison, G. W. 1993. The Beef Industry. Pages 34-74 *in* J. Martin, R. J. Hudson and B. A. Young, eds. *Animal production in Canada*. University of Alberta Press, Edmonton, AB T6G 2G4.

- Price, M. A. and White, R. G. 1985.** Growth and development. Pages 183-214 *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press Inc., Boca Raton, FL.
- Renecker, L. A. and R. J. Hudson. 1986.** Seasonal foraging rates of free-grazing moose. *J. Wildl. Manage.* **50(1)**: 143-147.
- Renecker, L. A. and R. J. Hudson. 1993.** Morphology, bioenergetics and resource use: patterns and processes. Pages 141-164 *in* J. B. Stelfox, ed. Hoofed mammals of Alberta. Lone Pine Publishing, Edmonton, AB.
- Renecker, L. A. and Samuel, W. M. 1991.** Growth and seasonal weight changes as they relate to spring and autumn set points in mule deer. *Can J. Zool.* **69**: 744-747.
- Ropstad, E., Helland, G., Hansen, H., Lenvik, D., and Solberg, E. T. 1993.** The effect of medroxyprogesterone acetate on pregnancy rates in reindeer calves (*Rangifer tarandus*). *Rangifer* **13 (3)**: 163-167.
- Rutley, B. D. and Jahn, C. M. 1997.** Reproductive performance of farmed Peace Country bison (*Bison bison*). *Can. J. Anim. Sci.* (submitted).
- Rutley, B. D. and Rajamahendran, R. 1995.** Circannual reproductive function of female bison (*Bison bison*). Proceedings, Western Section, American Society of Animal Science, Western Branch, Canadian Society of Animal Science, Vol. **46**: 242-245.
- Silver, H. H., Holter, J. B. Colovos, N. F., and Hayes, H. H. 1971.** Effect of falling temperature on heat production in fasting white-tailed deer. *J. Wildl. Manage.* **35**: 37.
- Stelfox, J. B. and J. G. Stelfox. 1993.** Population dynamics and reproduction. Pages 63-68 *in* J. B. Stelfox, ed. Hoofed mammals of Alberta. Lone Pine Publishing, Edmonton, AB.

Tolkamp, B. J. and Ketelaars, J. J. M. H. 1992. Toward a new theory of feed intake regulation in ruminants. 2. Costs and benefits of feed consumption: an optimization approach. *Live. Prod. Sci.* **30**: 297-317.

Walker, V. A. 1991. Photoperiod influences on the seasonal energy metabolism of ewes. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Appendices

Appendix Ia

Initial Survey for Peace Country Bison Producers December - February 1993

Name:

Farm:

Number of years farming bison:

1. Are your animals horned or dehorned?
2. Do you manage your herd as one large herd or as smaller, individual herds?
3. If you manage your herd in smaller units, on what basis do you form animal groups (i.e. gender, age, ration)?
4. Herd Information:

a. Females

Born	Total #	# Used for Breeding	# to be Culled	# Exposed to Bull, 1991	1992 # Calved	1992 # Open
pre- 1989						
born 1989						
born 1990						
born 1991						
born 1992						

b. Males

Born	# Animals	Breeding	Meat	Culled
1989 & before				
1990 (2 yr)				
1991 (yearlings)				
1992 (calves)				

5. What injections and vaccinations did your herd receive in 1992 (by age, group, number, and time of year)?
6. List calving problems encountered in 1992 and their frequency.
7. Describe any recurrent health problems, and treatments used (e.g. scours, eye problems, worms, etc.)
8. How many separate pastures were used for bison in the summer 1992, and what was the acreage of each?
9. Number of animals stocked in each pasture (where a cow/calf pair is counted as one animal).
10. Length of time bison were on pasture without additional feed (approximately).
11. Did you creep feed any of your stock in 1992? If so, please describe.
12. Did you flush any of your animals in 1992? If so, please describe.
13. Were there any other special feeding of your animals in 1992? If so, please describe.

14. What mineral or salt supplements were used (enclose mineral tag if available)?
15. Has any feed analysis been done on your farm? If so, how regularly and how is this information used? (Please enclose copies if possible.)
16. Which of the following best describes your winter feeding schedule: a) minimal; b) supplemental; c) planned feeding program? Please describe.
17. What amount of land base is available for bison?
 - Please draw a map of your farm on the grid paper provided. Draw approximately to scale, including all pastures, water sources, and other pertinent information. Number pastures as well, corresponding to the numbers given in one of the previous questions.
 - Producers were asked:
 - to list the number of calves born weekly between “before April 5 to August 29”.
 - total number of calves
 - 1992 spring calves
 - 1992 red calves
 - number calves born after August 29, 1992
 - weaning date
 - number of calves weaned

Appendix Ib

Follow-up Survey for Peace Country Bison Producers

1. Name:
2. Farm:
3. Do you manage your herd as one large herd or as smaller, individual herds (please describe)?
4. Herd Information:

a. Females

Born	Total #	# Used for Breeding	# to be Culled	# Exposed to Bull, 1992	1993 # Calved	1993 # Open
pre- 1990						
born 1990						
born 1991						
born 1992						
born 1993						

b. Males

Born	# Animals	# Breeding	# Used for Meat	# Culled
1990 & before				
1991 (2 yr)				
1992 (yearlings)				
1993 (calves)				

5. What injections and vaccinations did your herd receive in 1993 (by age, group, number, and time of year).
6. List calving problems encountered in 1993 and their frequency.
7. Describe any recurrent health problems, and treatments used (e.g. scours, eye problems, worms, etc.).
8. Length of time bison were on pasture without additional feed (approximately).
9. Did you creep feed any of your stock in 1993? If so, please describe.
10. Did you flush any of your animals in 1993? If so, please describe.
11. Were there any other special feeding of your animals in 1993? If so, please describe.
12. What mineral or salt supplements were used (enclose mineral tag if available)?
13. Which of the following best describes your winter feeding schedule? a) minimal, b) supplemental, or c) planned feeding program. Please describe winter feed program.
14. Calving Window: list number of calves in each category;

a. before April	h. beginning July
b. beginning May	i. middle July
c. middle May	j. end July
d. end May	k. beginning August
e. beginning June	l. middle August
f. middle June	m. end August
g. end June	n. after August 31
15. Report

a. total number of calves	d. weaning date
b. 1993 spring calves	e. # calves weaned
c. 1993 red calves	

Appendix Ic.

Description of Herd Management Survey Codes Summarized in Appendices Ia and Ib.

HEADING	DESCRIPTION
Herd Code	code assigned to each herd
Weaning Date	actual date calves weaned
Weaning Code (month weaned)	0 = did not wean 1 = October 2 = November 3 = December 4 = January 5 = February 6 = March 7 = April
# Animals in Herd	Actual
Years in Bison	Actual
Horn Status	1 = horned 2 = dehorned 3 = mixed
Birth Code	Method of recording births 1 = actual date 2 = week of birth 3 = month of birth 4 = not recorded
Herd Management Style	1 = one large herd 2 = split by sex 3 = split by age 4 = split by ration 5 = all three
Routine Injections	1 = no 2 = yes
Vaccinations	1 = no 2 = yes calves only 3 = all animals
Dewormer	1 = no 2 = 1/year 3 = 2/year 4 = 2/year, different ones 5 = pellets in feed
Calving Problems	1 = no 2 = yes
Herd Health	1 = no 2 = yes
Land Base	actual acres
Number of Pastures for Bison	Actual
Pasture season (months)	Actual
Creep Feeding	1 = no 2 = yes
Flushing	1 = no 2 = yes
Special Feeding	1 = no 2 = taming agent 3 = other
Winter Feed	1 = minimal 2 = supplemental 3 = planned feeding program

Mineral	1 = prescription 1 2 = prescription 2 3 = prescription 3 4 = prescription 4	5 = generic 1 6 = generic 2 7 = generic 3
Additional Salt	1 = no 2 = yes (iodized)	
Vitamins	1 = no 2 = in feed	3 = injection 4 = feed + injection
Feed Analysis	1 = no 2 = yes 3 = yes and used	
Fertilizer	1 = no 2 = yes	
Rain	actual mm	
Rotation	1 = pastures not rotated 2 = rotated "as needed" 3 = fixed rotation (preset)	
Overgrazing	1 = adequate pasture 2 = heavily grazed 3 = overgrazing occurred	
Winter Ration	1 = < 8% Crude Protein 2 = ~10% Crude Protein 3 = >12% Crude Protein	

Appendix Id.

Pasture Assessment Survey

1. Name:
2. Farm:
3. List plant species currently in each pasture used for bison (last seeded).
4. Date seeded.
5. Previous crop planted on this land.
6. Number of years in that crop.
7. Current prevalent weed species.
8. Other problems (i.e. erosion, overgrazing)
9. Chemical use (fertilizers, pest control) and dates used.
10. Describe winter grazing conditions, if applicable.
11. Number of animals grazing pasture in 1993; Cow/calf pairs, open cows, Bulls, 1992 calves (males and females).
12. Acres available for bison on pasture assessment date.
13. Date in present pasture.
14. Date out of present pasture.
15. Pasture rotation: please describe criteria and/or strategy.
16. Other pasture management strategies employed (e.g. aeration).

**Appendix II.
Pasture Survey Results Summary - 1993**

Predominant Cultivated Species:	
Alfalfa	A
Barley	Ba
Bluegrass	Bg
Brome	Br
Brome - meadow	M
Clover - unspecified	C
Clover - alsike	Ca
Clover - red	Cr
Fescue - Creeping Red	F
Oats	O
Ryegrass	Rg
Timothy	T
Wheatgrass - Crested	W
Formulated Pasture Mix	Mix

Predominant Weed Species:	
Dandelion	D
Fireweed	Fw
Foxtail	Fx
Hawkweed	H
Nettle	N
Quack Grass	Q
Rose - wild	Rw
Silkhweed	S
Sweetclover	Cs
Thistle	Th
Ticklegrass	Tg
Vetch	V
Yarrow	Y

Mix 1:	
BrFCaTWRg	

Mix 2:	
25% Rg	
25% F	
50% Highway Mix (TBrC)	

Mix 3:	
40% Cr	
20% F	
20% T	
20% W	

Herd Code	1	2	3	4	5	6	8	9	10	11	12	13	14
Cultivated Sp. Seeded	Mix 1	Mix 2	FCBrTA	ABrFT	FBrTA	ACrTBr	Mix 3	MTCWBrBa	OCrAFBrCa	RgFBgTC	CrBrFBa	FTBrCa	OBrcrBaM
Predominant Sp. - June	BrFTCr	CrCaFT	TABrW	BrTFA	ACaFBr	BrATC	ABr	BaTCBr	ACBrTF	RgTBgFBr	FCr	TCFA	MCBr
Predominant Sp. - August	BrTCa	TCaCrFRg	CTFM	TcaBr	BrCaAT	TCaBrMA	FCT	CaTBaAW	ABrTC	RgTBrCaF	CrFBaBr	ATFBrCa	OCBrTM
Predominant Weed Sp.	DHRwQY	HDSQFw	DFxThHCsQ	QDYFxFw	QFxVDY	QSDHN	HQFXTgD	DQFxrWYS	YDTgFxQ	DRwQSH	ODHSFxTg	DYHTgS	FxSHQDTg

CURRICULUM VITAE

CURRICULUM VITAE

Bruce David Rutley, B. Sc. (Agr.), M. Sc., Ph.D., P. Ag.

Post Secondary Education and Training Relevant to Proposal:

<i>Institution</i>	<i>Field of Specialization</i>	<i>Degree/Diploma</i>	<i>Location</i>
University of Alberta	Wildlife Ecology & Management	Ph.D. 1998	Edmonton
Macdonald College of McGill University	Animal Genetics	M. Sc. 1985	Ste. Anne de Bellevue
University of British Columbia	Animal Science	B. Sc. (Agr.) 1976	Vancouver

Relevant Professional Experience (Begin with present position):

<i>Dates</i>	<i>Position or Function</i>	<i>Employer</i>	<i>Location</i>
August 1996 to present	Dean, Agricultural Technologies	Fairview College	Fairview, AB
May 1996 to August 1996	Director of Research	Boreal R & D (self)	Fairview, AB
August 1994 to May 1996	Director of Research and Educational Services - Center for Agricultural Diversification (CAD)	Northern Lights College	Dawson Creek, BC
April 1990 to July 1994	Coordinator - CAD	Northern Lights College	Dawson Creek, BC
June 1985 to March 1990	Agriculture Program Coordinator	Northern Lights College	Dawson Creek, BC

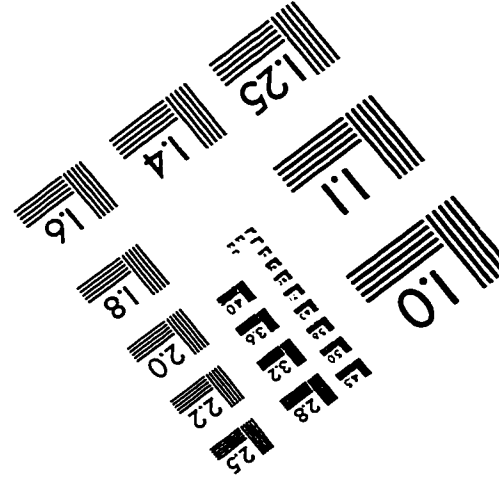
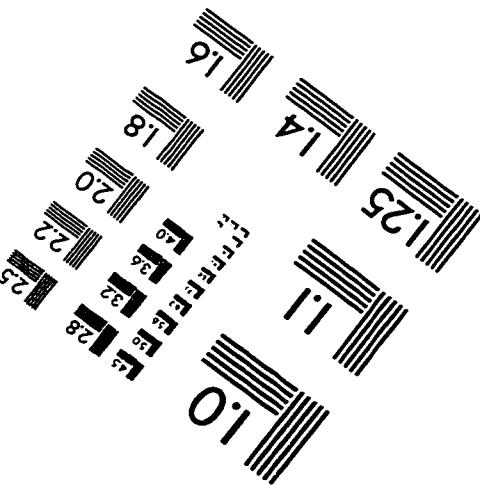
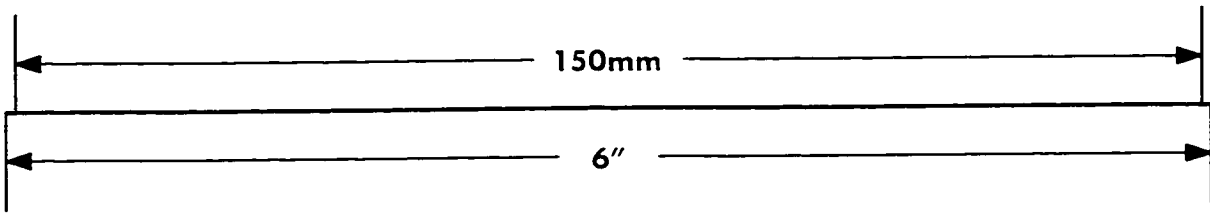
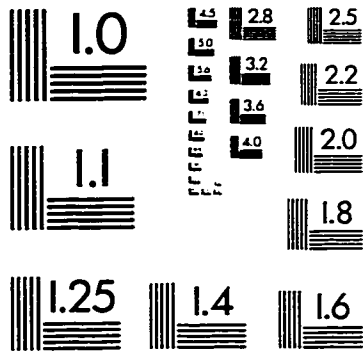
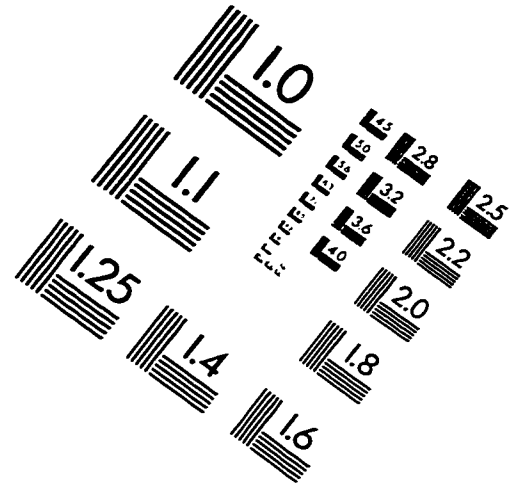
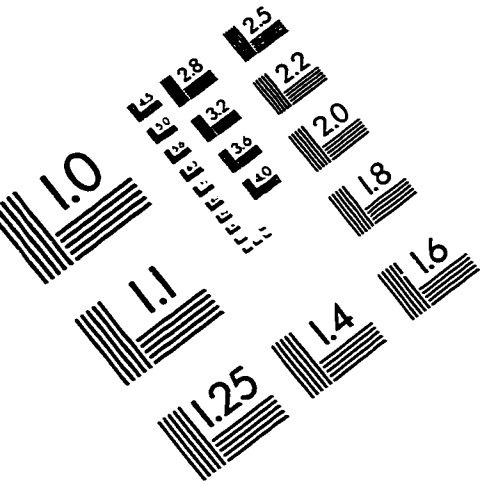
Research Activities Related to Research Proposal (list research project titles and dates):

1. Factors affecting growth and productivity in Peace Country bison. October 1992 to August 1994
2. Effect of time of year on ADG of plains bison bulls fed finishing feedlot rations. November 1992 - June 1995.
3. Feed-weight station as a method of grain finishing bison bulls. October 1992 - April 1995.
4. Reproductive function of bison females. January 1993 to February 1994.

Related Articles in Refereed Journals and Other Relevant Works Completed in the Last Three Years:

1. Rutley, B. D., Jahn, C. M. and Hudson, R. J. 1997. Management, gain and productivity of Peace Country bison (*Bison bison*). *Can. J. Anim. Sci.* 77: 347-353.
2. Rutley, B. D. and Hudson, R. J. 1997. Performance of bison on seasonal pasture. Pages 162-174 in L. Irby and J. Knight. eds. *International Symposium on Bison Ecology and Management in North America*, Montana State University, Bozeman, MO. June 1997.
3. Rutley, B. D. and Renecker, L. A. 1996. Serum vitamin and mineral levels of farmed reindeer. Pages 69-88 in B. D. Rutley, ed. *Factors affecting growth and productivity of Peace Country reindeer (Rangifer tarandus)*. Northern Lights College, Dawson Creek, BC. May 1996.
4. Rutley, B. D. and Renecker, L. A. 1996. Growth patterns and seasonal weight change of farmed reindeer (*Rangifer tarandus*). Pages 46-68 in B. D. Rutley, ed. *Factors affecting growth and productivity of Peace Country reindeer (Rangifer tarandus)*. Northern Lights College, Dawson Creek, BC. May 1996.
5. Rutley, B. D. and Church, J. S. 1995. Effect of time of year on average daily gain of feedlot finished bison (*Bison bison*). A report to the Peace Country Bison Association, November 1995, 32 pp.
6. Rutley, B. D. and Church, J. S. 1995. Feed-weight station as a method of grain finishing bison (*Bison bison*) bulls. A report to the Peace Country Bison Association, November 1995, 41 pp
7. Rutley, B. D. and Rajamahendran, R. 1995. Circannual reproductive function of female bison (*Bison bison*). Pages 242-245 in *Proceedings. Volume 46, Western Section, American Society of Animal Science and Western Branch, Canadian Society of Animal Science, Lethbridge, Canada, July 1995.*

IMAGE EVALUATION TEST TARGET (QA-3)



APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved