

**ELK/MOOSE POPULATION DYNAMICS IN  
THE RIDING MOUNTAIN NATIONAL PARK  
REGION**

**BY**

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**A Practicum  
Submitted to the Faculty of Graduate Studies  
in Partial Fulfillment of the Requirements  
for the Degree of**

**MASTER OF NATURAL RESOURCES MANAGEMENT**

**Natural Resources Institute  
University of Manitoba  
Winnipeg, MB**

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By

*Ms. Lisa Richards*

*A practicum submitted to the Faculty of Graduate Studies of the  
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## ABSTRACT

This study considered relative impacts of some important factors on elk (*Cervus elaphus manitobensis*) and moose (*Alces alces*) population trends in Riding Mountain National Park (RMNP). These factors included hunter success outside Park boundaries, beaver (*Castor canadensis*) populations, wolf (*Canis lupus*) populations, snowshoe hare (*Lepus americanus*) populations, and weather severity. Weather severity was represented by a winter severity index; however, individual parameters within the index were also examined, and consisted of yearly temperature indices (mean, minimum and maximum), snow accumulation, snow density and spring green-up value. This study was conducted under the assumption that if the relative impacts of these human-induced and natural factors on ungulates are understood, managers will be better able to make decisions to minimize human impacts on ungulate populations.

Cross-correlation analysis was used to determine the relationship between both elk and moose populations and each parameter. This type of analysis was essential to determine the lag effects of a particular parameter on the elk or moose population, if any. Graphs and correlograms were used to explore the relationships.

The elk population was significantly correlated to hunter harvest ( $r = -0.4812$ ,  $k=2$ ,  $n=22$ ), the beaver population ( $r=0.6271$ ,  $k=0$ ,  $n=14$ ), the snowshoe hare population ( $r=0.5628$ ,  $k=0$ ,  $n=10$ ), the winter severity index ( $r=0.5998$ ,  $k=4$ ,  $n=19$ ), all temperature indices ( $r=0.4800-0.5481$ ,  $k=0$ ,  $n=17$ ), and snow accumulation ( $r=0.6047$ ,  $k=4$ ,  $n=19$ ). The moose population was significantly correlated to hunter harvest ( $r = -0.4628$ ,  $k=4$ ,  $n=20$ ), the beaver population ( $r=0.5908$ ,  $k=0$ ,  $n=14$ ;  $r=0.6566$ ,  $k=1$ ,  $n=12$ ), the wolf population ( $r = -0.5839$ ,  $k=0$ ,  $n=17$ ), the snowshoe hare population ( $r=0.5967$ ,  $k=0$ ,  $n=10$ ) the minimum winter temperature index ( $0.4121$ ,  $k=1$ ,  $n=18$ ), snow accumulation ( $r=0.4821$ ,  $k=4$ ,  $n=19$ ) and snow density ( $-0.4756$ ,  $k=2$ ,  $n=19$ ).

Of the factors examined, hunter harvest and winter severity (specifically, winter temperature and snow accumulation) were suspected to be influencing the elk population. Both of these factors may be creating delays in the population response by the effects of winter mortality of calves, reduced recruitment and reduced fecundity. As

well, although no significant correlation was detected, it is possible that wolves are preventing the elk population from increasing dramatically, and therefore potentially eliminating conditions suitable for a population irruption. The moose population was suspected to be influenced by hunter harvest, beaver populations and winter severity (specifically, winter temperature, snow accumulation and snow density). Again, hunter harvest and winter severity conditions may be creating time-delayed population responses. Although the wolf population was found to be significantly correlated to the moose population, no lag effect implied that the populations were acting independently of each other. It was presumed that there was a common response of the herbivores (elk, moose, beavers and snowshoe hare) to winter severity due to the significant positive correlations found between these species.

## **ACKNOWLEDGMENTS**

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# TABLE OF CONTENTS

ABSTRACT .....	ii
ACKNOWLEDGMENTS .....	iv
LIST OF TABLES .....	ix
LIST OF FIGURES .....	xiii
<u>Chapter</u>	<u>page</u>
1. INTRODUCTION.....	1
1.1 Preamble .....	1
1.2 Background .....	1
1.3 Problem Statement .....	5
1.4 Research Objectives .....	6
1.5 Scope .....	6
2. REVIEW OF RELATED LITERATURE .....	8
2.1 Introduction .....	8
2.2 Natural History of Ungulates.....	8
2.2.1 Elk .....	8
2.2.2 Moose .....	9
2.3 Population Dynamics of Ungulates .....	11
2.3.1 Introduction .....	11
<i>Fluctuation and Regulation of Populations</i> .....	11
2.3.2 Food Limitation as a Limiting/ Regulating Factor .....	13
<i>Population Irruptions</i> .....	14
<i>Dynamics in a Predator-free Environment</i> .....	15
2.3.3 Predation as a Limiting/ Regulating Factor .....	19
2.3.4 Weather as a Limiting/ Regulating Factor .....	20
<i>Temperature</i> .....	20
<i>Snow Conditions</i> .....	21
<i>Spring Green-up Value</i> .....	22
3. POPULATION DYNAMICS IN RMNP .....	23
3.1 Introduction .....	23

3.2	Study Area .....	23
	3.2.1 <i>History</i> .....	23
	3.2.2 <i>Description</i> .....	24
	3.2.3 <i>Vegetation Composition</i> .....	24
	3.2.4 <i>Climate</i> .....	26
3.3	Historic Description of Elk and Moose in RMNP .....	26
	3.3.1 <i>Fluctuation in the Ungulate Populations Until 1950</i> .....	27
	<i>Elk</i> .....	27
	<i>Moose</i> .....	27
	3.3.2 <i>Fluctuations in the Ungulate Populations From 1950-1963</i>	28
	<i>Elk</i> .....	28
	<i>Moose</i> .....	28
3.4	Ungulate Population Monitoring .....	28
	3.4.1 <i>Purpose</i> .....	30
	3.4.2 <i>Survey Technique 1963-Present</i> .....	30
	3.4.3 <i>Reliability of Aerial Surveys</i> .....	32
3.5	Factors Influencing Elk and Moose Populations .....	33
	3.5.1 <i>Hunter Harvest of Ungulates in the RMNP Region</i> .....	33
	3.5.2 <i>Beaver</i> .....	39
	3.5.3 <i>Wolves</i> .....	40
	3.5.4 <i>Snowshoe Hare</i> .....	41
	3.5.5 <i>Winter Severity</i> .....	44
	<i>The Winter Severity Index</i> .....	44
	<i>Stelfox's WSI</i> .....	44
	<i>RMNP Ungulate-Winter Severity Relationships 1977-1980</i>	45
4.	METHODS .....	47
4.1	Introduction .....	47
4.2	Compilation of Data .....	47
	4.2.1 <i>Ungulate Aerial Survey Results</i> .....	47
	4.2.2 <i>Hunter Success Data</i> .....	47
	4.2.3 <i>Beaver Aerial Survey Results</i> .....	48
	4.2.4 <i>Wolf Ground Survey Results</i> .....	48
	4.2.5 <i>Snowshoe Hare Track Survey Results</i> .....	48
	4.2.6 <i>Winter Severity Data</i> .....	53
	<i>A Modified WSI</i>	
4.3	Analysis of Data .....	56
4.4	Development of Conceptual Models .....	57



5.	RESULTS AND DISCUSSION .....	58
5.1	Introduction .....	58
5.2	Autocorrelation Analysis .....	60
	5.2.1 <i>Elk</i> .....	60
	5.2.2 <i>Moose</i> .....	61
5.3	Relationship Between Ungulates and Hunter Harvest.....	62
	5.3.1 <i>Elk and Hunter Harvest</i> .....	62
	5.3.2 <i>Moose and Hunter Harvest</i> .....	64
5.4	Relationship Between Ungulates and Beaver .....	65
	5.4.1 <i>Elk and Beaver</i> .....	65
	5.4.2 <i>Moose and Beaver</i> .....	67
5.5	Relationship Between Ungulates and Wolves .....	68
	5.5.1 <i>Elk and Wolves</i> .....	68
	5.5.2 <i>Moose and Wolves</i> .....	69
5.6	Relationship Between Ungulates and Snowshoe Hare .....	71
	5.6.1 <i>Elk and Snowshoe Hare</i> .....	71
	5.6.2 <i>Moose and Snowshoe Hare</i> .....	74
5.7	Relationship Between Ungulates and Winter Weather .....	75
	5.7.1 <i>Elk and Winter Weather Severity</i> .....	75
	5.7.2 <i>Moose and Winter Weather Severity</i> .....	77
	5.7.3 <i>Elk and Winter Temperature</i> .....	77
	5.7.4 <i>Moose and Winter Temperature</i> .....	80
	5.7.5 <i>Elk and Snow Accumulation</i> .....	81
	5.7.6 <i>Moose and Snow Accumulation</i> .....	82
	5.7.7 <i>Elk and Snow Density</i> .....	83
	5.7.8 <i>Moose and Snow Density</i> .....	83
	5.7.9 <i>Elk and Green-up Value</i> .....	84
	5.7.10 <i>Moose and Green-up Value</i> .....	84
5.8	Conceptual Models .....	84
6.	RECOMMENDATIONS, SUMMARY AND CONCLUSIONS .....	87
5.1	Summary .....	87
5.2	Conclusions .....	89
5.3	Recommendations .....	90

<b>LITERATURE CITED .....</b>	<b>92</b>
<b>Appendix A. Sample dBase 4.1 Calculations .....</b>	<b>106</b>
<b>Appendix B. Methods of Wildlife Population Estimation in RMNP .....</b>	<b>112</b>
<b>Appendix C. Non-Significant Relationships .....</b>	<b>120</b>
<b>Appendix D. Scatterplots of Significant Relationships .....</b>	<b>130</b>
<b>Appendix E. Tables Corresponding to Correlograms .....</b>	<b>140</b>

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
1.	Estimated Number of Elk Bulls, Cows and Calves Harvested From 1971/72 to 1995/96 .....	36
2.	Estimated Number of Moose Bulls, Cows and Calves Harvested From 1971/72 to 1995/96 .....	37
3.	Estimate Elk and Moose Hunting Kill in RMNP .....	38
4.	Summary Table of Significant Relationships For Elk .....	58
5.	Summary Table of Significant Relationships For Moose .....	59

## **LIST OF TABLES IN APPENDIX B**

<u>Table</u>	<u>Page</u>
1. <b>Names, Lengths and Locations of Snowshoe Hare Transects in Nine Cover Types Within Riding Mountain National Park .....</b>	<b>118</b>

## LIST OF TABLES IN APPENDIX C

<u>Table</u>		<u>Page</u>
1.	Elk vs. Wolves .....	120
2.	Moose vs. Winter Severity .....	122
3.	Moose vs. Mean Winter Temperature Index .....	123
4.	Moose vs. Maximum Winter Temperature Index .....	124
5.	Elk vs. Snow Density .....	126
6.	Elk vs. Green-up Value .....	127
7.	Moose vs. Green-up Value .....	129

## LIST OF TABLES IN APPENDIX E

<u>Table</u>		<u>Page</u>
1.	Elk Autocorrelations .....	140
2.	Moose Autocorrelations .....	140
3.	Elk vs. Hunter Harvest .....	141
4.	Moose vs. Hunter Harvest .....	141
5.	Elk vs. Beavers .....	141
6.	Moose vs. Beavers .....	142
7.	Moose vs. Wolves .....	142
8.	Elk vs. Snowshoe Hare .....	142
9.	Moose vs. Snowshoe Hare .....	143
10.	Elk vs. Winter Severity Index .....	143
11.	Elk vs. Mean Winter Temperature Index .....	143
12.	Elk vs. Minimum Winter Temperature Index .....	144
13.	Elk vs. Maximum Winter Temperature Index .....	144
14.	Moose vs. Minimum Winter Temperature Index .....	144
15.	Elk vs. Snow Accumulation .....	145
16.	Moose vs. Snow Accumulation .....	145
17.	Moose vs. Snow Density .....	145

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Location of Riding Mountain National Park Within Manitoba .....	2
2. RMNP Elk and Moose Population Estimates 1963-1996 .....	4
3. RMNP Elk and Moose Population Estimates 1950-1963 .....	29
4. Transect Set-up for RMNP Ungulate Aerial Surveys 1963-Present .....	31
5. Game Hunting Areas 23 and 23A .....	35
6. Elk and Moose Harvest in GHAs 23 and 23A 1969-1996 .....	49
7. RMNP Beaver Cache Estimates 1973-1995 .....	50
8. RMNP Wolf Population Estimates 1975-1996 .....	51
9. RMNP Snowshoe Hare Activity Units 1978-1989 .....	52
10. RMNP Winter Severity Index 1966/67-1988/89 .....	54
11. Correlogram- Elk .....	60
12. Correlogram- Moose .....	61
13. Number of Elk vs. Elk Harvested .....	62
14. Correlogram- Elk vs. Elk Harvested .....	62
15. Number of Moose vs. Moose Harvested .....	64
16. Correlogram- Moose vs. Moose Harvested .....	64
17. Number of Elk vs. Beaver Caches .....	65
18. Correlogram- Elk vs. Beaver .....	66
19. Number of Moose vs. Beaver Caches .....	67
20. Correlogram- Moose vs. Beaver .....	68
21. Number of Moose vs. Wolves .....	69
22. Correlogram- Moose vs. Wolves .....	70
23. Number of Elk vs. Snowshoe Hare .....	71
24. Correlogram- Elk vs. Snowshoe Hare .....	72
25. Number of Moose vs. Snowshoe Hare .....	74
26. Correlogram- Moose vs. Snowshoe Hare .....	74
27. Number of Elk vs. Winter Severity .....	75
28. Correlogram- Elk vs. WSI .....	75
29. Number of Elk vs. Winter Temperature Indices .....	77
30. Correlogram- Elk vs. Mean Winter Temperature Index .....	78
31. Correlogram- Elk vs. Minimum Winter Temperature Index .....	78
32. Correlogram- Elk vs. Maximum Winter Temperature Index .....	79
33. Number of Moose vs. Winter Temperature Indices .....	80
34. Correlogram- Moose vs. Minimum Winter Temperature Index .....	80
35. Number of Elk vs. Yearly Snow Accumulation .....	81
36. Correlogram- Elk vs. Yearly Snow Accumulation .....	81
37. Number of Moose vs. Yearly Snow Accumulation .....	82
38. Correlogram- Moose vs. Yearly Snow Accumulation .....	82
39. Number of Moose vs. Snow Density Index .....	83
40. Correlogram- Moose vs. Snow Density Index .....	84
41. Elk Model .....	85
42. Moose Model .....	86

## LIST OF FIGURES IN APPENDIX B

<u>Figure</u>		<u>Page</u>
1.	Sample Hunter Survey .....	113
2.	Distribution of Sample Quadrats for Aerial Beaver Censuses in Riding Mountain National Park .....	115
3.	Location of the Study Area and Snowshoe Hare Activity Transects in Western Riding Mountain National Park .....	119



## LIST OF FIGURES IN APPENDIX C

<u>Figure</u>		<u>Page</u>
1.	Number of Elk vs. Wolves .....	120
2.	Correlogram- Elk vs. Wolves .....	121
3.	Number of Moose vs. Winter Severity .....	121
4.	Correlogram- Moose vs. WSI .....	122
5.	Number of Moose vs. Winter Temperature Indices .....	123
6.	Correlogram- Moose vs. Mean Winter Temperature Index .....	124
7.	Correlogram- Moose vs. Maximum Winter Temperature Index .....	125
8.	Number of Elk vs. Snow Density Index .....	125
9.	Correlogram- Elk vs. Snow Density Index .....	126
10.	Number of Elk vs. Green-up Value .....	127
11.	Correlogram- Elk vs. Green-up Value .....	128
12.	Number of Moose vs. Green-up Value .....	128
13.	Correlogram- Moose vs. Green-up Value .....	129

## LIST OF FIGURES IN APPENDIX D

<u>Figure</u>		<u>Page</u>
1.	Number of Elk vs. Elk (1-yr. Lag) .....	130
2.	Number of Moose vs. Moose (1-yr. Lag) .....	130
3.	Number of Elk vs. Elk Harvested (2-yr. Lag) .....	131
4.	Number of Moose vs. Moose Harvested (4-yr. Lag) .....	131
5.	Number of Elk vs. Beavers .....	132
6.	Number of Moose vs. Beavers (1-yr. Lag) .....	132
7.	Number of Moose vs. Wolves .....	133
8.	Number of Elk vs. Snowshoe Hare .....	134
9.	Number of Moose vs. Snowshoe Hare .....	134
10.	Number of Elk vs. WSI (4-yr. Lag) .....	135
11.	Number of Moose vs. WSI (4-yr. Lag) .....	135
12.	Number of Elk vs. Mean Winter Temperature Index .....	136
13.	Number of Elk vs. Minimum Winter Temperature Index .....	136
14.	Number of Elk vs. Maximum Winter Temperature Index .....	137
15.	Number of Moose vs. Minimum Winter Temperature Index .....	137
16.	Number of Elk vs. Snow Accumulation (4-yr. Lag) .....	138
17.	Number of Moose vs. Snow Accumulation (4-yr. Lag) .....	138
18.	Number of Moose vs. Snow Density Index (2-yr. Lag) .....	139

# **CHAPTER 1**

## **INTRODUCTION**

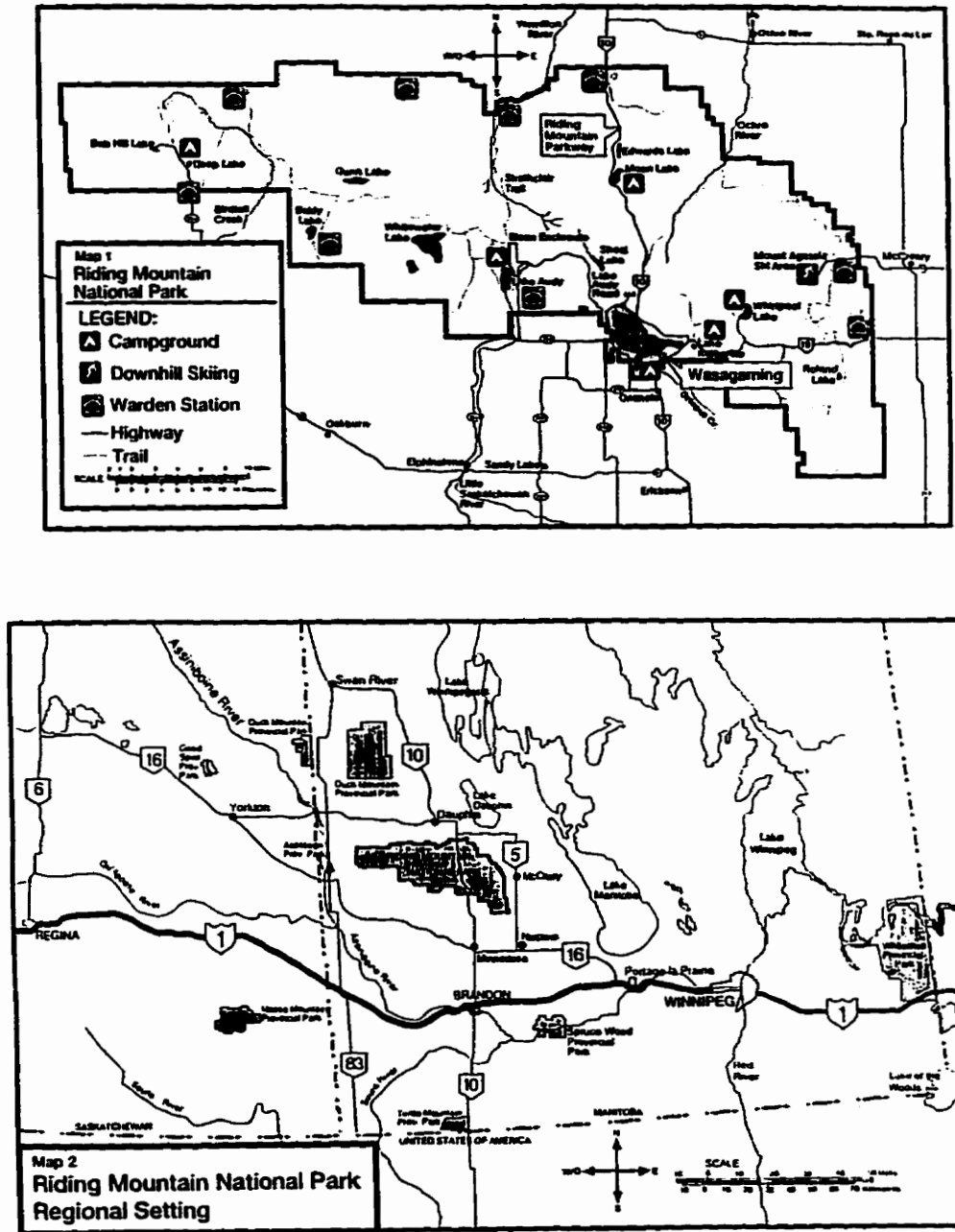
### **1.1 PREAMBLE**

Elk (*Cervus elaphus manitobensis*) and moose (*Alces alces*) are the dominant ungulates within Riding Mountain National Park (RMNP), and trends in their relative abundance are considered to be reflective of the integrity of the Riding Mountain region (Canadian Parks Service 1997). Managers in RMNP are faced with managing ungulate populations in an area increasingly influenced by anthropogenic factors. This study is conducted under the assumption that if the relative impacts of these human-induced and natural factors on ungulates are understood, managers will be better able to make decisions to minimize human impacts on ungulate populations.

### **1.2 BACKGROUND**

Riding Mountain National Park, established in 1930, includes 2978 km<sup>2</sup> of wilderness set amidst the agricultural landscape of southwestern Manitoba (Tarleton 1992a) (Figure 1). Despite the stark contrast between the Park and the surrounding agricultural landscape, RMNP cannot be considered a discrete ecological unit; wildlife movement, human activity, air circulation and drainage patterns intrinsically link the RMNP ecosystem with the surrounding area (Tarleton 1992a).

The park was a highly disturbed area at the time national park status was obtained- many flora and fauna were affected by logging, livestock grazing, wildfires, homesteading and hunting (Trottier *et al.* 1983). Vegetation succession has altered Park habitats and caused corresponding changes in relative distribution and abundance of wildlife. More recently, fire suppression policies, increasing park visitation and increasing isolation of the park as a wildlife refuge are steering the park away from a state of natural regulation (Trottier *et al.* 1983).



**Figure 1. Location of Riding Mountain National Park Within Manitoba (RMNP Round Table 1996)**

## Chapter 1- Introduction

Elk and moose are indigenous to RMNP and have been subject to the influence of human activity since settlement in southwestern Manitoba (Lothian 1976). These ungulates are an important component of the large mammal system in RMNP- they are powerful modifiers of habitat through their foraging activities, they are potential prey for wolves (*Canis lupus*) (Carbyn *et al.* 1979) and hunters outside Park boundaries, and they are in competition with snowshoe hare (*Lepus americanus*) populations for browse in winter (Trottier *et al.* 1983). Knowledge of the density and distribution of elk and moose, and changes in these parameters through time, allow park managers to assess the interactions of these ungulates with other herbivores and major predators. Ungulate censusing has therefore been a priority activity in the Park management plan to provide a course of action for ungulate protection and management (Barlow *et al.* 1980, Trottier *et al.* 1983, Tarleton 1992).

Annual aerial surveys of RMNP have provided information on ungulate population trends since 1963 (Figure 2). The use of these results are two-fold. First, they are released to the Manitoba Department of Natural Resources (DNR) to be used in the setting of yearly hunting regulations around Park boundaries. Second, they have the potential to be a predictive tool for managing ungulate populations within the Park. Unfortunately, however, after 40-odd years of data collection, there is no accurate model, based on observed correlations, which may be used to predict the impacts of management actions or climatic events on ungulate populations (Tarleton 1992a). Further, factors (and their interactions) responsible for the population fluctuations have not been previously identified. These factors may include hunter success around Park boundaries, winter severity, range condition (browse availability), beaver (*Castor canadensis*) populations, snowshoe hare populations, and wolf populations.

Park managers are now faced with the task of minimizing the extent of human impacts and encouraging the restoration of natural controls upon a system which has endured human influence throughout this century. The Natural Resource Management Process (NRMP) is a framework which Canadian Parks Service has adopted for providing a rational approach to the management of the resources in a national park (Parks Canada 1982). The Park Conservation Plan is a step in the NRMP which aims to

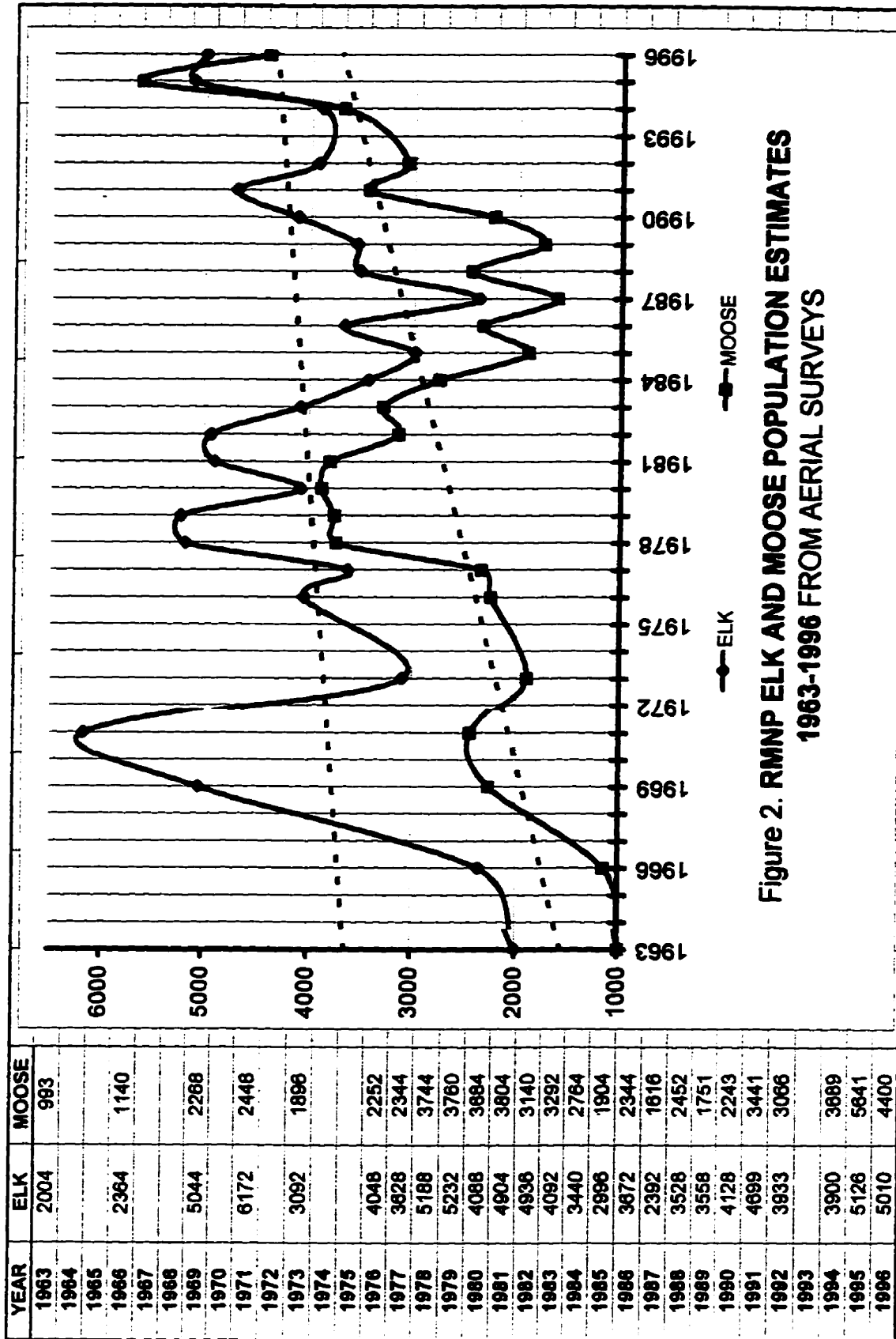


Figure 2. RMNP ELK AND MOOSE POPULATION ESTIMATES  
1963-1996 FROM AERIAL SURVEYS

provide "a documented, integrated and prioritized course of action for the management of parks' natural resources" (Parks Canada 1982). This step in the process "defines natural resource problems, proposes resource management actions and presents a documented, prioritized plan to prepare and/or implement them" (Parks Canada 1982). The 1987 *RMNP Park Conservation Plan* was recently revised and renamed *The RMNP Ecosystem Conservation Plan, 1997*. The purpose of the RMNP Ecosystem Conservation Plan is to prescribe actions to be taken to protect, restore and monitor both natural and cultural resources in the Park to ensure ecological integrity. Canadian Parks Service defines ecological integrity as "a condition where the structure and function of an ecosystem are unimpaired by stresses induced by human activity and are likely to persist (Canadian Parks Service 1994). An ecosystem-based management approach is proposed which implies the need to manage ungulate populations in concert with the rest of the ecosystem, including humans (Canadian Parks Service 1997).

"The ecological integrity of the resources in national parks will be protected through the elimination of threats and where possible, existing uses which compromise this integrity" (Canadian Parks Service 1990). Canadian Parks Service must identify, then revise management policies and activities which are not biologically compatible with this goal.

### **1.3 PROBLEM STATEMENT**

Canadian Parks Service is committed by its policy to maintain the ecological integrity of those areas within National Parks. Historic records show that elk and moose populations in RMNP have been subject to continued human influence since the settlement of southwestern Manitoba. However, the relative impacts of natural and human-induced factors upon these ungulates in RMNP have not been previously described or quantified. In order to enhance our management abilities for elk and moose and protect the Park's ecological integrity, it is necessary to understand what influences their population trends.

## **1.4 RESEARCH OBJECTIVES**

The primary objective of this study was to contribute to a management strategy for elk and moose populations in the RMNP region. Specific objectives are:

- 1) to examine factors (including hunter success, weather, and other wildlife populations), and their relative importance, that have influenced elk and moose populations in RMNP for the period 1963-1996;
- 2) to develop a conceptual model to aid in the understanding of ungulate population dynamics in RMNP; and
- 3) to provide information to all interested parties, and to recommend further research to be conducted, using information gleaned by the project.

## **1.5 SCOPE**

- This study is specific to the RMNP region and caution should be exercised when extrapolating results of this study to any other park or wilderness due to the Park's unique management strategy and geographical setting.
- The study will focus only on some of the major parameters that may influence ungulate populations, and will not, for example, examine the influence that the ungulates have on various other wildlife populations.
- A mathematical model to predict/ represent the influence that various parameters have on the ungulate populations will be precluded due to large gaps in the available data.



*Chapter 1- Introduction*

- Although the changes in range condition, or other habitat dynamics, over the period of 1963-1996 would be useful in helping to understand ungulate population trends, these changes will not be assessed in this study.
- The influence that predators, other than wolves (e.g. black bears), and disease have on the ungulate populations will not be examined due to non-existent or incomplete data sets.
- The effects of illegal human harvest and aboriginal harvest is not included in the hunter harvest estimates, and therefore will not be examined in this study.

## **CHAPTER 2**

### **A REVIEW OF RELATED LITERATURE**

#### **2.1 INTRODUCTION**

The following is a literature review dealing with ungulate population dynamics. The first section briefly describes the life cycle of elk and moose. The stages of the life cycle, and when they occur, may be pertinent to understanding delays that occur between a change in a parameter (e.g. hunter success) and the response to this change in the elk or moose population. The second section will examine the most current theories as to why ungulate populations fluctuate in an attempt to isolate some of the factors that may be influencing the elk and moose populations in RMNP.

#### **2.2 NATURAL HISTORY OF UNGULATES**

##### **2.2.1 Elk**

Elk are herbivores, and have a diverse diet consisting of sedges with lesser amounts of grasses and shrubs (Jones *et al.* 1984). Trottier and Hutchison (1980) studied diets of elk and moose in RMNP by tracking animals in snow to feed sites and by determining the botanical composition of fecal material. Elk were found to be dependent on shrubs in late winter when snow prevented access to grasses and sedges, but otherwise generally fed in meadowlands until snow limited grazing. Elk preferred mixedwood stands when snow thickness in meadows and deciduous forest impeded their movement.

Elk are a gregarious species. Bands of cows and their calves can be found foraging together during the summer months, while the bulls form bachelor bands. Young bulls do not usually mix with the cow-calf bands until late summer. Bulls' antlers commence their annual growth in April (after shedding their previous year's antlers in February, March and early April), and in mid-September bulls begin to rut (Banfield 1973). Bugling and harem formation begin with harems ranging from 15 to 30 cows

(consisting of cows with their calves) that are supervised by a mature bull. Young bulls hang around the edges of harems and opportunistically breed with the cows. Antler velvet is rubbed off in late August and early September. By early November most breeding has occurred and the bands join to form large herds of a hundred or more animals, composed of all ages and sex-groups. In these herds the social order is a matriarchy. The winter herds break up in spring as the cows separate to bear their calves and the bulls move off to form their bachelor bands (Banfield 1973).

The gestation period is about eight and a half months, with most calves being born in early June (Jones *et al.* 1984). Twins are uncommon, but if the range is good twins occur with a frequency of about 25 percent (Banfield 1973). Cows stay away from the herd for two to three weeks until the calves are capable of travel. By mid-July, cows and calves are concentrated in bands on summer ranges (Jones *et al.* 1984). By spring of the following year, the maternal ties slacken and the calves learn to fend for themselves. As yearlings, they may continue to follow their mothers, but the cow's attention is directed to her new calf (Banfield 1973).

Well-nourished female elk have been known to breed for the first time as yearlings (Buechner and Swanson 1955). However, breeding at two years of age is considered the norm for elk (Cowan 1950, Greer 1966, Gross 1969, Kittams 1953, Madson 1966, Murie 1951). The animals that ensure population survival are the experienced breeders- cows that are 4-12 years old (their pregnancy rate is stable at  $94 \pm 4$  percent) (Flook 1970).

The chief natural predators of elk, aside from man, are the mountain lion, the wolf, the grizzly bear, and occasionally the lynx and coyote. The golden eagle, bobcat, black bear, and wolverine sometimes kill unprotected young calves (Banfield 1973). From this list, only wolves, lynx, coyotes and black bears exist in RMNP.

### 2.2.2 Moose

Moose are primarily browsers that feed on stems, bark and leaves of many coniferous and deciduous trees as well as shrubs (Jones *et al.* 1984). Trottier *et al.* (1980) found that moose ate mainly shrubs during winter in RMNP, with beaked hazelnut being the

preferred species. Moose preferred deciduous forest and shrublands in the winter, and were not restricted by the thick snow cover which affected elk. Grasses, sedges and aquatic plants are also eaten, especially during summer (Jones *et al.* 1984). These animals prefer early successional vegetation and therefore commonly are found in areas that have been recently cut over, burned, or otherwise manipulated. Diet studies in RMNP (Trottier *et al.* 1980) indicated a potential for competition between elk and moose only if populations exceed the carrying capacity of shrub-dominated ranges and winter snow conditions are severe.

Moose appear to be the least sociable of the ungulates, and are basically solitary animals (Banfield 1973). Bulls' antler growth commences in April, after having dropped their previous year's antlers in December to late February. The breeding season is from mid-September to late November. Rutting bulls are restless during this season and spend much of their time trotting through the forests searching for cows and challenging other bulls. The bull is polygamous, but remains with one cow until she reaches her oestrous period before abandoning her to find another pre-oestrous cow. The bulls carry large velvety antlers until late August or early September, when they begin to rub them clean on shrubs.

The gestation period for moose is approximately eight months, and most calving takes place in late May or early June (Jones *et al.* 1984). Usually twins are born on adequate range, but births vary from singles to triplets (Banfield 1973). The cow usually seeks secluded shrubby lake borders or islands to serve as a nursery where she guards the new-born calf for several weeks. The calves remain with their mothers for the first year of their lives but the cows drive them off as the time approaches for the birth of the new calves (Banfield 1973).

Peterson (1955) found that a few female moose are successfully bred at the age of sixteen months, and produce offspring on their second birthday. More recently, however, Saether and Andersen (1996) studied life history variation in the moose by examining moose at four different latitudes. The authors found that the age of maturity is delayed in the northern population- only 50% (n=16) of the calves matured at 2.5 years of age, and the other half matured at older ages. Similarly, Skuncke (1949) reported that often cows

do not become pregnant until they are four years old in Scandinavia, and Jones *et al.* (1984) suggested that most reproduction in moose is by animals that are from four to 12 years old. Moose have been known to live twenty years (Banfield 1973).

Bears, wolves and man prey on the moose (Jones *et al.* 1984). Wolves take their toll on the aged, weak and younger animals, and predation is enhanced by severe weather conditions. Bears have been shown to target moose calves in the spring (Jones *et al.* 1984).

## **2.3 POPULATION DYNAMICS OF UNGULATES**

### **2.3.1 Introduction**

A 'population' can be described as a group of organisms of one species that is separated in some degree from other groups of the same species, by geographical or topographical barriers, or by some arbitrary boundary chosen by the investigator (Solomon 1976). The term 'population dynamics', then, is applied to "the study of changes in the numbers of organisms in populations and of the factors influencing these changes; also it includes the study of the rates of loss and replacement of individuals, and of any regulatory processes tending to keep the numbers steady, or at least prevent excessive change" (Solomon 1976).

#### ***Fluctuation and Regulation of Populations***

The study of animal populations embraces two fundamental questions: what creates year-to-year variations in animal numbers (population limitation), and what, in the long term, imposes an upper ceiling to population growth (population regulation)?

Populations may fluctuate irregularly in response to changes in weather or under the influence of other environmental factors. A 'limiting factor' (Messier 1991) is any process that quantifiably affects population growth. Limiting factors "are responsible for inducing year-to-year changes in the rate of population growth and, by extension, in animal abundance" (Watson and Moss 1970).

However, although populations change in abundance from generation to generation, they tend to preserve a characteristic level of abundance as long as the habitat retains its essential features, a feature central to the idea of 'regulation'. 'Regulating factors' are "any density-dependent processes that ultimately keep populations within normal density ranges" (Fowler 1987). Regulating factors are, then, a subset of limiting factors, characterized by negative-feedback mechanisms that depress population growth as animal abundance increases.

This characteristic level of abundance is, in many cases, due to the observed fact that, as abundance increases there is a progressive building up of resistance. For example, at high densities of moose there may be a shortage of food, or the animals may continually disturb each other, or wolves may exploit the large numbers better than they did the small numbers. Finally, the moose numbers are forced down again.

If the increase of a population is to be limited in this way, there must be at least one adverse influence/ factor that comes into play more strongly when the numbers rise, and ultimately stops further increase. These factors are called 'density-dependent' and can operate at different times and places, or at different levels of abundance, or all together, to contribute to the regulation of populations. It is necessary to have a long series of observations so that the regulatory trends may appear through the non-regulatory fluctuations.

Factors that affect a population in a way which is unrelated to its density are called 'density-independent'. For example, the number of elk in RMNP killed in a season by severe weather is density-independent- it is probable that the percentage affected will not depend upon whether these elk are sparse or abundant. However, even if the weather itself is not a function of population density, the animals may have been abundant enough to eat down the vegetation which would have otherwise provided food in their time of need. So, in effect the proportion that is killed by severe weather may be influenced by the abundance of the animals. This does not necessarily mean that the effect of weather is density-dependent- an inadequate supply of anything that is needed by the animals has density-dependent consequences (by process of competition for resources). A fair

statement would be that weather, availability of food and the number of elk jointly produce a density-dependent process.

The effectiveness of ecological controls on ungulate populations, even in the largest wildlife reserves, is still debated. Ungulate populations may be regulated without human interference through food limitation (Caughley 1976, Bobek 1977, Sinclair 1977, Bayliss 1985, Sinclair *et al.* 1985, Skogland 1985, 1990, Fryxell 1987, Dublin *et al.* 1990), predation (Bergerud *et al.* 1983, Messier and Crete 1985, Van Ballenburghe 1987, Bergerud and Snider 1988, Larsen *et al.* 1989, Ballard *et al.* 1991), weather (Picton 1979, 1984, Mech *et al.* 1987, Merrill and Boyce 1991) and disease (Sinclair *et al.* 1985). In the following sections, I summarize the literature in an attempt to assess the roles that food limitation, predation, and weather play in limiting/regulating ungulate populations.

### **2.3.2 Food Limitation as a Limiting/Regulating Factor**

While many studies have shown that populations of ungulates exhibit density-dependent changes, only a few studies have actually documented that food resources are limiting or have measured their regulatory effects on ungulate populations. Lack (1954) was among the pioneers of the theory that range condition is the determinant of ungulate population status. He postulated the food-limiting hypothesis, which is summarized for North American deer as follows:

"The numbers of North American deer are limited by food shortage, which causes a rise in the death rate, especially among the young and senile, and a fall in fecundity. The reduction is density-dependent, though precipitated by heavy snowfalls. Disease seems secondary. The effect of predators (scarce because destroyed) is uncertain."

Lack tried to include both density-dependent and density-independent factors in a general hypothesis by suggesting that in a seasonal environment the fecundity rate will be determined in a density-independent way by the amount of resources available for breeding in the favorable part of the year. Regulation of population size would then occur

through density-dependent mortality through resource limitation during the non-breeding season (Lack 1966).

Similarly, many authors have argued that forage quality represents a key element of ungulate population dynamics (Peek 1974, Oldmeyer *et al.* 1977, Peterson 1977, Franzmann and Schwartz 1995). For example, Peterson (1977) found that food supply played a major role in moose population dynamics on Isle Royale, supported by increased signs of malnutrition and reduced calf production in early 1970s when moose numbers were at high levels. These findings were confirmed by Messier (1991) who found that forage competition influenced population growth and had a further regulatory effect on moose numbers.

### ***Population Irruptions***

A major food limitation theory has sprung from observations of population irruptions. Caughley (1970, 1976, 1979) studied irruptive behavior in several ungulate species and concluded that the irruption was the typical pattern of population growth for large herbivores. Peek (1980) defined 'irruption' as "an abrupt increase, initial stabilization, and decline of the population, peaking well above the normal fluctuations and related to an abrupt decrease in limiting factors". Predators may delay or promote the population fluctuations, but are unnecessary (since it is the rapid increase of forage supplies that is thought to initiate the irruptive sequence)(Caughley 1970).

There is a major problem with Caughley's hypothesis- all documented irruptions recorded in North America have also been preceded by human interference with the ecosystem in some manner (Peek 1980). As well, it has been found that Caughley's assumptions usually hold for ungulates where there is little or no predation (Blood 1974, Staines 1978, McCullough 1979).

For these reasons, RMNP may be a prime target for a population irruption. In fact, a population irruption has already occurred in the Park. Investigations into the population irruption of elk that occurred in RMNP in the fall of 1946, and the subsequent decrease in the population after the winter of 1946/47 were undertaken by Banfield (1949). The winter was characterized by exceptionally deep snow and low temperatures in the early



winter, and thaws followed by cold snaps creating thick crusts on the snow in the late winter. It was found that the severe winter conditions of 1946/47 caused an estimated drop from 77.1 to 58.7 elk per square mile on the concentrated elk ranges, which are an estimated 180 square miles. This meant an estimated mortality of 20 per cent due to winter kill. It was suggested that the severe winter conditions affected the calf crop by losses of pregnant cows (several observed), still births (one was found) and by re-absorption of embryos. As well, 63.6 per cent of the 1946 calves which survived until January perished before May, 1947; of the ten newborn calves examined, eight were females, suggesting a possible high prenatal mortality among the males. An analysis of the 59 carcasses examined showed that the youngest and senile classes suffered the greatest losses. There were widespread infestations of external and internal parasites which could have been an important secondary lethal factor.

According to the literature, there are two very different views about the causes of irruptions among ungulates. The traditional idea is that decimation of large predator populations reduces regulative mortality and thereby initiates a phase of unimpeded growth (Leopold 1943). Riney (1964) suggested that irruptions are triggered by a major discrepancy between existing population levels and environmental carrying capacity (food and cover).

### ***Dynamics in a Predator-free Environment***

Recently, the results from several long-term individual-based population studies of ungulates have been synthesized (Saether 1997), allowing the addressal of an important question in population ecology- can a stable equilibrium between a herbivore and its food resources exist in the absence of predation? One major conclusion is that the population dynamics of ungulates in predator-free environments is strongly influenced by a combination of stochastic variation in the environment, and population density (Saether 1997). The following sections outline evidence that supports Lack's hypothesis, that density-dependent and density-independent factors act in concert to regulate a population.

*Factors Influencing Mortality in Ungulates*

A necessary condition for population regulation is that there exists a 'return tendency' (i.e. a tendency for the population to recover after a small perturbation away from equilibrium) in the population through density dependence (Turchin 1995). In long-lived species, such as ungulates, with a high degree of age dependence in both fecundity and mortality, it is difficult to show significant density-dependent effects by statistical analyses of such time series. This is because such age-specific events are likely to generate delays in the density-dependent response of the population and thereby further increase the length of the study period necessary for detecting density-dependence (Peterson *et al.* 1984a, Fryxell *et al.* 1991).

According to Lack's hypothesis, in temperate ungulates we expect the highest losses to occur during winter because of density-dependent resource limitation. In red deer (*Cervus elaphus elaphus*), the major density-dependent mortality losses occur among calves during their first winter (Houston 1982, Clutton-Brock and Albon 1982, Clutton-Brock *et al.* 1987). No density-dependence occurred in the mortality of adults (Saether 1997).

As well, a strong interaction was found between the effects of population density and abiotic factors on recruitment rate (number of calves per female). The recruitment rate was influenced by a combination of population density and winter severity in white-tailed deer (McCullough 1979), elk (Boyce 1989) and mountain goats (*Oreamnos americanus*) (Swenson 1985). Similarly, in mule deer (*Odocoileus hemionus*) (Picton 1984), white-tailed deer (McRoberts *et al.* 1995), red deer (Clutton-Brock and Albon 1982) and moose (McRoberts *et al.* 1995), the calf:female ratio was highly correlated with variation in winter severity.

In a comparison of the mortality rate of wild reindeer populations living in almost predator-free environments with different resource availability during the non-breeding period, it was found that there was a relationship between calf survival rate and population density. This relationship was related to the amount of available forage during late winter (Skogland 1985). However, in a similar comparison among different Norwegian moose populations, no relationship was found between winter food supply

and calf mortality (Saether *et al.* 1996). In fact, most losses occurred during the summer season as neonatal mortality.

Finally, it is noticeable that in some temperate species, predation is not necessary for large neonatal losses in ungulates, and population regulation or limitation by juvenile losses may occur even during the favorable part of the season despite an absence of large predators (Clutton-Brock *et al.* 1985, Clutton-Brock *et al.* 1992, Saether *et al.* 1996).

#### *Factors Influencing Fecundity in Ungulates*

Population density was found to influence the fecundity rate in red deer and Soay sheep (*Ovis spp.*) (Clutton-Brock *et al.* 1987, Jorgenson *et al.* 1993, Clutton-Brock *et al.* 1997). In both these species, the age at maturity increased with increasing population density.

Climatic conditions also exert a strong influence on the fecundity rate in red deer as well as in other temperate ungulates (Milner-Gulland 1994, Langvatn *et al.* 1996, Saether *et al.* 1996). In particular, the climatic conditions during winter or spring are of particular importance for age at maturity. For example, female moose matured significantly earlier after two winters with almost no snow cover in southern Norway (Saether *et al.* 1996).

In several temperate ungulates, it has been shown that changes in body weight affect the fecundity rate through size-dependent onset of reproduction (Gaillard *et al.* 1992, Festa-Bianchet *et al.* 1994, Langvatn *et al.* 1996). For example, Gaillard *et al.* (1992) found that body weight of young roe deer often decreases with population size, in particular at very high densities, possibly leading to a delay in the age of maturity at high densities. Long-term studies of annual variation in body weight have indicated that these variations are related to stochastic variation in the summer and the winter climate (Solberg and Saether 1994), probably through an influence on the quality or quantity of the food (Saether and Heim 1993, Langvatn *et al.* 1996). For example, body weight of moose calves, and thereby their age of maturity, is related to the biomass of favorable summer food on the mother's home range (Saether and Heim 1993).

*Results from Key-Factor Analyses*

Key-factor analysis is a commonly used technique for examining quantitatively the effect of changes in different demographic variables, at different stages of the season, on population fluctuations (Sinclair 1989). This method assumes that differences in population size can be interpreted as changes in mortality in different stages of the season. Although key-factor analysis is based on several assumptions that are not truly fulfilled in any ungulate population (Royama 1996), key-factor analyses have been conducted in four different ungulate populations: red deer on Rhum (UK) (Clutton-Brock *et al.* 1985), elk in Yellowstone National Park (Houston 1982), Soay sheep on St. Kilda (UK) (Clutton-Brock *et al.* 1991) and the African buffalo in the Serengeti (Tanzania) (Sinclair 1977). In two of the studies (Soay sheep and red deer) winter losses were the key factor, whereas neonatal calf loss and juvenile mortality were the key factors in the elk and wildebeest populations, respectively. In all four cases, the populations were regulated mainly through density-dependent mortality in the non-breeding season.

*Population Cycles of Ungulates*

Population fluctuations in large mammals has traditionally been attributed to variation in extrinsic factors, such as food, predation, pathogens or parasites (Caughley and Krebs 1983). However, very little empirical evidence exists to suggest that variation in one or a combination of extrinsic factors can generate cyclic variation in the population sizes of large ungulates (Saether 1997). Both long delays and over-compensation in the density-dependent feedback (Peterson *et al.* 1984, Grenfell *et al.* 1992) or stochastic variation in climate (Caughley and Gunn 1993) can easily generate large fluctuations in population size of large ungulates, often of an apparently cyclic nature. Thus, an irruption-like pattern of variation in population size with the lack of a stable resource-dependent equilibrium seems to be characteristic for population fluctuations of many large ungulates in the absence of predators (Messier 1994, Saether *et al.* 1996).

### *Conclusions*

The results of the study by Saether (1997) suggest that a stable equilibrium between ungulates and their resource supply as expected from Lack's food limitation hypothesis is unlikely without predation. This is due to the fact that, in the absence of predation, the regulatory mechanisms in population dynamics of large ungulates will operate very slowly, giving long return times in the population dynamics. As a result, large fluctuations in the population size, possibly overshooting the carrying capacity, will occur.

### **2.3.3 Predation as a Limiting/Regulating Factor**

The effect of predation on population dynamics of ungulates continues to be a topic of considerable debate (Boutin 1992). Predation has been described as exerting a significant element of control (Keith 1974), the limiting factor (Bergerud *et al.* 1983, Bergerud and Snider 1988, Larsen *et al.* 1989) and the regulating factor in North American ungulate populations (Messier and Crete 1985, Van Ballenburgh 1987, Ballard *et al.* 1991). Predation on elk has received far less attention than that on moose or white-tailed deer, probably because the sympatric distribution of elk and wolves has been restricted (Carbyn 1983). Furthermore, the numerous studies that have been conducted on wolf-moose interactions have taken place in areas where elk and moose do not coexist. Since RMNP contains both moose and elk populations, caution must be exercised in extrapolating the results of these studies to the predator-prey relationships of the Park.

Little information exists on the influence of alternate prey on moose-wolf interactions (Messier 1994). Theoretically, one can postulate two outcomes with opposite effects. First, an increase in alternate prey could decrease predation on the primary prey by dilution of the functional response (how the number of prey consumed per predator varies with prey density), particularly if the alternate prey is preferred by the predator (Real 1979). For example, the presence of elk in RMNP, with a higher degree of vulnerability than moose, may dilute wolf predation and allow for a greater abundance of moose than otherwise expected (Messier 1994). Studies by Pimlott *et al.* (1969), Carbyn (1983) and Potvin (1988) support this interpretation. Second, the presence of an alternate

prey may increase predation by promoting a favorable numerical response (changes in predator numbers with prey density). Gates and Larter (1990) have proposed that the recent eruption of wood bison (*Bison bison athabascae*) in the Mackenzie Bison Sanctuary, Northwest Territories, may exaggerate predation on moose, rather than diverting it. Here, the increase in bison appears to favor higher wolf abundance, although wolves probably exploit moose preferentially. An analogous situation has been described by Bergerud and Elliot (1986), Edmonds (1988) and Seip (1992) with regard to the decline of woodland caribou (*Rangifer tarandus*) with expanding moose populations within the range distribution of woodland caribou.

#### **2.4.4 Weather as a Limiting/Regulating Factor**

##### ***Temperature***

Low temperature and wind chill increase energy expenditure by ungulates (Trottier and Hutchison 1982). Deer experience significant body heat loss during extreme cold and strong winds (Verme 1968, Ozoga and Gyzel 1972, Moen 1976). Ungulates mitigate such losses through morphological, physiological, and behavioral adaptations. They are insulated by hair and spend less time searching for food (Short *et al.* 1969, Thompson *et al.* 1973, Moen 1978). Energy conservation is also assisted by lowered basal metabolic rates (Silver *et al.* 1969, Seal *et al.* 1972, Wallmo *et al.* 1977). Therefore, animals search for vegetation that provides protective cover in winter, usually of coniferous species, that reflect radiation back to the emitting body, offering protection from winds, and minimizing extremes in ambient temperature (Ozoga 1968, Moen 1968, Lyon 1980). Prolonged periods of cold weather or high wind chill will affect physical condition and subsequent reproductive potential of the animal or population (Ransom 1967, Moen 1978).

Cold weather has an indirect effect on animal condition because it forces animals to seek cover in areas where little forage is available. Therefore, food intake is often reduced because food is scarce and because less time is spent feeding (Ozoga and Verme 1970). Prolonged 'yarding' in areas with good cover leads to range overuse in those areas and subsequent food shortage if severe conditions persist.

### ***Snow Conditions***

Snow thickness, hardness and density are important in the analysis of ungulate relationships to snow (Trottier and Hutchison 1982). In fact, Coady (1974) stated that depth, density and hardness of snow were probably the characteristics most important to moose. For elk, moose and white-tailed deer, snow places restrictions on movements (Telfer and Kelsall 1971) and forage quality and availability (Mautz 1978, Verme and Ozoga 1981). Nasimovich (1955) observed that European red deer (*Cervus elaphus elaphus*) in Russia dig for food from under the snow only while snow density is low and thickness does not exceed 30 to 40 cm. Coblentz (1970) found that white-tailed deer shifted from eating grasses and forbs to a browse diet after about 17 cm of snow accumulated on the ground. Moose were found to seldom paw through snow to feed but will often move fresh, low-density snow with their snouts to uncover food (Nasimovich 1955).

Telfer and Kelsall (1971) found that snow thickness exceeding two-thirds the chest height of ungulates impedes locomotion. Foot-load-on-track (FLOT) in turn determines the ability of animals to cope with varying density and hardness of snow (Nasimovich 1955, Pruitt 1959, Skogland 1978, Telfer and Kelsall 1979). Moose are morphologically well adapted to cope with deep snow typical of boreal forests (Messier 1991). Kelsall and Prescott (1971) observed that moose sunk to 88% of the snow thickness but can tolerate sinking 40 cm. Coady (1974) reported that snow depths less than 70 cm cause little hindrance to the movements of moose. Elk are not as well adapted to snow because of their higher FLOT (Telfer and Kelsall 1979) and avoid areas of deep snow whenever possible (Telfer 1978, Lyon 1980). Subadults of all species are at a disadvantage in thick snow because they have lower chest heights than adults (Telfer and Kelsall 1979). More important are the negative effects of year-to-year winter snow on the vulnerability of calves to wolf predation (Messier 1991).

Mech *et al.* (1987) analyzed long term data on the demography of moose on Isle Royale and white-tailed deer in northeastern Minnesota with the objective to identify primary predictors of population productivity and changes in abundance. They proposed that winter conditions represent the primary determinant of population changes in moose

and deer. Further, snow accumulation during consecutive winters has a cumulative influence on the nutritional status of females and therefore on female reproductive success. Finally, they asserted that "although wolf predation is the main direct mortality agent of fawns and calves, wolf density itself appears to be secondary to winter weather in influencing the deer and moose populations" (Mech *et al.* 1987, p. 615).

### ***Spring Green-up Value***

The timing of spring green-up and the subsequent length of the growing season affect the condition of ungulates and ultimately, their reproductive potential. Mautz (1978) found that winter survival of deer depends, to a large extent, on fat reserves built up during the summer when growing plants are available. This fat serves as insulation against heat loss and is catabolized during winter to compensate for lower food intake and poorer forage quality. Stewart *et al.* (1977) concluded that the energy budget of moose in northern Saskatchewan was highly dependent on annual variations in quality of available browse which in general was correlated with the timing of plant phenological events such as spring leaf flush and autumn leaf abscission. The significance, then, of a one month range in leaf flush (from early May to early June in RMNP) may be considered to have a large effect on the reproductive potential of these and other cervids.



## **CHAPTER 3**

# **POPULATION DYNAMICS IN RIDING MOUNTAIN NATIONAL PARK**

### **3.1 INTRODUCTION**

The following is a review of Park records relating to ungulate population dynamics. The chapter provides a description of RMNP and a brief history of ungulate population dynamics within the Park. The bulk of the chapter outlines several factors that may be contributing to the elk and moose population fluctuations, and speculates as to how these factors may be influencing elk and moose.

### **3.2 STUDY AREA**

#### **3.2.1 History**

Prior to settlement, the forests, prairies and lakes of Riding Mountain were favorite hunting grounds for aboriginal peoples, including the Woodland Cree, who lived in the highlands; and the Assiniboine, a tribe that lived off bison herds on the surrounding prairie (Dunbar 1991). In 1741, Pierre de la Verendrye, an explorer of the area, established a post at Dauphin Lake at the request of the Cree. By 1800, trading posts ringed the mountain which yielded a rich harvest of furs. The easiest way to ascend the highland was by horseback, hence the mountain's name (Dunbar 1991).

By the 1850s, many species such as bison (*Bison bison*), wolverine (*Gulo gulo*), river otter (*Lutra canadensis*), martin (*Martes americana*) and fisher (*Martes pennanti*) had disappeared from the area; beaver hovered on the brink of extirpation (Dunbar 1991). After the Canadian Pacific Railway reached the area in 1881, homesteaders began farming the areas surrounding the plateau. The upland was withdrawn from settlement at the end of the last century. It was designated a Forest Reserve in 1906 and a National Park in 1930 (Dunbar 1991).

### 3.2.2 Description

Riding Mountain National Park is located 225 km northwest of Winnipeg and approximately 100 km north of Brandon in western Manitoba. The Park consists of forested, low hills and catchment basins and is completely surrounded by farmland. The Manitoba Escarpment is clearly visible along the eastern edge of Riding Mountain, rising abruptly 427 m above the surrounding plain. Most of the Park, however, is situated above the escarpment of the Second Prairie Steppe of the Great Plains (Ehrlich *et al.* 1956). Elevations average 610 m, and range from 319 m to 756 m on the escarpment.

The bedrock is Cretaceous in origin and consists of silt deposits laid down in ancient seas (Trottier *et al.* 1983). The Park can attribute its present landform configuration to subsequent uplift followed by glaciations and deglaciations. The Park landform consists of deep gorges with eroding shales and glacial over-burden on the escarpment which contrast with rolling boulder till, knob and kettle stagnation moraine, and lacustrine plains dissected by glacio-fluvio outwash channels over the majority of the Park.

### 3.2.3 Vegetation Composition

The Park contains three vegetation zones- the Boreal Forest, the Eastern Hardwood Forest, and the Prairie Grasslands.

The Boreal Forest supports a mixedwood forest with varying proportions of aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and Jack pine (*Pinus banksiana*). Aspen and mixed aspen- white spruce forests occupy approximately 70% of the Park area (Rounds 1977). Poorly drained sites may be sedge fens (*Carex* spp.), black spruce (*Picea mariana*) bogs, or tamarack-sphagnum (*Larix laricina*- *Sphagnum* spp.) bogs. Riparian areas along the escarpment (and sporadic areas throughout the Park) consist of stands of white elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), bur oak (*Quercus macrocarpa*) and Manitoba maple (*Acer nugundo*). Bur oak can also be found in pure stands on coarse alluvium.

Grasslands, shrublands, and several coniferous formations account for about 20 % of the remaining vegetation. Approximately 2.5% of the Park consists of grassland (Bailey 1968); 0.7% of this is rough fescue (*Festuca scabrella*) native grassland; and the remainder is upland meadows of wheat grass- blue grass (*Agropyron trachycaulum- Poa pratensis*) which resulted from clearing of forest cover by fires, and lowland meadows of pure sedge (*Carex* spp.) and/or slough grasses (*Glyceria* sp., *Calamagrostis* spp.)

Approximately 2% of the Park consists of upland shrub meadows, dominated by hazel (*Corylus cornuta*), with lesser amounts of willow (*Salix* spp.), saskatoon (*Amelanchier alnifolia*), choke cherry (*Prunus virginiana*) and aspen; and lowland shrub meadows consisting primarily of willows and speckled alder (*Alnus rugosa*).

A fine-grained interspersed of ponds, marshes and lakes, and small stands of vegetation differing in species composition and structure (with much edge between types), is created by the Park's irregular surface features. Disruptive factors such as fire and logging, livestock grazing and haying have had a variable effect on the structure and succession of stands (Bailey 1968). As a result, there are few extensive stands of climax vegetation; instead, there is a rather high habitat diversity in any given area for use by wildlife.

Areas burned by wildfires occupy 10% of the land and are in various stages of succession (Rounds 1977). In approximately 1890, a drought period coincident with settlement of the region by Europeans was the setting for two large wildfires which swept across the Riding Mountain (Dickson 1909). In 1909, only 23% of the area was described as 'timbered' (i.e. trees over 20 cm DBH); of this 23%, 52% was poplar, 20% was white spruce, and the remainder was grassland, shrubland and young stands of poplar forest. In 1930, serious attempts to conserve the timber virtually eliminated fire as a modifier of vegetation types in the area (Bailey 1968). The Gunn Lake burn in 1961 and the Rolling River burn in 1980 were two major exceptions to the 'stamp-it-out' policy. As a result, about 54% of the forests are mature poplar stands (Bailey 1966, cited in Trottier *et al.* 1983) originating in the 1890's. Even today, many of these stands are still in a secondary successional stage where conifers are scarce.

More recently, the vegetation of the area is a complex of seral stages with high productive capacity capable of supporting dense herbivore populations (Trottier *et al.* 1983). This variety of seral stages is a result of many anthropogenic influences. For example, selective logging has altered mean stand ages and opened the canopy, thereby promoting patches of shrub growth (Bailey 1968). Similarly, grazing and haying changed species composition of the native grasslands (Blood 1966), while irruptive populations of elk and beaver have had an impact on shrub species and forest regeneration (Banfield 1949).

#### **3.2.4 Climate**

The climate of Riding Mountain is continental and typical of the Canadian prairies, with short warm summers (mean daily temperature for July = 20°C) and long cold winters (mean daily temperature for January = -19.5°C). The growing season is short (mean = 65 days, range = 43-106), and snow cover persists for about five months (mean = 152 days)(Keck 1975). Elevation has a moderate control over temperature and precipitation with the highest regions of the escarpment receiving significantly greater amounts of snow and recording lower temperatures. Total precipitation is about 50 cm per year.

### **3.3 HISTORIC DESCRIPTION OF ELK AND MOOSE IN RMNP**

Elk and moose were plentiful in Manitoba prior to settlement by Europeans (Bird 1961), and the creation of the Riding Mountain Forest Reserve was the first step in protecting the area and its indigenous wildlife for future generations of Manitobans. It was officially set aside by Departmental Order on 13 July 1895 to conserve the timber resources (Report of the Superintendent of Forestry, Canada Department of the Interior 1909). In 1900, however, a 13 x 39 km game reserve was established, and the rest of the forest reserve was open to hunting, regulated by the provincial government.

### **3.3.1 Fluctuations in Ungulate Populations Until 1950**

#### ***Elk***

With intensified settlement, elk herds were reduced by both slaughter and loss of habitat, especially along the southern boundary of the reserve. By 1900, only a 'few hundred' elk remained (Green 1933). These small numbers were probably a result of the opening of the reserve to sport hunting and periodic severe winters. Until 1909, there were about 50 settled families in the reserve, and they likely used ungulates as a food source. In addition, during the open hunting season an estimated 500-600 hunters created further pressure on ungulate herds.

In 1914, an estimated 500 elk remained and a closed season was recommended by forestry officials (Green 1933). Photographs exist that depict railway flat cars loaded with elk and moose carcasses from the Riding Mountain awaiting shipment from Dauphin to Winnipeg (Carbyn 1980). As a result, the whole forest reserve was closed to hunting by Legislative decree in 1917. After several years of protection from hunting, the elk herd was estimated to contain 2500 animals in 1925 (Green 1933).

After national park status was obtained, population estimates for elk indicated quick recovery (3500 in 1933, 5000-7000 in 1941 and 12000 in 1946) to a situation of over-population by 1946 (Banfield 1949). Although early records are too incomplete to reveal year-to-year fluctuations in the population, Banfield (1949) states that the increase was not steady, citing a severe winter kill in 1935-36 as evidence.

The elk population eventually peaked at approximately 16800 in fall 1946. Harsh winter conditions in 1946-47, and habitat deterioration caused by several successive years of over-browsing resulted in a dramatic decline in elk numbers during the late 1940's (Rounds 1977).

#### ***Moose***

The moose population of RMNP was not as closely monitored (Rounds 1977), and early accounts make infrequent mention of this species (Green 1933). The first estimate of moose numbers was made in 1950, when the first aerial survey of the area was conducted. In 1950, there were an estimated 250 moose (Rounds 1977).

### **3.3.2 Fluctuations in the Ungulate Populations from 1950-1963**

#### ***Elk***

The elk population stabilized at about 4500 animals between 1950 and 1952 (Figure 3). A harvest of 938 elk in winter 1951-52 accounted for a major part of the stabilization and an additional kill of 1766 animals in 1952-53 likely caused a population decline to 2500 (Rounds 1977).

In 1955, there were an estimated 1132 elk in the Park. However, this survey can be deemed invalid since the survey report states that ground conditions were poor for sighting animals. A count conducted under good conditions in 1956 resulted in an estimate of 5200 elk, which further invalidates the previous estimate. The population subsequently declined to 2500 in 1957, showed a slight increase in 1958, and expanded rapidly in 1959 and 1960, to a population of approximately 4800 in 1960 (Rounds 1977).

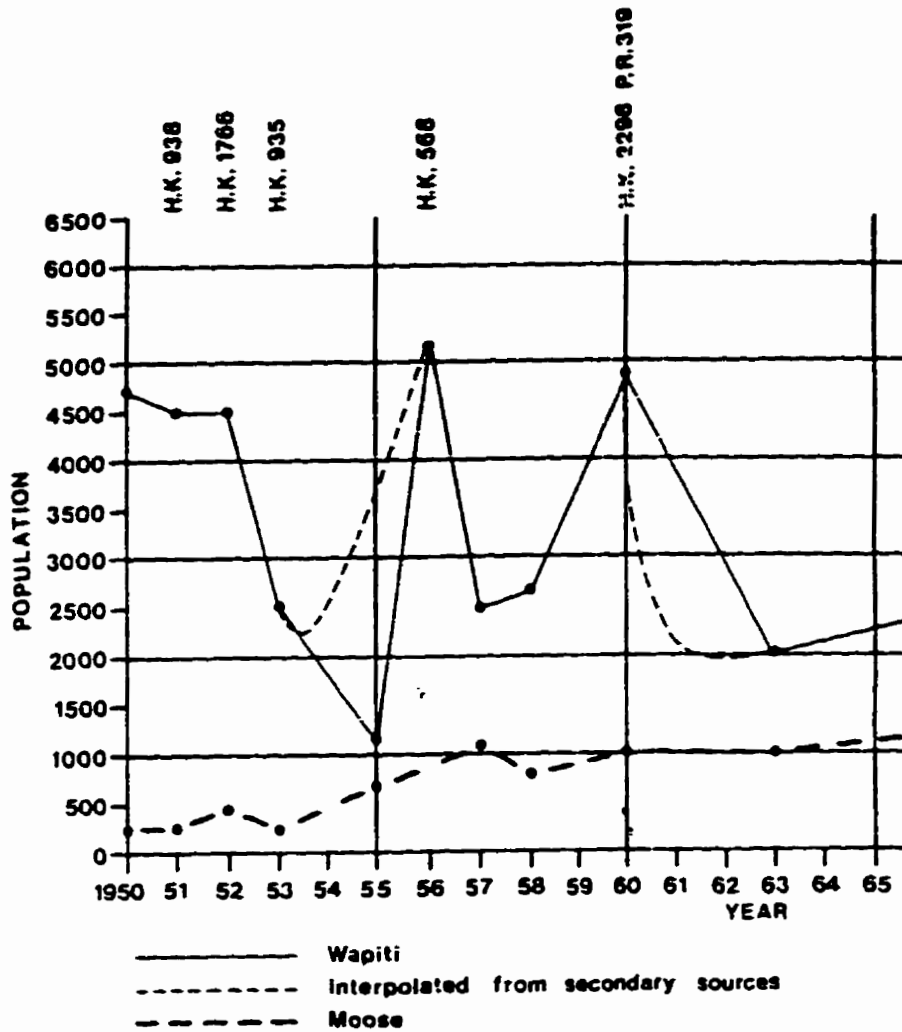
Following this, apparent range deterioration and extensive depredation on private lands surrounding the Park resulted in a re-opening of hunting around the Park and a planned reduction of the number of animals within the Park. In total, more than 2500 elk were harvested in 1960. The next survey that was conducted was in 1963, when the population was estimated at about 2000 elk (Rounds 1977).

#### ***Moose***

Moose numbers were relatively low during early survey years but a noticeable increase occurred during the mid- to late 1950's (Figure 3). The population remained near 1000 animals from 1957-1963 (Rounds 1977).

## **3.4 UNGULATE POPULATION MONITORING**

Population estimates of elk and moose in RMNP since 1950 are based on aerial surveys using a fixed-wing aircraft on north-south transects (a strip census sampling method). Survey techniques, however, have varied considerably over the years. The number of transects flown ranged from 16 to 68, flying height from 30 to 125 m, and strip width from 0.4 to 0.8 km. Resulting coverage varied from 6.2 to 25% of the Park. These



H. K. 500 - Hunter kill-wapiti  
 P. R. 319 - Park reduction-wapiti  
 H.K.(155) - Hunter kill-moose

**Figure 3. RMNP Elk and Moose Population Estimates 1950-1963**  
(Rounds 1977)

variations in survey techniques probably result in significant differences in accuracy of population estimation (Rounds 1977). Since 1963, however, the survey technique has remained the same, and thus an analysis of these data can be made to reveal valid trends (the years 1974 and 1975 are an exception whereby a different methodology was used).

### **3.4.1 Purpose**

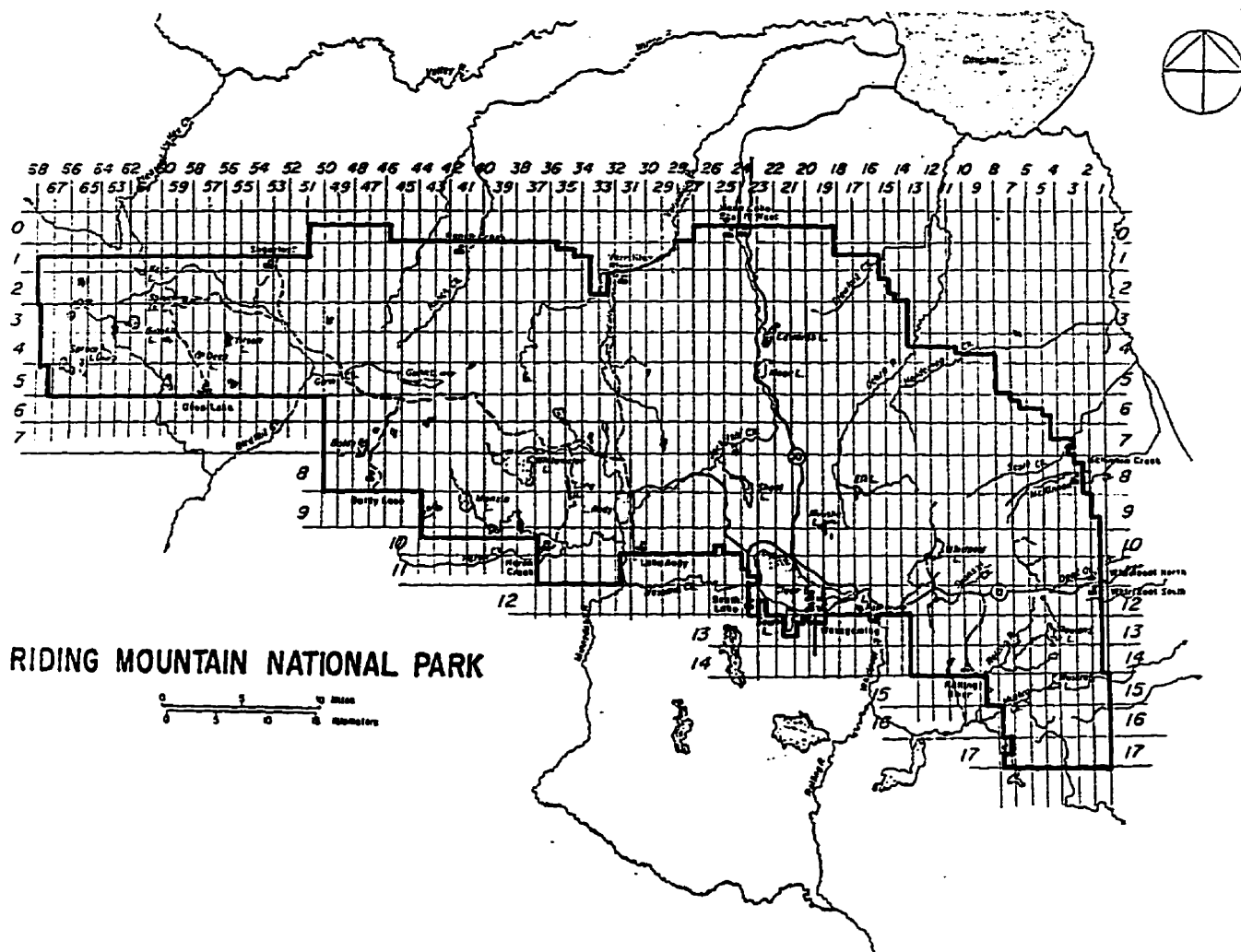
The purpose of the RMNP monitoring program for elk and moose is to provide trend information which can be employed to inform and direct management strategies. Trend data are provided to the Manitoba Department of Natural Resources (DNR) and are used by them in the annual assignment of hunting seasons in Game Hunting Areas (GHAs) 23 and 23A with a year's delay. The data are also used internally as indicators of effectiveness of the resource management and protection strategies undertaken within RMNP. The data are intended to be used primarily as indices of real population trends. These data are some of the most consistent data about a specific North American elk or moose population (Tarleton 1992b).

### **3.4.2 Survey Technique 1963-Present**

Tarleton (1992b) described the methodology for ungulate aerial surveys in the Park. Sixty-eight north-south transects spaced at 1.6 km (one mile) intervals cover approximately 25% of the Park in east-west dimensions (Figure 4). All surveys were conducted in January, February or March. The first transect began exactly on the most easterly portion of the Park boundary. Some transects (e.g. number one) were not complete transects, and one observer was observing outside the Park. Animals observed outside the Park were not included in the estimate. Transect areas were calculated so as to exclude the portions of transects which were outside the Park.

Each transect was 0.4 km wide (0.2 km on each side of the aircraft). To delineate the 0.2 km width of view, the aircraft flew above a field which was marked off at 0.4 km sections. The observers on each side of the aircraft were able to mark off 0.2 km on each side of the aircraft when it flew down the center of the field at the survey height of 125 m. The observers restricted their width of view by placing a piece of masking tape on the





**Figure 4. Transect Set-up for RMNP Ungulate Aerial Surveys 1963-Present (Tarleton 1992b).**

window such that the area below the tape was within the transect.

Observers communicated with the recorder via voice-activated headsets, calling out each sighting according to species and group size. The recorder noted each sighting on a 1:25000 map of RMNP. Different pen colors were used to distinguish between elk and moose observations. The recorder noted the time on and time off (or elapsed time) for each transect. The survey crew consisted of a pilot, a navigator, a left and right observer and a recorder. Preliminary data analysis was performed on dBase version 4.1. Transect areas were recorded on a separate dBase file. A dBase report was used to generate the standard error, sums of squares, and populations estimates (Appendix A). Data were stored on 3.5" disks and have been filed at warden stores.

### **3.4.3 Reliability of Aerial Surveys**

Visibility bias can occur when an observer fails to see and count every animal within the survey area. Caughley (1977) has observed that undercounting is usually serious enough to invalidate the use of an aerial survey as estimation of absolute abundance, although the survey result may still be useful as an index of population size.

Species behavior and dispersion, observers, weather, habitat type and methodology are factors that also create visibility bias. LeResche and Rausch (1974) found an observer with current aerial survey experience counted an average of only 68 percent of the moose present in an area under excellent viewing conditions. Hauge and Keith (1981) reported an observation efficiency of 50 percent for aerial surveys of moose from fixed wing aircraft. Similarly, MacLennen (1975) calculated a 'miss factor' for elk in the Porcupine forest of Saskatchewan of 20-40 percent.

Increased visibility bias can result from increased survey speed, height and width of transects (Caughley *et al.* 1976). Similarly, observer fatigue (including time-of-day), boredom and airsickness were found to be responsible for as much as 26 percent of the variation in an aerial survey (Norton-Griffiths 1976). Norton-Griffiths (1976) recommended that survey flights be no more than three hours in order to minimize this visibility bias. Caughley *et al.* (1976) demonstrated that the use of different observers resulted in significantly different counts; while LeResche and Rausch (1974) showed that

inexperienced observers saw approximately 20 percent fewer moose than experienced observers under all types of viewing conditions. They recommend that aerial moose surveys should only be conducted by experienced observers under conditions of complete, fresh snow cover.

Weather factors increase variation between yearly survey results by influencing ungulate behavior and aerial visibility. Severe weather conditions, particularly deep snow and late winter conditions, may cause both elk and moose to seek shelter in coniferous or mixedwood areas (Trottier and Hutchison 1982), thus reducing aerial visibility and negatively biasing the count. For example, Trottier *et al.* (1983) employed 19 aerial surveys during the winters 1977-78, 1978-79 and 1979-80 in a study of elk and moose habitat selection. They found that late winter surveys produced lower counts than early winter surveys (particularly for elk), and attributed this discrepancy to shelter-seeking behavior.

Population estimates are not accurate predictions of population size, but should be precise estimates of trends. Therefore, the population statistics should be treated as indices to the statistics of interest. When resources are not available to control or estimate biases, the chief value of these population statistics, as indices, is in their ability to be compared from year to year (such as the aerial surveys from 1963 to present).

### **3.5 FACTORS INFLUENCING UNGULATE POPULATIONS**

The following section outlines and describes some of the factors that may have influenced elk and moose populations in RMNP in the past in an attempt to illustrate some of the reasons why each of these factors were explored in this study.

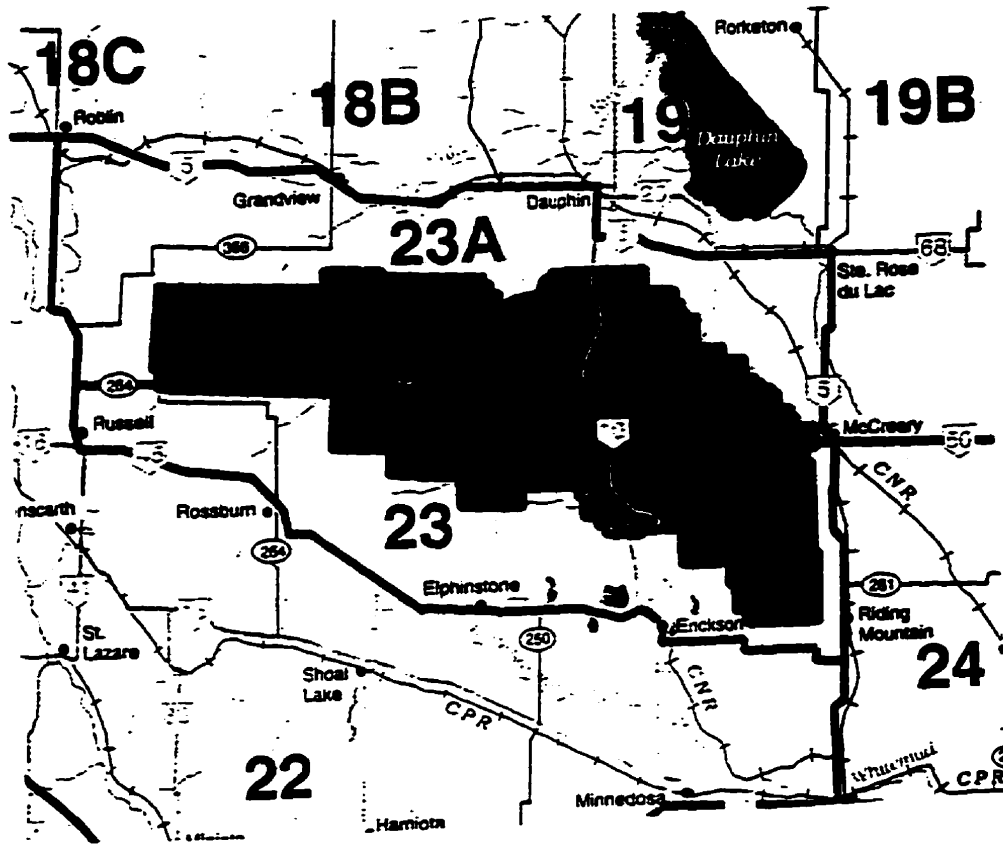
#### **3.5.1 Hunter Harvest of Ungulates in the RMNP Region**

The Manitoba Department of Natural Resources (DNR) also takes some responsibility for managing the RMNP region. Hunting is an important regional economic/ recreational activity that DNR uses as a tool to manage the wildlife populations in the Province (Tarleton 1992a). As well, the Province of Manitoba is responsible for compensating

affected farmers for lost income from depredation of standing crops and stored hay by elk herds (Tarleton 1992a). Unfortunately, the two agencies which share responsibility for managing the elk and moose of RMNP on behalf of Manitobans and Canadians have not developed common objectives for elk and moose. Two jurisdictions (provincial and federal) with different mandates, and with different tools to achieve those mandates, managing lands adjacent to one another will obviously create transboundary issues. For example, RMNP pays for and distributes the results of its annual aerial surveys to DNR early in each calendar year. Yet, these results are not figured into the setting of seasons or tags issued by DNR until the following year due to the lead time needed to approve regulations, print licenses, etc. As a result, there is a one-year delay in the Province's managing of the ungulate populations surrounding RMNP (based on the population estimates from the surveys).

Presently, elk and moose are legal to harvest by Manitoba residents in the Bowhunting, Landowner and Firearm season types during set periods from late August until late January within GHAs 23 and 23A (Figure 5). The number of tags is limited and allocated by draw, with only one tag being issued to every two hunters for the Firearm draw season (Manitoba Natural Resources 1997). One animal may be taken per tag, but both hunters must buy a license.

Game Hunting Areas 23 and 23A differ from other Manitoba GHAs (and jurisdictions) in that there are no restrictions as to the sex of the animal taken for the bag limits- in all cases the bag limit is one elk or one moose. However, with elk, for example, regulations designed to focus harvest on particular portions of a population are necessary in some management systems (Mohler and Toweill 1982). To keep a population at maximal level, for example, it is thought that the total size of the population must be controlled, and, in most areas, each sex harvested in such proportions as necessary to maintain the optimal sex ratio for herd productivity. Most states and provinces have an antlered-only season, followed or preceded by a season during which any elk, antlered or antlerless, may be harvested. The reasons for this strategy relate to elk behavioral patterns (Mohler and Toweill 1982).



**Figure 5. Game Hunting Areas 23 and 23A (Manitoba Department of Natural Resources 1997)**

It is difficult to predict the impact of no restrictions in sex for the bag limit. With no protection of the cows, there is a possibility that this might skew the sex ratios, causing ungulate populations to fluctuate with lag effects. For example, antlerless elk i.e. cows and calves, hunted in an either-sex or antlerless-only season, are somewhat less vulnerable than bulls during the rut, because the former are silent during this period and do not move about as widely as bulls do (Mohler and Toweill 1982). After the rut, however, antlerless elk move in groups toward wintering areas. Their movements are more predictable and their collective presence makes them more noticeable, and hence more vulnerable to hunters than are bulls. And because cow elk tend to take over leadership of elk bands during this period, they often are the first to expose themselves to opportunistic hunters. Following the rut, bull elk lose their aggressiveness and tend to become solitary or follow elk bands led by mature cows (Mohler and Toweill 1982). Anderson (1958) confirmed the speculation that elk cows are more vulnerable later in the hunting season by reporting that, in Wyoming, more bulls than cows were killed during the early part of the hunting season, but the reverse was true after elk grouped along migration routes.

Tables 1 (elk) and 2 (moose) represent the estimated number of bulls, cows and calves harvested from 1971/72 to 1995/96 (Source: Brian Knudson, DNR). With elk, in 50% of the observations, there were more cows harvested than bulls (and in one case there was as much as 3.5 times as many cows harvested). Similarly, with moose, more cows were harvested than bulls 36% of the time.

Table 1. Estimated Number of Elk Bulls, Cows and Calves Harvested from 1971/72 to 1995/96

	Bulls	Cows	Calves	Cows/ Bulls
1971/72	217	291	63	1.3410
1972/73	50	103	36	2.0600
1973/74	188	154	44	0.8191
1974/75	0	0	0	-
1975/76	0	0	0	-
1976/77	32	94	27	2.9375
1977/78	37	130	50	3.5135
1978/79	151	123	37	0.8146
1979/80	51	109	22	2.1373
1980/81	78	61	22	0.7821
1981/82	34	74	30	2.1765
1982/83	55	200	56	3.6364

1983/84	64	81	21	1.2656
1984/85	430	186	38	0.4326
1985/86	22	38	9	1.7273
1986/87	143	147	56	1.0280
1987/88	65	33	7	0.5077
1988/89	99	10	2	0.1010
1989/90	228	3	0	0.01316
1990/91	n/a	n/a	n/a	-
1991/92	137	59	6	0.4307
1992/93	77	14	2	0.1818
1993/94	76	69	8	0.9079
1994/95	46	85	16	1.8478
1995/96	233	120	36	0.5150

Table 2. Estimated Number of Moose Bulls, Cows and Calves Harvested from 1971/72 to 1995/96

	Bulls	Cows	Calves	Cows/ Bulls
1971/72	67	58	22	0.8657
1972/73	58	67	30	1.1552
1973/74	147	79	19	0.5374
1974/75	0	0	0	-
1975/76	0	0	0	-
1976/77	73	58	30	0.7945
1977/78	44	115	60	2.6136
1978/79	87	73	13	0.8391
1979/80	54	36	19	0.6667
1980/81	58	53	19	0.9138
1981/82	43	57	25	1.3256
1982/83	75	92	31	1.2267
1983/84	71	57	21	0.8028
1984/85	89	103	38	1.1573
1985/86	6	19	15	3.1667
1986/87	43	50	32	1.1628
1987/88	31	0	0	0
1988/89	33	39	7	1.1818
1989/90	17	4	0	0.2353
1990/91	n/a	n/a	n/a	-
1991/92	21	20	6	0.9524
1992/93	11	7	5	0.6364
1993/94	26	17	5	0.6538
1994/95	30	10	6	0.3333
1995/96	85	57	24	0.6706

Rounds (1991) presented a preliminary analysis of what is known about the effect of hunting seasons on the populations of elk and moose in RMNP. He found that, between 1951 and 1980, there was no significant relationship between total ungulate populations and total hunter kill ( $df=19$ ,  $r=0.12$ ;  $p>0.10$ ). In fact, he found that less than two percent of the population variation is accounted for by total kill ( $R^2=0.015$ ). Similar patterns were apparent for each species. Elk kill was weakly related to elk populations ( $df=17$ ,  $r=0.40$ ;  $p>0.10$ ), but accounted for only 16 percent of population variation.

Moose kill showed no long-term relationship to moose population ( $df=9$ ,  $r=0.22$ ;  $p>0.10$ ). He concluded that the available information indicated that licensed hunting has had virtually no effect on population fluctuations. Potential lag effects were not examined.

Rounds (1991) also examined the percentage of the ungulate population that was taken by hunters on a yearly basis. He estimated that, between 1951 and 1980, hunters harvested between 11 and 53 percent of the elk during early seasons (Table 3). Because elk far outnumbered moose, the percentage kill of all large ungulates approximated that for elk. Moose kill was reported only in 1974, when it was estimated that 18 percent of the herd was harvested. From 1980 and on, though, Rounds (1991) found that the legal harvest of elk was less than five percent in five of the nine years of record, less than ten percent in eight of the years, and reached 23 percent only in 1984. Moose harvests were less than five percent of populations in six of nine years, and never exceeded nine percent. Total legal harvest of both populations was less than five percent in seven of 12 years of record and exceeded ten percent only in 1984, when 17 percent of all large ungulates were harvested. Using only years in which both harvest and population records were available, hunters harvested 16 percent of all available elk, five percent of moose, and 11 percent of all animals. Numbers, however, are heavily skewed by harvests in early years (Rounds 1991).

Table 3. Estimated Elk and Moose Hunting Kill in RMNP

Year	Elk			Moose			Combine		
	kill	pop.	% pop. <sup>1</sup>	kill	pop.	% pop.	kill	pop.	% pop.
1951	938	4500	21	0	250	0	938	4750	20
1952	1766	4500	39	0	400	0	1766	4900	36
1953	935	2500	36	0	250	0	935	2850	33
1956	568	5200	11	0	800	0	568	6000	10
1960	2617	4900	53	0	1000	0	2617	5900	44
1971	806	6172	13	0	2448	0	806	8620	9
1974	385	1392	28	245	1338	18	630	2730	23
1980	161	4088	4	130	3880	3	291	7968	4
1981	139	4904	3	125	3804	3	264	8708	3
1982	312	4936	6	198	3140	6	510	8076	6
1983	315	4092	8	166	3292	5	481	7384	6
1984	780	3440	23	242	2764	9	1022	6204	17
1985	129	2996	4	54	1904	3	183	4900	4
1986	—	3672	—	—	2344	—	378	6016	6
1987	106	2392	4	42	1616	3	148	4008	4
1988	111	3628	3	85	2452	4	196	6080	3
1989	243	3558	7	19	1751	1	262	5309	5
1990	—	4470	—	—	2434	—	100 est.	6904	1
1991	—	4699	—	—	3441	—	100 est.	8140	1
Totals	10,311	63,298 <sup>2</sup>	16/14	1306	25,941 <sup>2</sup>	5/4	12,195	115,447	11/10

(Rounds 1991)

<sup>1</sup> Harvests were not added back in to populations, so these percentages are higher than actual numbers.  
<sup>2</sup> Calculated using only populations in years with hunting seasons.



There is no sure way to determine if a population, or subset of a population (e.g. cows), is being overharvested in a particular year. Rounds (1991) suggested that most elk (and moose, by implication) herds can withstand 20-30 percent annual mortality. However, one has to take into account all mortality factors, including predators and winter severity, in this estimate. The 1974-1976 management framework for elk in Colorado included a provision that annual harvest would not exceed 30 percent of the pre-season elk population (Caudill 1976). Since 1980, at least, harvest percentages in RMNP have rarely approached either of these figures.

Although mortality relating to hunting has been reported to be a minor and insignificant component of total mortality in RMNP, it is likely to be more important at the same time as other mortality is high (Rounds 1991). For example, elk leave the highlands of RMNP for the lowland areas in severe winters (Rounds 1991) (presumably to escape the deep snow of the highlands). If this phenomena occurs during the hunting season, hunter success around Park boundaries would presumably increase, therefore potentially increasing total mortality of elk in a particular year. Weather must also directly influence hunter effort, i.e. person hours in the field, and thus also influence harvest.

### **3.5.2 Beaver**

The successional change of vegetation from grassland to large areas of aspen since Park establishment, coupled with minimal beaver control in the Park, are undoubtedly responsible for the current high beaver population levels. Each year the activities of beaver cause large cash expenditures for the surrounding landowners due to damage to hay, pasture, and cropland on farms (Carbyn 1980).

Although no detailed studies have been carried out in the Park, it is very likely that the beaver population directly affects habitats of ungulates (Carbyn 1980). Peterson (1955) noted that moose and beaver often appear to be directly associated in a common habitat. He also suggested that beaver dams are responsible for maintaining the water levels in streams and lakes, thus, in turn, allowing aquatic vegetation to be established and maintained as a source of food for moose during the summer. Occasionally, flooding

of lowlands kills some moose food plants; however, the maintenance of water levels in swampy areas undoubtedly increases the growth of various plants that moose use for food. However, since shrubs (especially beaked hazelnut, poplar and willows) make up >60% of the moose's diet for most of the year (with shrubs being >80% during the winter months), the influence of beaver may be in creating conditions favorable for these shrubs (Trottier *et al.* 1983).

### **3.5.3 Wolves**

The role of predation in shaping and maintaining the structure of animal communities in RMNP is not clearly understood. A review of wolf population fluctuations suggests that when the intensive wolf studies began in 1975, wolf numbers were at, or near, peak densities (Carbyn 1980). Since then, the population has dropped from an estimated 120 wolves (1975) to an estimated 28 wolves in 1996. The reasons for this population decline is unknown, but could include harvest by hunters and trappers along Park boundaries (Carbyn 1980) and mange (G. Goulet, pers. comm.). Ungulates, on the other hand, seem to be increasing in number.

Carbyn (1983) has suggested that wolf predation on elk in RMNP reduces rates of increase and possibly prevents an irruption like that documented in 1947 (Banfield 1949). However, he also found that wolves killed a larger proportion of young and old elk when compared to hunter kills adjacent to the Park, suggesting the wolf predation may be compensatory rather than regulatory.

An important consideration of whether a predator 'limits' a prey population or just provides compensatory mortality (kills only surplus animals) is an analysis of the predator/ prey ratios and the examination of the availability of alternate or buffer prey species (Carbyn 1980). Carbyn (1980) found that, from 1975 to 1978, in six wolf packs territories examined in RMNP, the wolf: elk ratio equaled or exceeded the wolf: moose ratio. The number of elk per wolf ranged from 22 to 90 and the number of moose per wolf ranged between 14 and 34. The mean wolf: ungulate ratio for all packs was 1:83 (55 elk and 28 moose). In 1996, the number of elk per wolf was 179, and the number of moose per wolf was 157, the highest ratios ever recorded in the Park. Obviously, there

has been an increasing number of ungulates for every wolf from 1963 to present, as the wolf population has steadily declined, whereas the elk and moose populations have steadily increased.

Mech (1970) considered predator: prey ratios in terms of biomass per wolf. His tentative conclusion was that wolf predation is a population controlling factor when prey: wolf ratios are 11,000 kg or less per wolf. Carbyn (1980) estimated the biomass ratio to be approximately 22,041 kg per wolf at that time in the Park. Based on Mech's model, the prey base in RMNP could have supported twice as many wolves, or alternately the prey could have decreased to half of its population size before predation could be considered the primary controlling influence. Obviously, the prey base in RMNP is considerably higher now, and could probably support many times more wolves. The question then becomes, with such a large prey: predator base, could the wolves be significantly impacting the ungulate populations? As mentioned, it is possible that elk, with a higher degree of vulnerability than moose, may dilute wolf predation and allow for more moose than otherwise expected (Messier 1994).

#### **3.5.4 Snowshoe Hare**

Samoil (1979) attempted to define the role of the snowshoe hare as a consumer and, more specifically, answer the question of whether snowshoe hares compete with ungulates for browse during the winter. Competition is only one of the many ways in which snowshoe hares may be affecting ungulate populations. Amensalism (when one species is inhibited and the other is unaffected) and commensalism (where both benefit by this association) as defined by Odum (1971) are two other possible interactions.

Competition as defined by Pianka (1976:114) "occurs when two or more organisms, or other organismic units such as populations, interfere with or inhibit one another." Competition may be classed as direct or interference type, as in the case of interspecific territoriality, or indirect or exploitive, arising from the joint use of the same resources (Pianka 1976). In Samoil's (1979) study in RMNP, the hypothesis that was tested was restricted to whether exploitive competition exists between the snowshoe hare and one or more species of ungulates.

The alternative hypothesis was that the species are coexisting in the same habitat. Cody (1974: 7) suggested that "coexistence is achieved by the evaluation of some minimal degree of difference in resource use." He suggested that competition can be avoided by species having differences in the selection of horizontal and vertical habitats (feeding areas), and timing of feeding activities.

Cole (1958) describes four requirements for determining the existence of exploitive competition among herbivores: 1) the potentially competing species must use the same area; 2) they must both use the same forage plants; 3) the forage plants must be important sources of food for both species involved; and 4) the forage plants being used must be in limited supply or deteriorating as a result of combined use. After comparing the interactions between ungulates and snowshoe hares, Leonard (1980) examined an additional condition- the species must use the same feeding space in RMNP.

In Samoil's study (1979), the first condition of competition was examined through selection of representative vegetation cover types and through track count surveys conducted to determine whether hares and ungulates occupied that same habitats in the same areas. The condition was satisfied (Samoil 1979).

The second condition, that of use of the same browse species, was investigated by tracking animals and recording the species of plants on which they browsed. Data presented in Trottier and Samoil (1978) showed that there was a considerable overlap in use of the browse resource by the ungulates and snowshoe hares. To quantify the degree of overlap in usage of woody browse species, and index of similarity (Krebs 1972) was calculated based on the number of species of browse occurring in the late winter diets of snowshoe hares, moose, elk, and deer. The amount of overlap varied from 47.6 to 66.7%. The second condition also appeared to be satisfied (Samoil 1979).

The third condition, that the browse species must be important food sources for the animal species involved, would also seem to be satisfied. Beaked hazel was the most frequently used species by snowshoe hares, moose, elk and white-tailed deer, and nine species of browse accounted for 95% of the diets of these four herbivores (Trottier and Samoil 1978).

The fourth condition, if the forage plants being used are in limited supply, was examined by Trottier and Hutchison (1980). They noted that beaked hazelnut was in good to excellent condition at all range transects, and that its utilization appeared to be far less than production in all situations. As well, they found that at sites where beaked hazelnut was frequently browsed, productivity appeared greater because annual growth and suckering were stimulated by the impact of utilization. The results imply that this condition was not satisfied.

The last condition, if the species used the same feeding space was addressed by Leonard (1980). He found that use of ungulate feeding sites by hares was low since those sites were mostly openings in the forest with poor cover for hares if the snow was thick. However, as hare numbers increase such marginal sites may be occupied by dispersing individuals because the food supply would be attractive. Samoil (1979) and Leonard (1980) reported that the percentage of plants browsed by hares that were also browsed by ungulates increased as the winter progressed. Elk and white-tailed deer take the bulk of their food from the same stratum, but moose take the bulk of their food from a higher stratum than other ungulates. Hares are capable of overlapping vertically with ungulates (Trottier and Samoil 1978, Leonard 1980) depending on snow thickness and shrub stem diameter. Moreover, girdling of stems by hares kills plants and constitutes an additional mode of vertical overlap. Therefore it appears that elk and hare use the same feeding space, but moose and hare do not.

In summary, four of the five conditions are satisfied for elk and three of the five conditions are satisfied for moose. Competition, then, may occur at selected times, especially for hares and elk. The model of the snowshoe hare cycle proposed by Keith and Windberg (1978) postulates a hare-vegetation interaction in the peak years, during which overbrowsing causes deterioration in range condition, which in turn contributes to a decline in the hare population. Given the similarity in food habits of hares and the ungulates studied, if the vegetation is damaged by one species (i.e. hares) to the detriment of other species dependent on that resource (i.e. elk and moose), poor performance by the dependent species would be expected. As Trottier and Samoil (1978) have suggested, this might explain the observations by Rounds (1976) that elk and moose populations

survived the mild winters of 1972-73 in poor condition and suffered significant losses in their cow-calf cohorts. This followed a regional peak in hare abundance during the 1970-71 period (Rusch *et al.* 1978). There is evidence, however, that suggests that competition does not occur when the supply of hazel is sufficient to support several herbivore species (Trottier and Samoil 1978).

### **3.5.5 Winter Severity**

Trottier and Hutchison (1982) examined ungulate-winter severity relationships in RMNP from 1977-1980. The following section is largely based on their study.

#### ***The Winter Severity Index***

The apparent inseparability of factors in the winter environment has led researchers to devise indices of winter severity which express the cumulative effects of those factors on the energy budgets of ungulates. There are no reports which present a fully satisfactory equation defining the relationship between winter regime and animal energetics. Each species has a unique strategy for coping with winter, and each area has a unique combination of parameters that influence ungulates; therefore, individual indices have to be developed (Trottier and Hutchison 1982).

A severity index is useful because it recognizes that some factors in the winter environment are inseparable and, whereas one factor alone may not be critical in influencing the populations, a combination of factors may. However, severity indices reflect winter-long average or cumulative conditions and, consequently, are insensitive to short periods of extremely severe weather (Coughenour and Singer 1996). For example, alternative periods of warm and freezing temperatures can be detrimental to elk or moose because the insulating capacity of their coats might be decreased. If this is the case, then it is possible that an index could not pick up this event because the event would be averaged over time and therefore lose its significance.

### **Stelfox's WSI**

From 1977 to 1980, winter severity data were collected in RMNP and a winter severity index (WSI) was calculated for those years according to Stelfox (1976). A monthly winter severity index (November to April) was derived using the following additive relationship:

$$MSI = T + D + H + MT \text{ (if } > 0^{\circ} \text{ C) or } -MT \text{ (if } < 0^{\circ} \text{ C)}$$

T = mean snow thickness (cm) (this is the reading at the end of the calculation period).

D = mean snow density x 100.

H = snow hardness

(0 = supports nothing; 5 = supports hares, lynx; 10 = supports squirrels, mink, porcupine; 15 = supports wolves, coyotes; 20 = supports deer, sometimes elk, moose).

MT = mean temperature ( $^{\circ}$  C).

A yearly severity index (WSI) was calculated as follows:

$$WSI = \sum MSI + GU$$

MSI values were derived from November through April

GU = spring green-up value

[the difference between the date of green-up- when grass growth on grassland ranges reaches 10 cm- and the normal green-up date for the Park (May 11th) (Dolan and Tempny 1980)].

### **RMNP Ungulate- Winter Severity Relationships 1977-1980**

A die-off of elk and deer in the Park during late winter 1978-79 coincided with abnormally high snowfall, late snow melt and delayed green-up of the vegetation. The subsequent calf crop for elk was low and together the effects of winter accounted for a population decrease. There was insufficient information on the reaction of moose to these conditions to observe the impact of such things as late green-up and low temperatures on its population dynamics.

Mobility of adult elk was restricted only during late winter 1978-79, while moose mobility was not likely adversely affected except for a brief period during late April 1979. Elk calves were likely restricted in movement in March of 1979-1980 and from February to May of 1978-79. Moose calves were likely only affected in late winter to early spring of 1978-79. When snow cover restricts mobility, ungulates travel in dense

canopy white spruce and mixedwood which have good snow interception qualities. These vegetation types account for only 14% of the study area; therefore overlap in range use is likely during prolonged periods of thick snow cover. Observations during March 1979 indicated that elk avoided meadowland and deciduous forest by moving into the small amount of mixedwood and coniferous habitat, whereas moose were seen regularly throughout the study area mostly in deciduous stands (Trottier and Hutchison 1980).

Snow conditions influence vulnerability of ungulates to predation. In late winter 1978-79 snow crusts in the Gunn Lake area supported wolves and coyotes, but ungulates penetrated the crust. Carbyn (1980) reported increased kill rates and surplus killing by wolves in the study area during this period.

Increases in snow thickness coincided with reduced intake of grass, sedge and forbs by all ungulates in the study area. This effect was more dramatic for elk than for moose or deer because from October through May, 60 to 70% of the elk diet may be obtained from grazing sedges and grasses if snow is absent, patchy, or less than about 30 cm thick and of low density (Trottier and Hutchison 1982).



## **CHAPTER 4**

### **METHODS**

#### **4.1 INTRODUCTION**

This chapter provides an overview as to the methods that were used in the study of population dynamics in RMNP. First, data were compiled from RMNP records, Manitoba Department of Natural Resources (DNR) and Environment Canada. Since historical data sets provided most of the information needed in this study, many of the methods used in this study can be found in an appendix. Trends in elk and moose in RMNP were then analyzed in relation to other parameters for the period 1963-1996 by simple methods of time series analysis. Finally, a conceptual model was created to visually represent the factors that were found to be significant in contributing to elk or moose population dynamics.

#### **4.2 COMPILATION OF DATA**

##### **4.2.1 Ungulate Aerial Survey Results**

Moose and elk population estimates from the 1963-1996 aerial surveys were compiled from RMNP records (Figure 2). The survey usually took place for 4-6 days in early to mid-February each year. Yearly counts were assessed for uniformity of method and validity (i.e. recommendations by the report author to ignore results). The quantitative results from the 1974 and 1975 survey (Rounds 1974, 1975) were ignored since a different aerial survey technique was used. All other aerial surveys were considered valid for further statistical analysis. An expanded description of the survey technique can be found in Section 3.4.2.

#### **4.2.2 Hunter Success Data**

Annual harvest estimates for elk and moose were obtained from the Department of Natural Resources (DNR) for Game Hunting Areas (GHAs) 23 and 23A surrounding RMNP (Figure 5) for the period 1969-1996 (Figure 6). Each year, harvest statistics for various species of big game are estimated by a questionnaire method, conducted by DNR. This methodology is described in Appendix B (Hummelt 1990).

#### **4.2.3 Beaver Aerial Survey Results**

Beavers may influence ungulate population trends because the caches they build modify water levels and therefore the amount of habitat available for ungulates. Beaver population trends were taken as an index from beaver cache counts (4-7 beavers/cache; Trottier 1982) from the 1973-1995 aerial surveys (no surveys were flown prior to 1973) (Figure 7). These data were compiled in a similar manner as the ungulate surveys. The surveys were flown in October as soon as leaf-fall was complete and, if it was possible, before freeze-up (since ice on ponds and subsequent snowfall would make it difficult to see food caches. Trottier (1980) described the sampling technique for the beaver aerial surveys (Appendix B).

#### **4.2.4 Wolf Ground Survey Results**

Wolf population estimates were taken from the 1975-1996 predator ground survey reports (Figure 8). Estimates were mainly derived from an intense five-day wolf tracking survey in February. Hoggins (1993) described the methodology for the ground surveys (Appendix B).

#### **4.2.5 Snowshoe Hare Track Survey Results**

Studies of abundance of snowshoe hares in RMNP were initiated in the winter of 1977 while hare populations were increasing, and continued until 1989 to provide a temporal index of hare abundance and distribution (Figure 9). Samoil (1979) described the methodology (Appendix B).

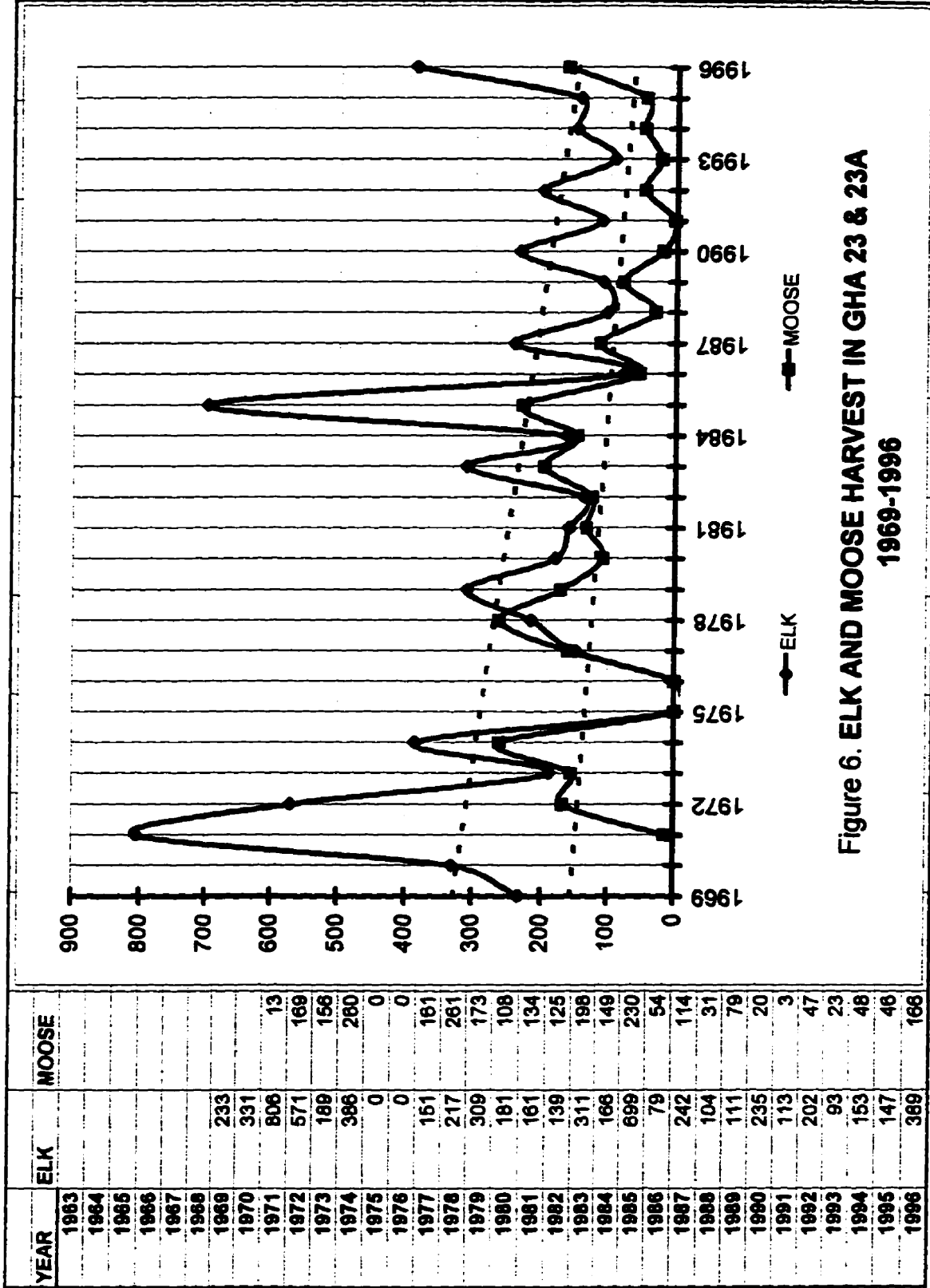


Figure 6. ELK AND MOOSE HARVEST IN GHA 23 & 23A  
1969-1996

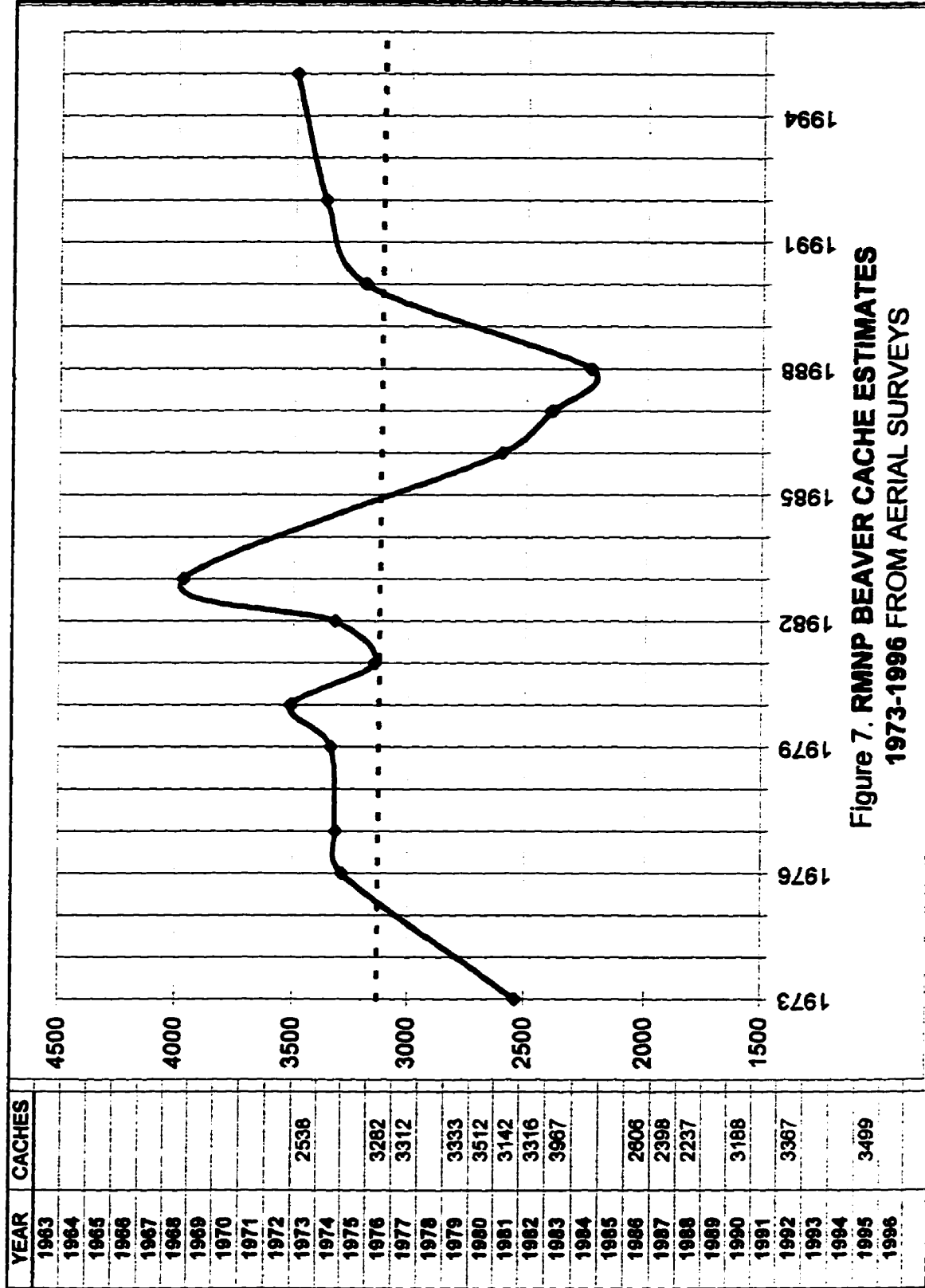


Figure 7. RMNP BEAVER CACHE ESTIMATES  
1973-1996 FROM AERIAL SURVEYS

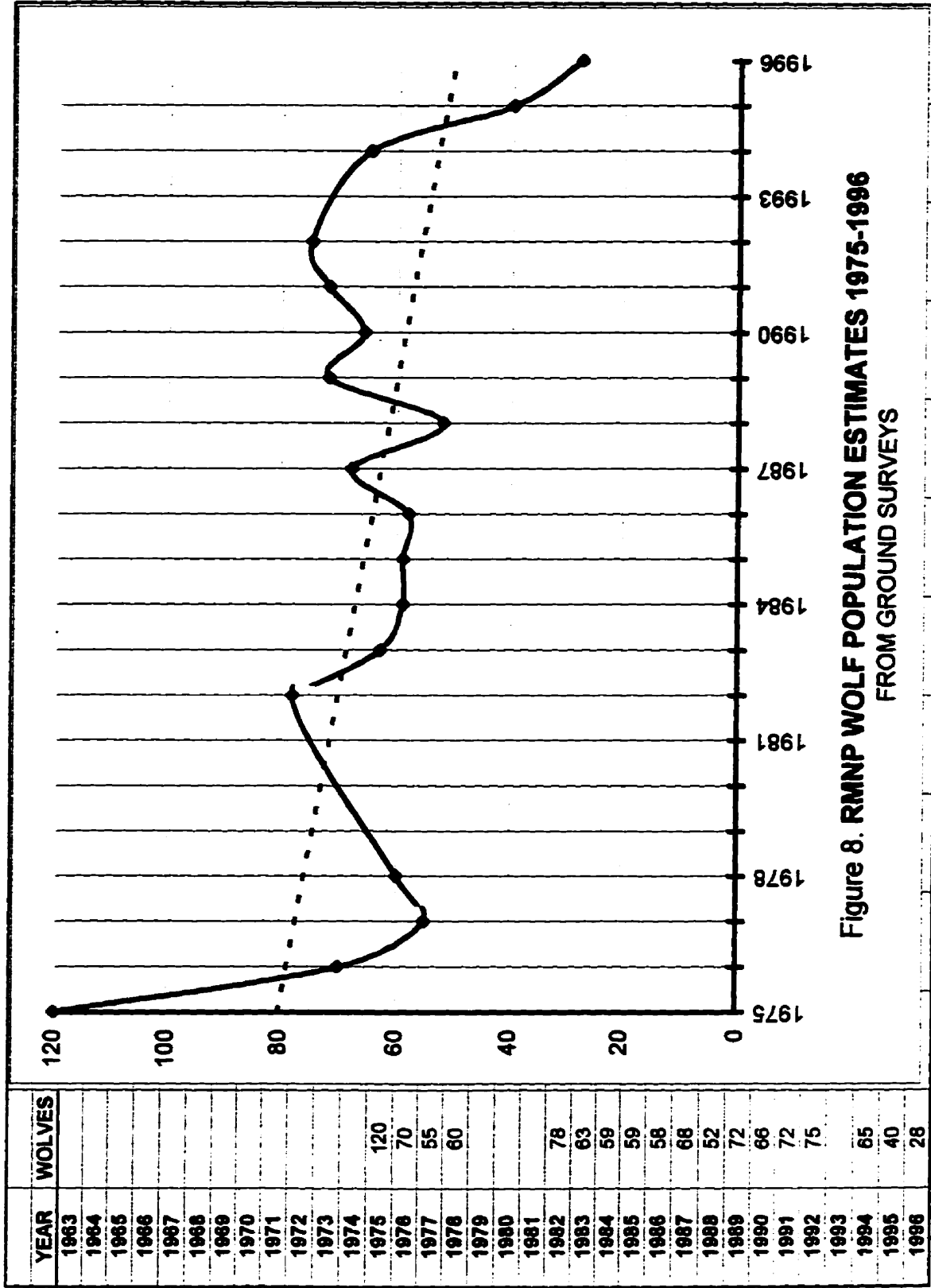


Figure 8. RMNP WOLF POPULATION ESTIMATES 1975-1996 FROM GROUND SURVEYS

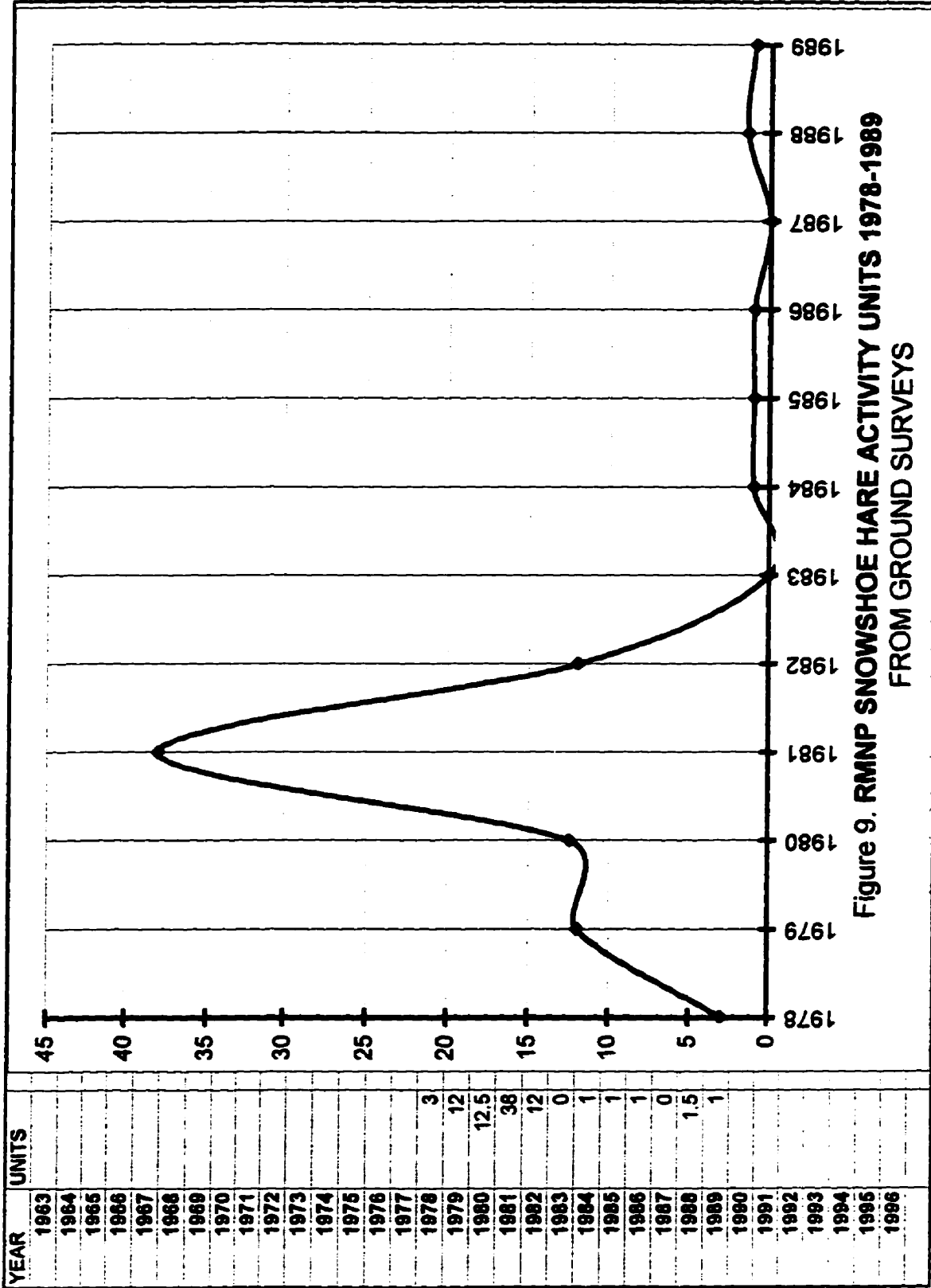


Figure 9. RMNP SNOWSHOE HARE ACTIVITY UNITS 1978-1989 FROM GROUND SURVEYS

#### 4.2.6 Winter Severity Data

From 1977 to 1980, winter severity data were collected in RMNP and a winter severity index (WSI) was calculated for those years according to Stelfox (1976). Unfortunately, most variables included in the WSI were not sampled in the years following 1980 (mean snow thickness, mean snow density, snow hardness and spring green-up value). It was necessary to modify Stelfox's WSI (p. 45) to include data that were available to create a WSI from 1967-1989 (Figure 10).

##### *A Modified WSI*

Daily and monthly temperature and precipitation data were acquired from Environment Canada from 1967-1989 (consistent data were not available from 1990-1996). Winter weather parameters (snow accumulation, snow density, mean temperature and number of degree days) were incorporated into a modified WSI for this period. Monthly winter severity indices (November to April) were derived using the following additive relationship:

$$MSI = A + MT \text{ (if } > 0^{\circ} \text{ C) or } -MT \text{ (if } < 0^{\circ} \text{ C)}$$

A = snow accumulation (cm) for that month

MT = mean temperature ( $^{\circ}$  C) for that month

A yearly severity index (WSI) was calculated as follows:

$$WSI = \sum MSI + GU + DI$$

MSI values were derived from November through April

GU = in theory, the difference between the date of green-up for that year and the normal green-up date for the Park (May 11th). The mean degree day requirement for the park (estimated at 44.7 + or - 2.6 days) can be used to estimate green-up of previous years by examining temperature records and determining:

$$\sum [h - 12.22^{\circ} \text{ C}] = 44.7 = \text{mean degree day requirement for RMNP}$$

h = maximum daily temperature

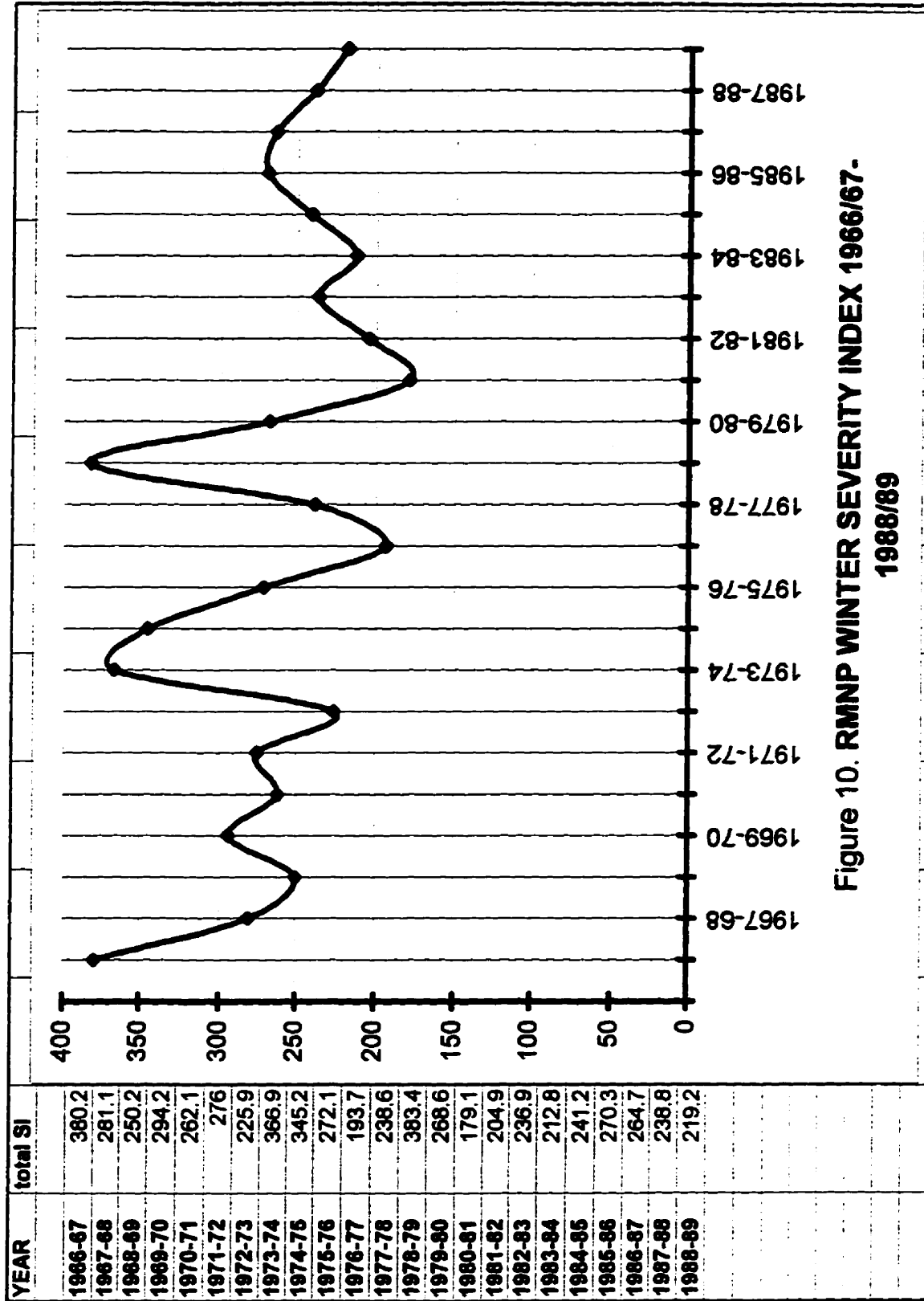


Figure 10. RMNP WINTER SEVERITY INDEX 1966/67-1988/89



DI = an index representing the snow density (measured only in February and March) for a particular year. The index was calculated as follows:

$$DI = [d(\text{feb}) + d(\text{march})] * 200$$

Note: It was necessary to create a snow density index that was proportional to Stelfox's (1976) mean monthly snow density (calculated from November to April). Therefore, the density values for February and March were multiplied by a factor of two hundred.

Since the validity of Stelfox's WSI in RMNP has not been tested, and due to the substantial modification of the WSI, each parameter included in the WSI (temperature, snow accumulation, snow density and green-up value) was analyzed individually. As well as examining mean winter temperatures (incorporated into the WSI), maximum winter temperatures and minimum winter temperatures were also examined as potentially more appropriate indicators of winter severity. To further analyze the winter weather parameters, it was necessary to modify the MSI values (temperature and snow accumulation) and represent them as yearly values. These yearly values (summed from monthly values calculated from November to April) were calculated as follows:

$$MEANTI = \sum -MEANT$$

$$MINTI = \sum -MINT$$

$$MAXTI = \sum -MAXT$$

$$ATOT = \sum A$$

TI = yearly winter temperature index (° C)

T = monthly temperature (° C)

ATOT = yearly snow accumulation (cm)

A = monthly snow accumulation (cm)

### 4.3 ANALYSIS OF DATA

This analysis was exploratory in nature, and looked for structure in multivariate data. Therefore it was necessary to initially graph each relationship so general patterns of structure could emerge. Secondly, correlation analysis was used to quantify the strength of the relationship. In correlation analysis, the degree to which two variables are interdependent, or vary together, is estimated. Unlike regression analysis, one variable is not expressed as a function of the other, and there is no distinction between independent and dependent variables (Sokal and Rohlf 1995).

Due to the complex population interactions, though, direct correlations may not give accurate results. This is primarily due to the fact that there can be lag effects of a particular factor on the elk or moose population. To make the interactions even more complicated, we are dealing with synergistic effects in population studies, or the joint action of each discrete factor that results in a greater effect than the sum of their effects when acting independently.

To account for the fact that there may be lag effects, auto- and cross-correlation analyses were undertaken to determine what the lag effect might be, if any. Autocorrelation is an approach to time-series analysis whereby the evolution of a process through time can be described. A series of quantities called sample correlation coefficients measure the correlation between observations at different distances apart (correlation between  $X_t$  and  $X_{t+k}$ ). Similarly, cross-correlation also measures correlation between successive observations, but focuses on observations in two time series (correlation between  $X_t$  and  $Y_{t+k}$ ). Sets of auto- or cross-correlation coefficients were presented using a graph called a correlogram in which  $r_k$  was plotted against the lag  $k$ . Inference was based on these functions and is known as an analysis in the time domain (Chatfield 1989). Under the hypothesis of normality, confidence intervals ( $\alpha = 0.05$  and  $\alpha = 0.10$ ) were computed and drawn on the correlogram, in order to test whether the autocorrelation is significantly different from zero (Legendre and Legendre 1983). When the number  $n$  of terms in a series is high,  $r_k \sqrt{n-1-k}$  is normally distributed, so that the hypothesis  $r_k = 0$  must be rejected when

$$r_k > \pm \frac{1.96}{\sqrt{n-1-k}} \text{ (probability } < 0.05)$$

$$r_k > \pm \frac{1.64485}{\sqrt{n-1-k}} \text{ (probability } < 0.10)$$

k = lag period

n = number of observations

Significant correlation coefficients were examined together with scatterplots since the same coefficient can result from very different underlying relationships. For example, a correlation coefficient of zero can result from a completely random plot of variables, or a cluster of points more or less forming a concave. As well, a few outlying points can result in a significant correlation, where most of the points are clustered in no discernible pattern. Scatterplots were graphed for all relationships that were found to be significant.

#### 4.4 DEVELOPMENT OF CONCEPTUAL MODELS

Once the results were computed, conceptual models were developed for both elk and moose in an attempt to outline the factors examined in this study that were potentially influencing the populations. The conceptual models did not simply represent the results of the statistical analyses, though. Instead, the models attempted to incorporate any inferences that were made after careful consideration of the results of the analyses, and the recent literature. Thus, these factors were determined from an in-depth consideration of the results of the statistical analyses, literature findings, and local observations. Further discussion of the rationale supporting the models is provided throughout Chapter 5.

## CHAPTER 5

### RESULTS AND DISCUSSION

#### 5.1 INTRODUCTION

This chapter presents exploratory data analyses performed on available data to further understand the relationship between ungulate populations and various parameters. It explores several approaches to time series analysis, focusing on 1) the analysis of two time series by an initial plotting on the data series, and 2) more quantitative approaches, i.e. autocorrelation and cross-correlation analyses.

Twelve parameters were examined in this study against elk and moose populations. For elk, nine of the twelve parameters were statistically significant ( $\alpha = 0.05$  or  $\alpha = 0.10$ ) when correlated with the elk population. Many of these parameters had a lag effect on the elk population of up to four years. Similarly, for moose, eight of the twelve factors examined were found to be statistically significant with lag effects. Tables 4 and 5 represent a summary of the results of these analyses.

Table 4. Summary Table of Significant Relationships for Elk

<i>Parameter</i>	<i>Correlation</i>	<i>n</i>	<i>Lag</i>	<i>Possible Explanation</i>
Elk	0.4668 <sup>†</sup>	18	1-year	• Elk population one year is dependent on the elk population the year before.
Hunter Harvest	-0.4812 <sup>*</sup>	22	2-year	• High harvest of cows reduces recruitment of calves, causing delays in population effects.
Beavers	0.6271 <sup>*</sup>	14	none	• Beavers and elk are reacting negatively to severe winters and positively to mild winters.
Wolves	none	-	-	
Snowshoe Hare	0.5628 <sup>†</sup>	10	none	• Hare and elk are reacting negatively to severe winters and positively to mild winters.
Winter Severity Index	0.5998 <sup>*</sup>	19	4-year	• Winter mortality of calves, reduced recruitment rate and reduced fecundity cause delays in population effects.
• Temperature				
• Mean	0.5310 <sup>*</sup>	17	none	• Aerial survey bias or immediate mortality due to extreme temperatures.
• Min.	0.4800 <sup>†</sup>	17	none	
• Max.	0.5481 <sup>*</sup>	17	none	

• Snow Accumulation	0.6047*	19	4-year	• Winter mortality of calves, reduced recruitment rate and reduced fecundity cause delays in population effects.
• Snow Density	none	-	-	
• Spring Green-up	none	-	-	

**Table 5. Summary Table of Significant Relationships for Moose**

<i>Parameter</i>	<i>Correlation</i>	<i>n</i>	<i>Lag</i>	<i>Possible Explanation</i>
Moose	0.6497* 0.4865 <sup>+</sup>	18 19	1-year 2-year	• Moose population one year is dependent on the moose population the years before.
Hunter Harvest	-0.4628 <sup>+</sup>	20	4-year	• High harvest of cows reduces recruitment of calves, causing delays in population effects.
Beavers	0.5908* 0.6566*	14 12	none 1-year	• Beavers and moose are reacting negatively to severe winters and positively to mild winters. • Beavers are creating favorable habitat for moose.
Wolves	-0.5839*	17	none	• Both populations are acting independently of each other.
Snowshoe Hare	0.5967 <sup>+</sup>	10	none	• Hare and elk are reacting negatively to severe winters and positively to mild winters.
Winter Severity Index	none	-	-	
• Temperature • Mean • Min. • Max.	none 0.4121 <sup>+</sup> none	18	1-year	• Winter mortality of calves, reduced recruitment rate and reduced fecundity cause delays in population effects.
• Snow Accumulation	0.4821 <sup>+</sup>	19	4-year	• Winter mortality of calves, reduced recruitment rate and reduced fecundity cause delays in population effects.
• Snow Density	-0.4756 <sup>+</sup>	19	2-year	• Winter mortality of calves, reduced recruitment rate and reduced fecundity cause delays in population effects.
• Spring Green-up	-	-	-	

\* = statistically significant,  $\alpha = 0.05$  (Legendre and Legendre 1983)

<sup>+</sup> = statistically significant,  $\alpha = 0.10$  (Legendre and Legendre 1983)

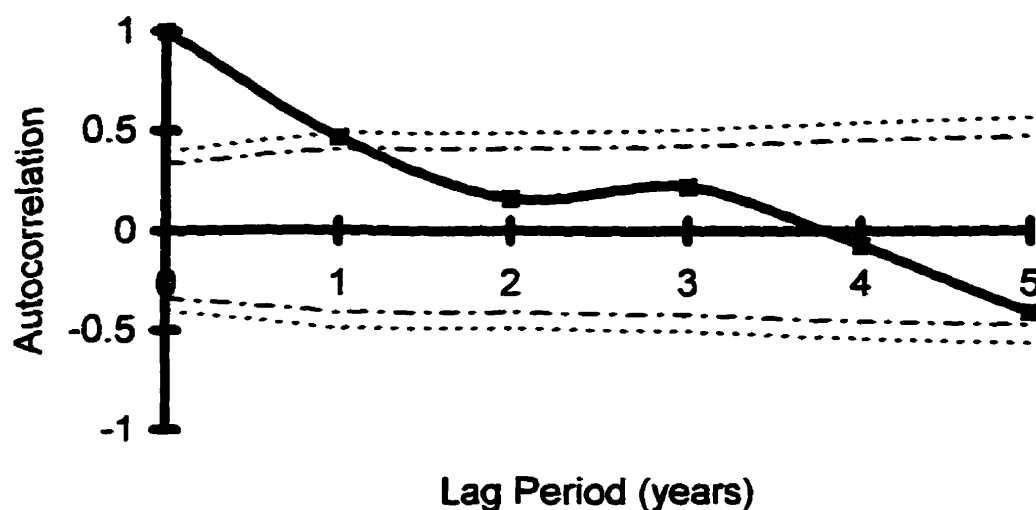
Each of the following sections explores a relationship between elk or moose and another parameter by presenting a line graph and correlogram of the relationship. (All analyses of relationships that were not found to be statistically significant can be found in Appendix C). Scatterplots of the significant relationships can be found in Appendix D. Tables that represent values plotted in the correlograms (for significant relationships) can be found in Appendix E. A discussion follows each section, examining the possible reasons why the relationship and time lags, if found, might exist.

## 5.2 AUTOCORRELATION ANALYSIS

### 5.2.1 Elk

The elk population in a particular year was significantly correlated to the elk population in the previous year (i.e. a one-yr. lag) ( $r=0.4668$ ,  $n=18$ ,  $p<0.10$ ) (Figure 11).

Figure 11. Correlogram- Elk



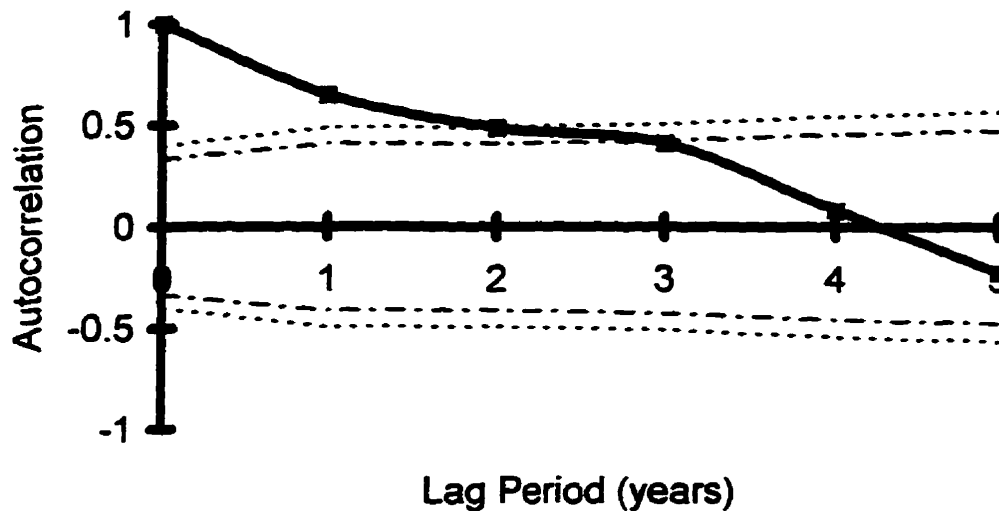
-----  $\alpha = 0.05$  confidence interval (Legendre and Legendre 1983)  
 .....  $\alpha = 0.10$  confidence interval (Legendre and Legendre 1983)

The relationship observed in the correlogram is not at all unexpected, and characteristic of a short-term correlation- a fairly large value of  $r_t$  followed by a few further coefficients which, while greater than zero, tend to get successively smaller (Chatfield 1989). It is expected that the elk population in a particular year is dependent upon the population the year before, and less and less influenced by the population in each preceding year. Thus the population in a particular year acts as a baseline for the population the next year, with some modifications (either an increase or a decrease due to a variety of factors).

### 5.2.2 Moose

The moose population was statistically significant and positively correlated with the moose population the year before ( $r=0.6497$ ,  $n=18$ ,  $p<0.05$ ). The moose population was also significantly correlated to the moose population two years before ( $r=0.4865$ ,  $n=19$ ,  $p<0.10$ ) (Figure 12).

Figure 12. Correlogram- Moose

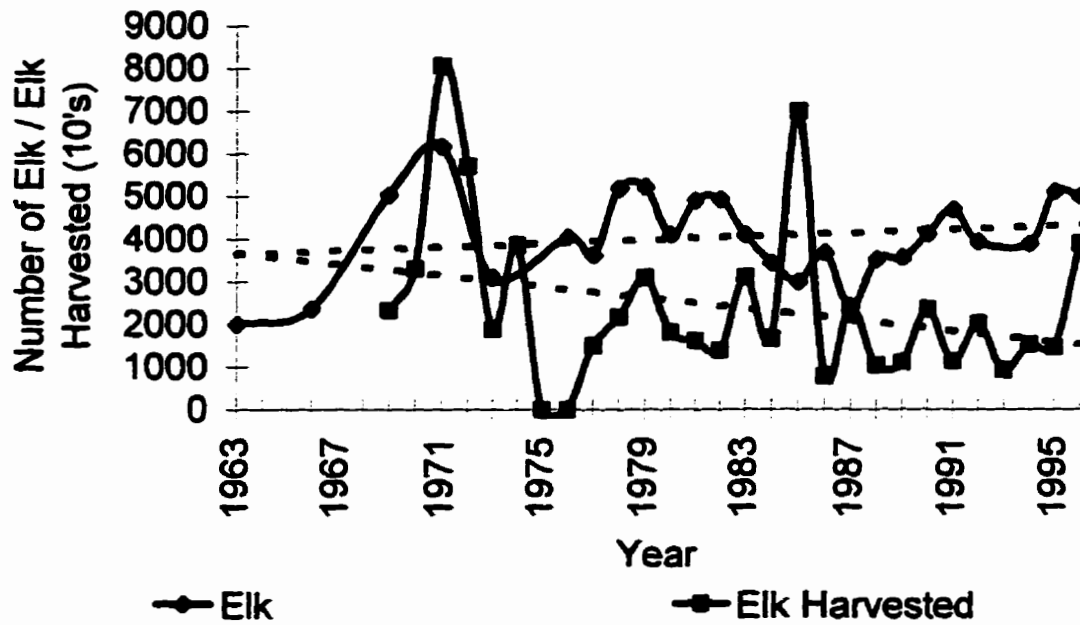


The relationship observed in the correlogram follows the same pattern as with the elk autocorrelation. However, it can be noted that the moose exhibit a much stronger positive correlation with a one-year lag, as well as a statistically significant and strong positive correlation with a two and three-year lag, respectively. This discrepancy may relate to age-specific events such as the length of time to reach sexual maturity. Whereas elk tend to reach sexual maturity at two years of age (Murie 1951), moose do not reach sexual maturity until approximately four years of age (Skuncke 1949). With a longer time to reach sexual maturity, moose could be expected to have a strong positive correlation with a two-year and a three-year lag. For example, a moose that was born in 1992 would still be immature in 1995, 3 years later; whereas an elk that was born in 1992 would be mature in 1994, causing the age structure of the population to change within a shorter period.

### 5.3 RELATIONSHIP BETWEEN UNGULATES AND HUNTER HARVEST

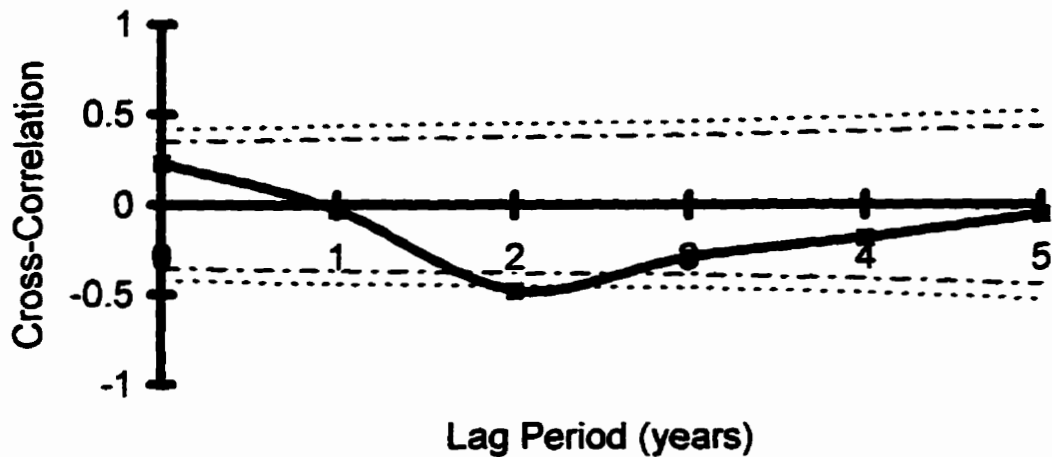
#### 5.3.1 Elk and Hunter Harvest (Figure 13)

Figure 13. Number of Elk vs. Elk Harvested



Correlation analysis produced a statistically significant correlation coefficient with a 2-year lag effect ( $r = -0.4812$ ,  $n=21$ ,  $p < 0.05$ ) (Figure 14).

Figure 14. Correlogram- Elk vs. Elk Harvested





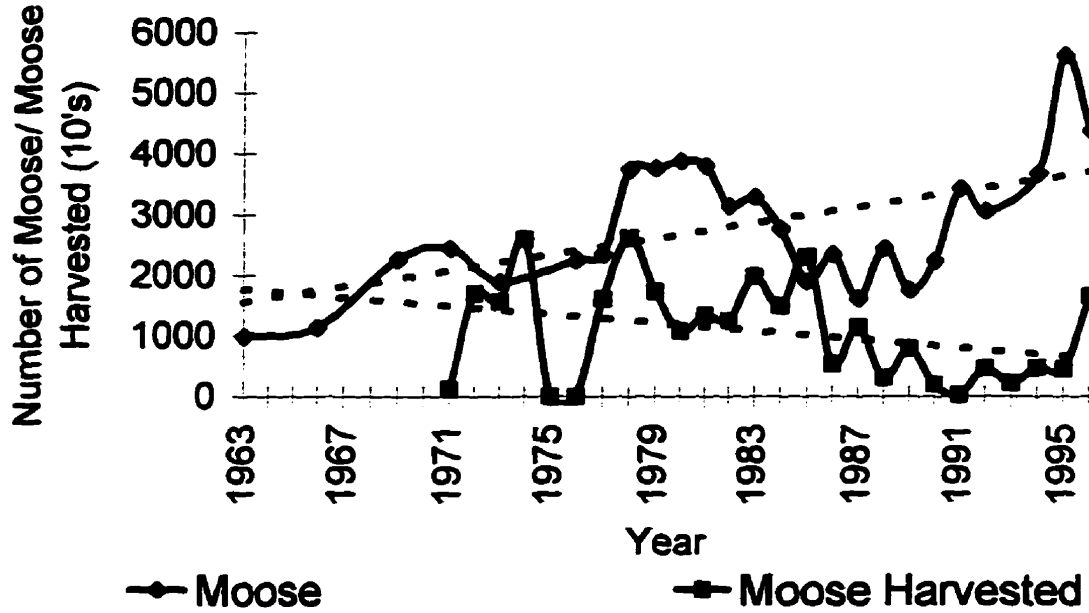
Although these analyses may suggest that hunter harvest does have some influence on the elk population trends, the scatterplot of this relationship showed that there were some outlying points (Appendix D). These outlying points could be misrepresentative of the trend, but since both points are representing years where the elk harvest was large, one must be cautious in removing them.

If it is assumed that the negative correlation is valid, a lag of two years might seem illogical- if an elk is harvested in a particular year, there will be one less elk that year, and the reduction should show up that same year (the elk are harvested before elk numbers are estimated in a particular year). For example, if a cow is harvested in 1991 (in the 1990/91 season, all elk harvested were taken as being harvested in 1991), then one would expect a high negative correlation with no lag effect, since cows taken and their potential calves that would not be born in the summer would doubly negatively impact the elk population that year.

In fact, a negative correlation with a two-year lag implies that after a high hunter harvest the elk population declines for two years. A *two-year* lag effect might suggest that the negative correlation relates to both the life history of elk (i.e. that the females do not produce offspring until they are two years of age) and that harvest of cows has traditionally been uncontrolled. If elk cows are being heavily harvested, as Table 1 suggests, then it could make sense that the two years following a high elk harvest may affect the elk population dynamics. Cows that are 4-12 years old are the experienced breeders, and ensure population survival (Flook 1970). In years of high harvest, these elk cows that are harvested will not be able to produce calves for the following summers, causing the population to decline. However, it must be assumed that a harvest will increase calf survival, since winter competition will be reduced as the number of senescent cows in the population decreases (Taber *et al.* 1982). If this is true, then harvest of cows actually immediately benefits calves, the future source of new offspring. Thus it is possible that two years after a high hunter harvest, the elk population may be able to recover due to the survival of many of these calves.

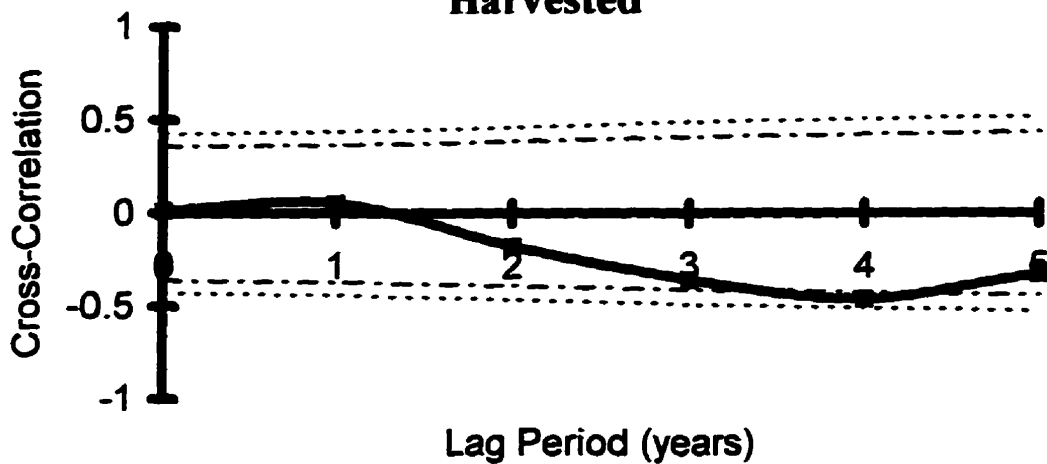
5.3.2 Moose and Hunter Harvest (Figure 15)

Figure 15. Number of Moose vs. Moose Harvested



Correlation analysis produces a statistically significant negative correlation coefficient with a 4-yr. lag ( $r=-0.4628$ ,  $n=20$ ,  $p<0.10$ ) (Figure 16).

Figure 16. Correlogram- Moose vs. Moose Harvested



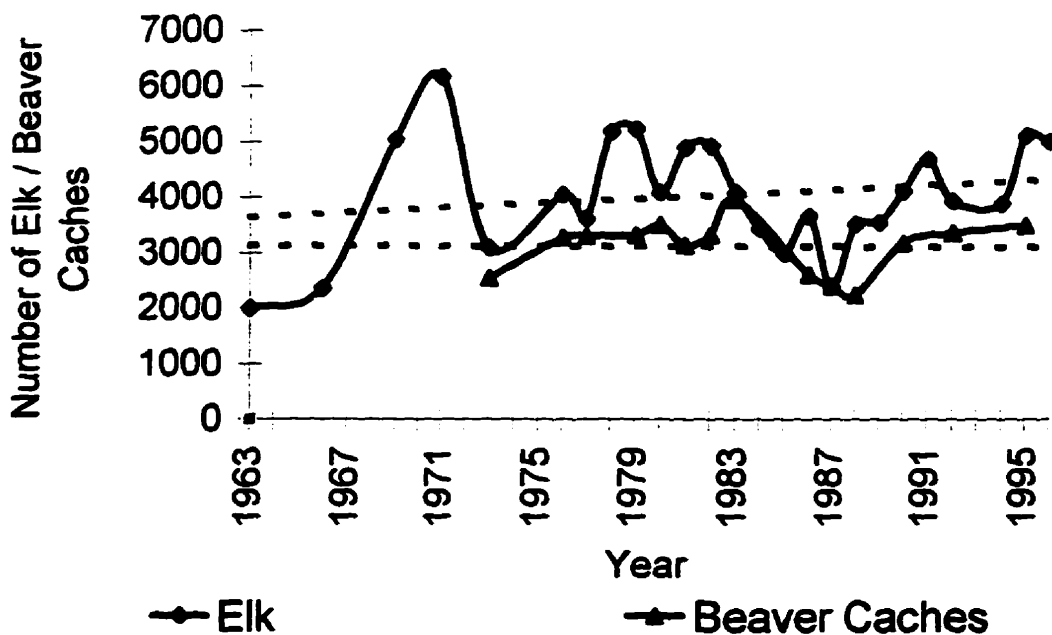
An examination of the scatterplot creates some uncertainty as to if a relationship actually exists, though (Appendix D). The distribution of the points is rather scattered and no clear negative correlation is evident. However, if we assume that hunter harvest does have some influence on the moose population trend, it is possible that, again, the four-year lag effect has something to do with the life history of moose and the high proportion of cows harvested.

The arguments are essentially the same as for elk. If moose cows are being heavily harvested, as the numbers may suggest, in years of high harvest, these experienced breeders would not be able to produce calves in the summers to follow. However, assuming that most of the female calves that survived that winter will begin to produce offspring in four years, the moose population may recover four years later.

## 5.4 RELATIONSHIP BETWEEN UNGULATES AND BEAVERS

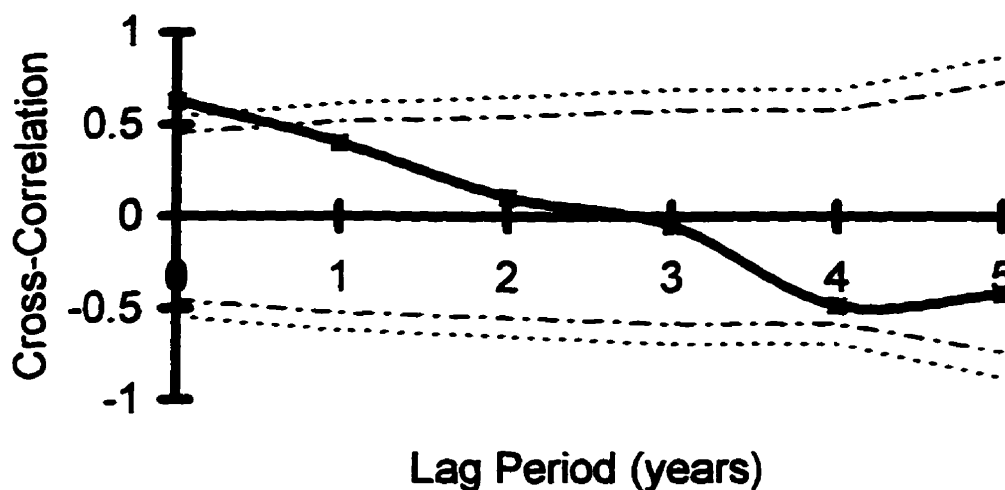
### 5.4.1 Elk and Beavers (Figure 17)

Figure 17. Number of Elk vs. Beaver Caches



Correlation analysis illustrated that there is a statistically significant positive correlation with no lag effect (i.e. the population fluctuations of beaver and elk are in virtual synchrony) ( $r=0.6271$ ,  $n=14$ ,  $p<0.05$ ) (Figure 18).

**Figure 18. Correlogram-Elk vs. Beaver**



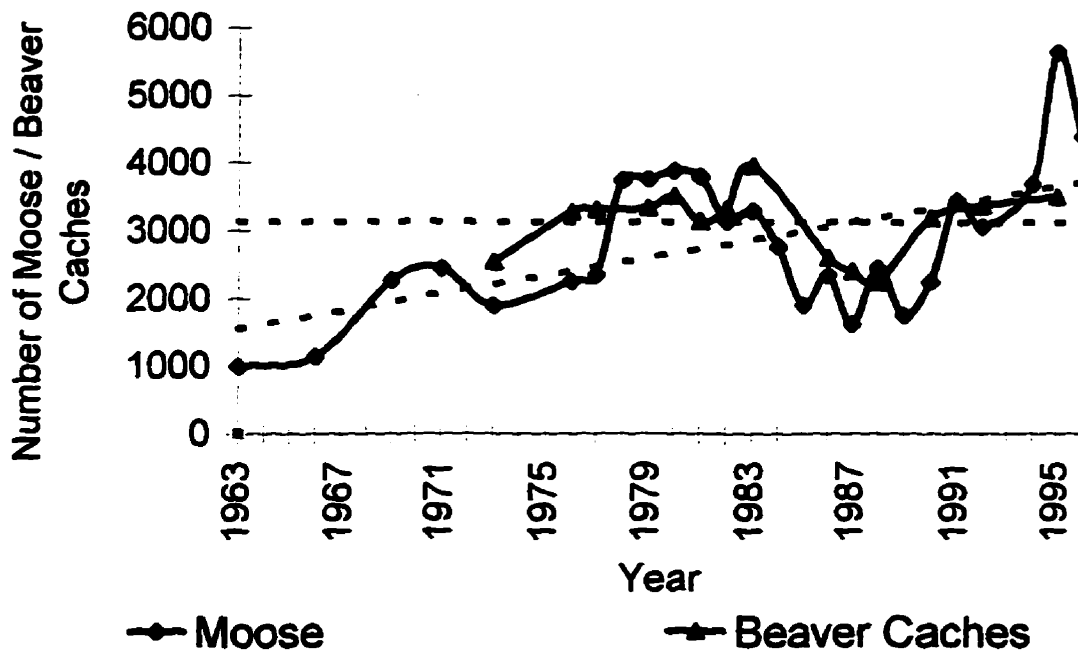
The explanation for this relates to the time of year that the aerial surveys are done. Since the beaver population is estimated in the fall (mid-October) and the ungulate populations are estimated in late winter (early to mid- February) of a particular year, it is quite possible that some underlying factor, such as winter severity, is causing both of the populations to fluctuate virtually in perfect synchrony.

Beavers have unique adaptations to survive winter with limited access to forage apart from woody stems stored in an underwater food cache and some use of aquatic macrophytes (Jenkins and Busher 1979). However, violent spring breakups and melt after a high winter snowfall can raise water levels in streams and may destroy lodges and occupants or drown large numbers of beaver under the ice (Hakala 1952, Boyce 1974). Starvation at northern latitudes has also been noted as a mortality factor (Gunson 1970, Bergerud and Miller 1977). Dyck and MacArthur (1993) suggested that, based on previous estimates of the energy content and digestibility of forage cached prior to freeze-up, it is unlikely that the winter energy requirements of this species can be met solely from the submerged food cache. These calculations suggest that northern beavers

balance their energy budget in winter by supplementing food resources in the cache with aquatic vegetation acquired away from the pile. As well, the beaver is most vulnerable to predation by mammalian predators such as wolves (Young and Jackson 1951, Mech 1966) when it is away from water. Where these large predators occur, food shortages that require beaver to forage great distances from water cause greater exposure to predation.

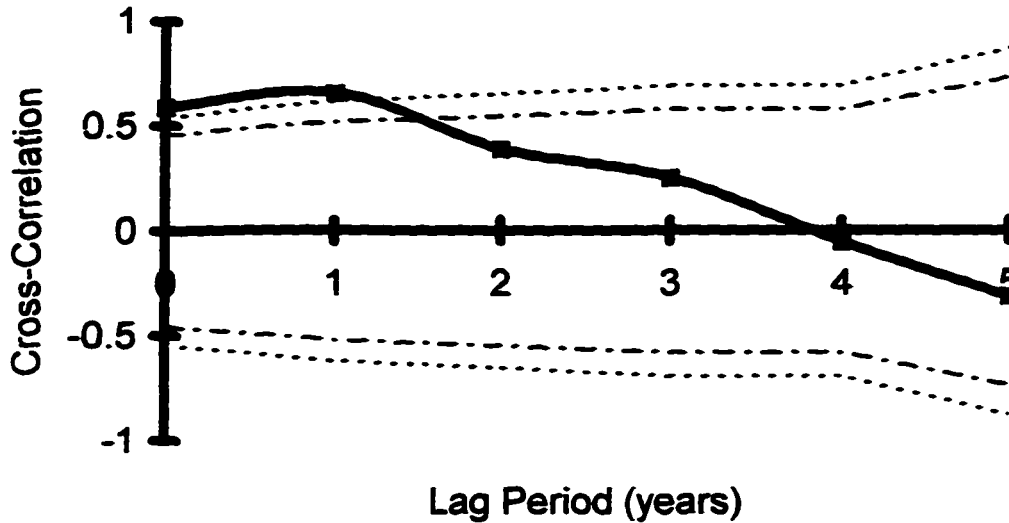
5.4.2 Moose and Beaver (Figure 19)

Figure 19. Number of Moose vs. Beaver Caches



There was a statistically significant correlation coefficient for both no lag ( $r=0.5908$ ,  $n=14$ ,  $p<0.05$ ) and a 1-yr. lag ( $r=0.6566$ ,  $n=12$ ,  $p<0.05$ ) (Figure 20).

Figure 20. Correlogram- Moose vs. Beaver



Again, no lag suggests that there is some underlying factor influencing the moose and beaver populations, as discussed above.

If there is a 1-year lag effect, this would suggest that the beaver population is somehow positively influencing the moose population trend, perhaps by creating more favorable moose habitat (i.e. as beavers increase in number, so does the amount of land flooded and potentially the amount of habitat available for moose).

For example, if the beaver population is found to be high in 1995 (measured in the fall), then, in the summer of 1995 the beaver may have had an opportunity to create favorable habitat for moose, allowing the population to flourish (including newborn moose calves). An increase in the population of moose, then, could be detected in the 1996 ungulate population estimates.

## 5.5 RELATIONSHIP BETWEEN UNGULATES AND WOLVES

### 5.5.1 Elk and Wolves

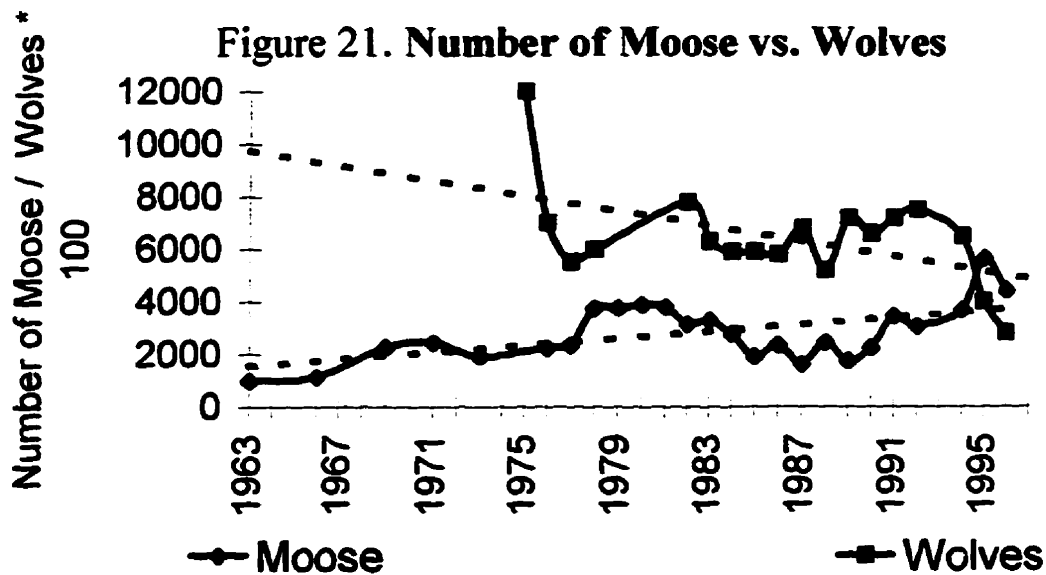
There was no significantly large positive or negative correlation between elk and wolves (Appendix C). This would lead one to conclude that wolves are having no major

impacts on the elk population. This finding supports the fact that, with such a large prey: ratio in the Park, wolves may not be significantly impacting the ungulate population (Carbyn 1980).

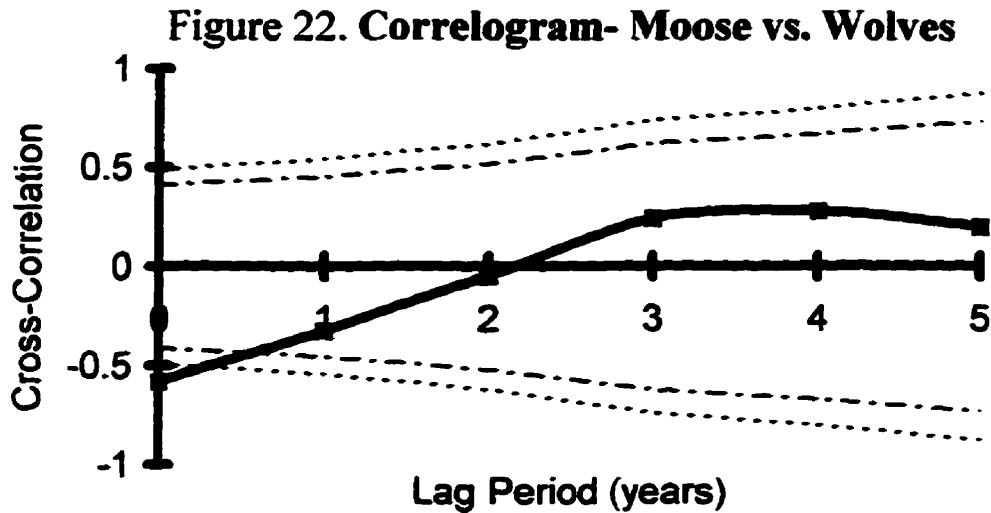
However, this finding contradicts previous studies that reported that wolves may exist largely on elk. Carbyn (1980) studied the frequency of occurrence of food items in scat, and found that elk was the most important year-round prey species in RMNP. Of 520 winter food items and 1,196 summer food items recovered from 1,626 scat samples, the percent occurrence of elk was 52% and 37% (26% adult, 11% calf) for winter and summer, respectively. Moose (12% in winter, 2% in summer) and deer (16% in winter, 2% in summer) were less important. Taber *et. al.* (1982) confirm these observations, by reporting that, where wolf and elk exist together, wolf may exist largely on elk.

It could be presumed, then, that it would be the elk population, rather than the moose population, that would be influenced by the wolf population. And the upward trend of both the elk and moose populations would, presumably, cause the wolf population to increase as well. However, no such trend is shown- the wolf population has been steadily decreasing since 1975. This leads us to believe that the ungulate population and the wolf population are fluctuating independent of each other.

### 5.5.2 Moose and Wolves (Figure 21)



There is a statistically significant correlation coefficient (-0.5839) when there is no lag effect (Figure 22).



The scatterplot, though, suggests that this negative correlation may be invalid due to two outlying points (Appendix D). However, caution must be exercised in ignoring these points since these represent a low number of wolves corresponding with a high number of moose.

In effect, as the moose population increases, the wolf population continues to decline. No lag effect seems to imply no causality, i.e. there are factors that are allowing the moose population to increase, and factors (the same or unrelated) that are causing (or contributing) to the decline of the wolf population. This would support the findings in the previous section.

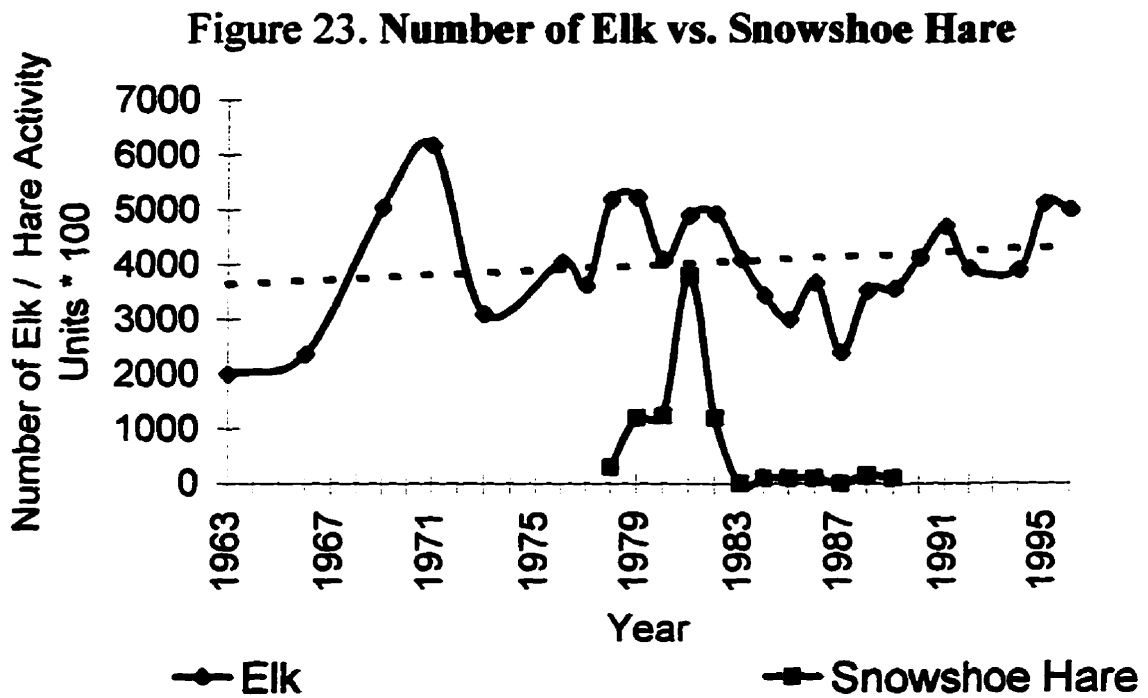
Theoretically, constant predation pressures on some prey populations could prevent any ungulate from becoming dominant at the expense of other species. Moose populations in the Park are currently expanding despite wolf predation. It is possible that because wolf predation is disproportionately heavy on elk, a competitive advantage is gained by moose. This would support the hypothesis that the presence of an alternate prey species (i.e. elk) that is preferred will dilute wolf predation causing the primary prey species (i.e. moose) to flourish (Real 1979). At the same time, even if wolf populations have ample prey available, there is a possibility that their numbers may have continued to decline due to little breeding stock, hunter harvest and mange. No studies of the wolf



population of the region have been done recently to examine potential causes of the decline. This would lead to relatively independent fluctuations of the moose and wolf populations.

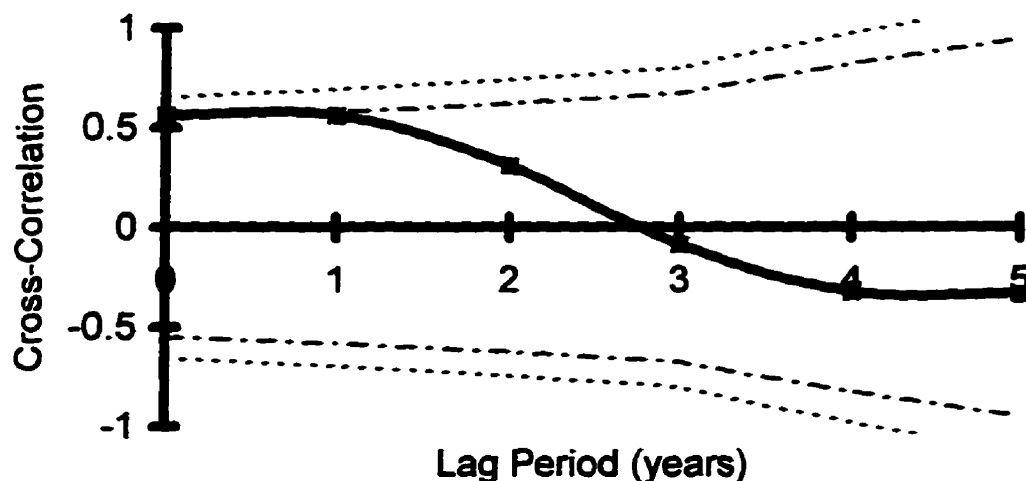
## 5.6 RELATIONSHIP BETWEEN UNGULATES AND SNOWSHOE HARE

### 5.6.1 Elk and Snowshoe Hare (Figure 23)



The highest correlation factor ( $r=0.5628$ ,  $n=10$ ,  $p<0.10$ ) occurred when there was no lag effect (Figure 24).

Figure 24. Correlogram- Elk vs. Snowshoe Hare



Unfortunately, the sample size was small ( $n=10$ ), and therefore a significant correlation may not have been detected or, alternately, the analysis may have identified a relationship that may not exist. Appendix D includes the scatterplot for this relationship.

A high positive correlation with no lag suggests, then, that there is some underlying factor, such as winter severity, as discussed previously with beavers, that is causing these two populations to fluctuate nearly in synchrony. Poll (1981) studied snowshoe hare population dynamics in RMNP during winter 1979-80. He examined why the relative abundance of hares was very similar between 1978-79 and 1979-80 within RMNP when Leonard (1980) predicted the hare cycle was in an increasing phase. [Keith and Windberg (1978) found that, during the cyclic increase near Rochester, Alberta between 1966 and 1971, the annual rate of increase averaged two-fold for five consecutive years.]

Poll (1981) examined winter weather parameters as potential factors reducing the expected rate of increase. Meslow and Keith (1971) reported significant negative correlations between winter temperature and snowfall, and survival of adult snowshoe hares in northern Alberta. Conway and Wight (1972) found that, in cottontail populations in Missouri, onset of breeding could be delayed by severe weather conditions resulting in the loss of one litter from the annual production. Winter weather was also discussed by previous investigators of the snowshoe hare study (Samoil 1979, Leonard 1980) as well

as elsewhere (Bider 1961) in terms of its influence on winter movements of hares. Bider (1961) concluded that wind, light and snow are independent factors which play a restrictive role in winter movements of hares. In addition, both fresh snowfall and cold temperatures have been observed to markedly decrease activity of snowshoe hares (Meslow and Keith 1971) and the mountain hare (Lindlof *et al.* 1974).

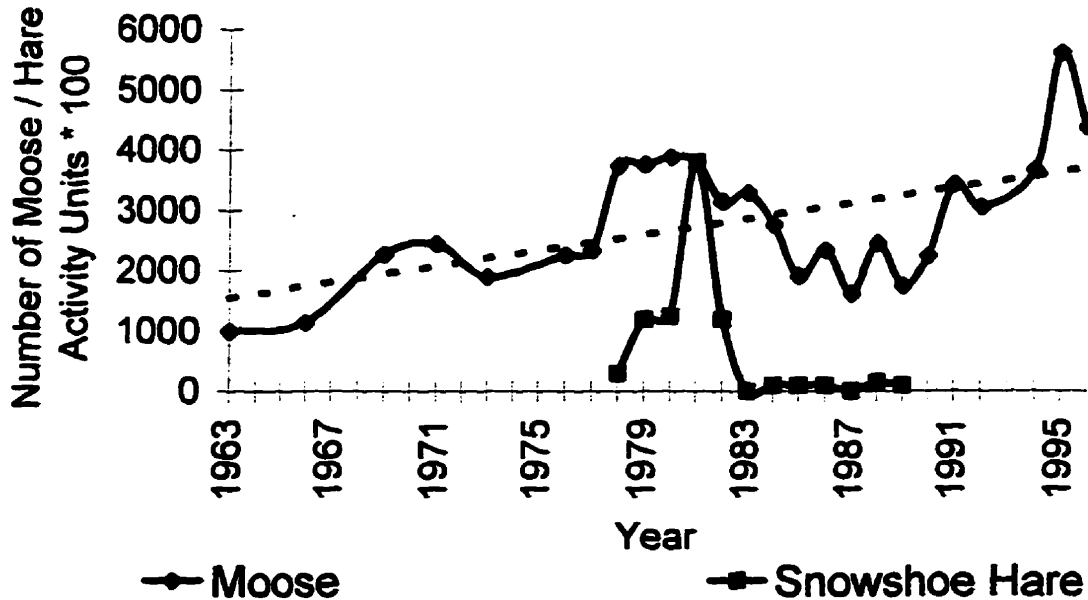
Leonard (1980) suggested that the observed synchrony of intercount fluctuation in hare activity, regardless of cover type, during winters 1977-78 and 1978-79 was due to external factors. Although he found no significant correlations between various environmental parameters and hare activity, there was a strong similarity between the patterns of fluctuation in activity and temperature, particularly when the mean temperature from the two-day period preceding track counts was compared. Data from the past winters' observations supports these findings (Poll 1981). Although few significant correlations were found between temperature and activity, the patterns of increase and decrease in hare activity and temperature were closely associated.

Poll (1981) suggested that the increased severity of the winter of 1978-79 was responsible for dampening the increasing hare population within the study area by reducing both adult winter survival and the length of the breeding season. In fact, the winter of 1978-79 was one of the three most severe winters. Evidently, winter severity affects snowshoe hare populations, and may be responsible for causing herbivore populations to fluctuate, to some extent, in synchrony.

It was hypothesized that snowshoe hare might be competing with elk (and possibly moose) for browse, especially in severe winters. In fact, no relationship was found ( $p < 0.10$ ), implying that competition is not a significant factor influencing elk population trends. Perhaps, though, during the study period there was never a coincidence of the right factors, e.g. high numbers of all species and a severe winter.

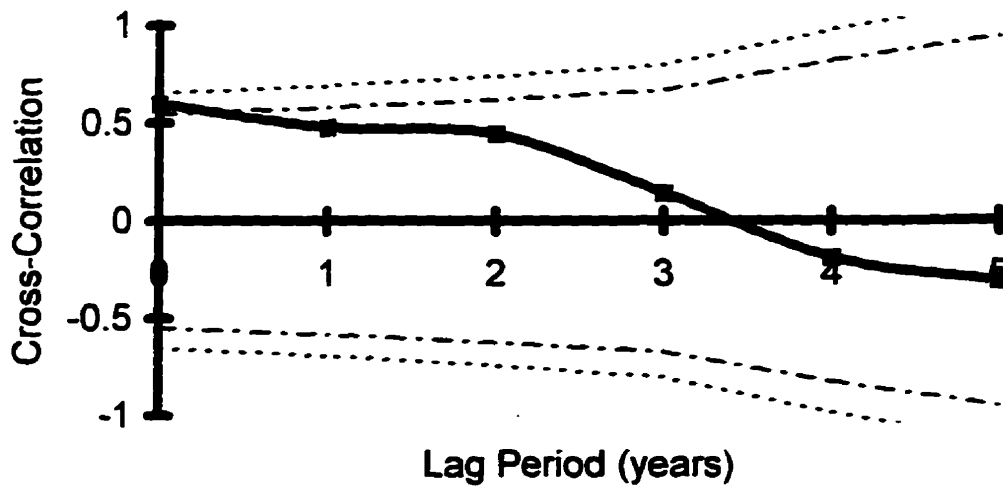
5.6.2 Moose and Snowshoe Hare (Figure 25)

Figure 25. Number of Moose vs. Snowshoe Hare



Again, the highest correlation factor ( $r=0.5967$ ,  $n=10$ ,  $p<0.10$ ) occurred when there was no lag effect (Figure 26).

Figure 26. Correlogram- Moose vs. Snowshoe Hare

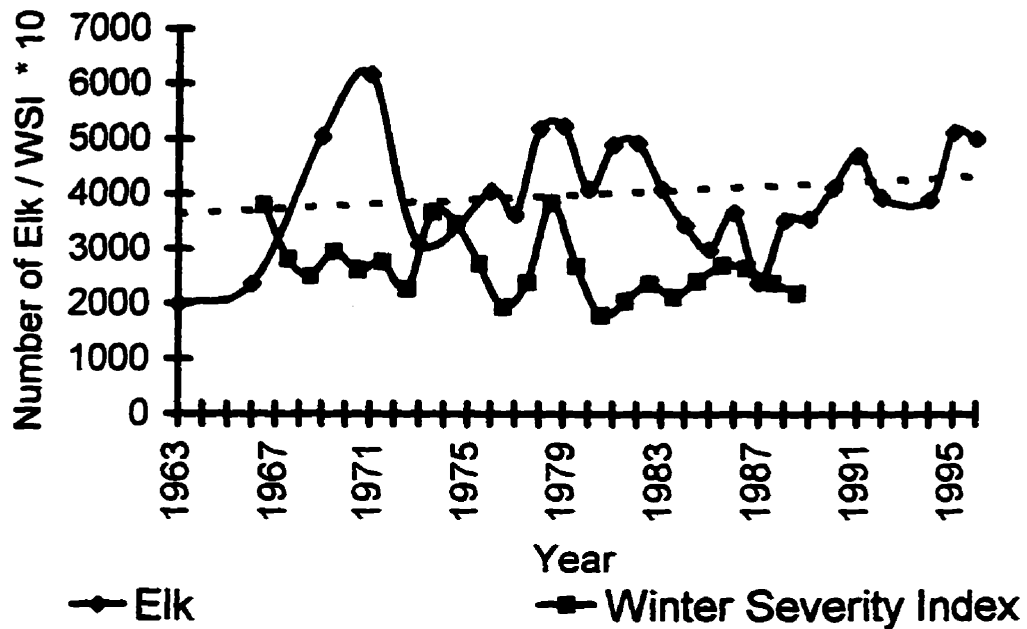


The same assumptions are valid as in the previous section. Moose and snowshoe hare may be highly positively correlated due to similar responses to severe weather. The results also suggest that moose and hare were not competing for browse.

## 5.7 RELATIONSHIP BETWEEN UNGULATES AND WINTER WEATHER

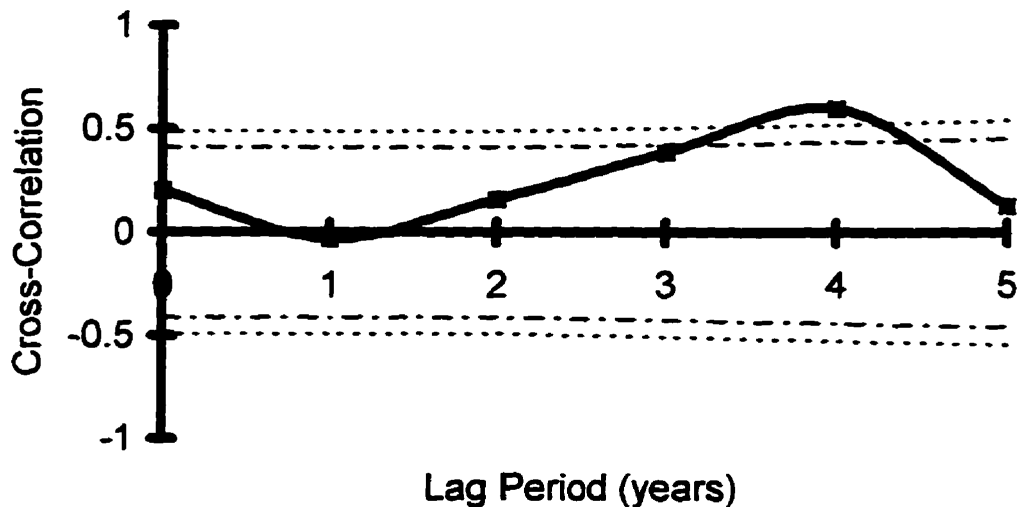
### 5.7.1 Elk and Winter Weather Severity (Figure 27)

Figure 27. Number of Elk vs. Winter Severity



A statistically significant positive correlation at a four year lag was found for elk and winter severity ( $r=0.5998$ ,  $n=19$ ,  $p<0.05$ )(Figure 28).

Figure 28. Correlogram- Elk vs. WSI



In effect, there were three very severe winters during the study period- 1966-67, 1974-75 and 1978-79. Severe winters were usually preceded and proceeded by mild winters. Thus a rising and falling trend of a severe winter is followed by a rising and falling trend in the elk population approximately four years later. It appears that after a very severe winter the elk population continued to increase for approximately four years before it began a descending trend. For example, after the severe winter of 1966-67, the elk population continued to increase, began to plummet in 1971 and finally recovered after 1973. The severe winter of 1974-75 and 1978-79 followed a similar pattern.

If Lack's hypothesis is right, in a seasonal environment (with little or no predation) the fecundity rate will be determined in a density-independent way by the amount of resources available for breeding in the favourable part of the year. Regulation of population size would then occur through density-dependent mortality through resource limitation during the non-breeding season. Assuming this hypothesis holds true, and with such a high degree of age dependence in both fecundity and mortality in ungulates, lag effects in the response of the population are likely to occur. Such time delays are likely to generate complex population fluctuations (May 1981).

According to Lack's hypothesis, in temperate ungulates we expect the highest losses to occur in winter because of density-dependent resource limitation. If these losses are occurring in severe winters among elk calves during their first winter, as found in previous studies, then a whole age class of the population may disappear. This would have delayed effects on the population since these calves would not get a chance to mature and produce offspring until two years later. As well, it has been found that variation in winter severity affects recruitment rate. If this is true, then the calf:female ratio will be lower after severe winters. Again, a delay in this effect will be evident since there will be fewer newborns that would have eventually produced offspring two years later.

Similarly, climatic conditions may exert an influence on fecundity rate in elk. In a severe winter the quality and quantity of food may be poor. This may cause large losses in body weight which will affect the fecundity rate through size-dependent onset of reproduction (small females mature later than large females). A consequence of this is

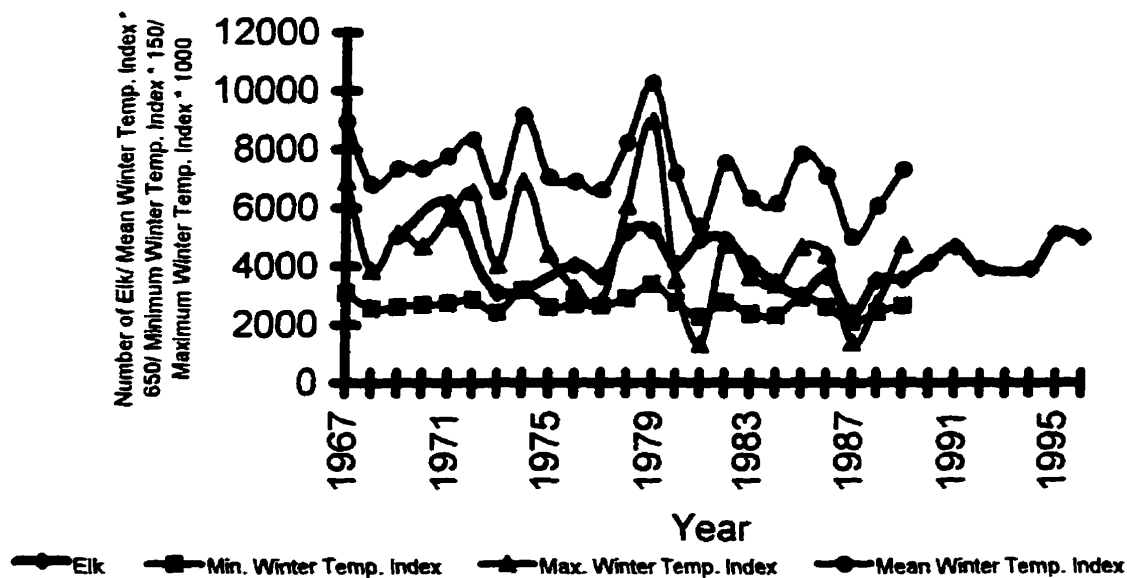
that a delay will occur between the occurrence of the ecological change (change in the winter feeding conditions) and the response to this change in the population. This delay could be up to four years, since the normal age of maturity of elk is two years.

### 5.7.2 Moose and Winter Weather Severity

Although there was a similar pattern of this correlogram (Appendix C) to the elk and winter severity correlogram (Figure 28), no significant correlations were found. The highest positive correlation *did* occur at a four-year lag (Appendix C). Although not considered significant, there is definitely a pattern that can be observed with the moose population as well. After the severe winter of 1966-67, the moose population increased for approximately four years, declined after 1971, and recovered after 1973. The severe winters of 1974-75 and 1978-79 seemed to act in concert, increase and fluctuate from 1973 to 1981, and plummet after this (recovering in the late '80's). This pattern and time frame is almost identical to the pattern of the elk population, but is slightly less severe. An examination of the factors that are included in the winter severity index (below) may give some hints as to which winter parameter(s) moose might be most/ least sensitive to.

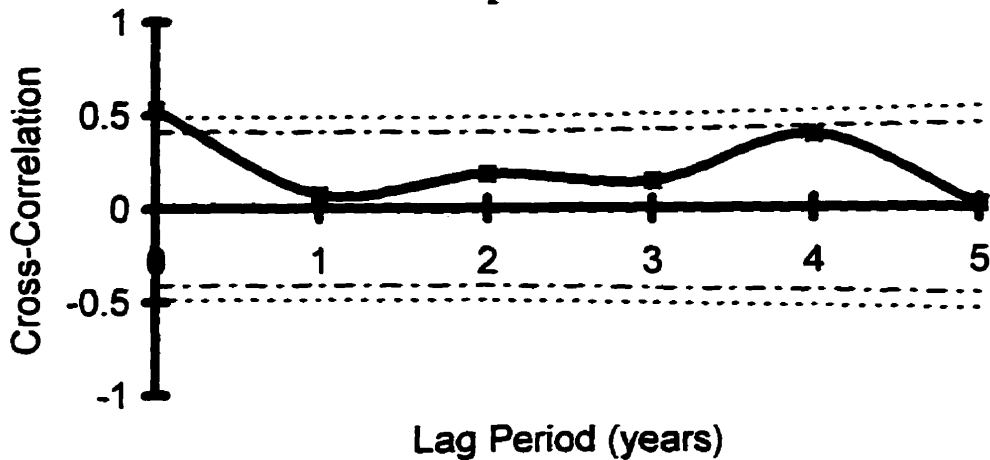
### 5.7.3 Elk and Winter Temperature (Figure 29)

Figure 29. Number of Elk vs. Winter Temperature Indices

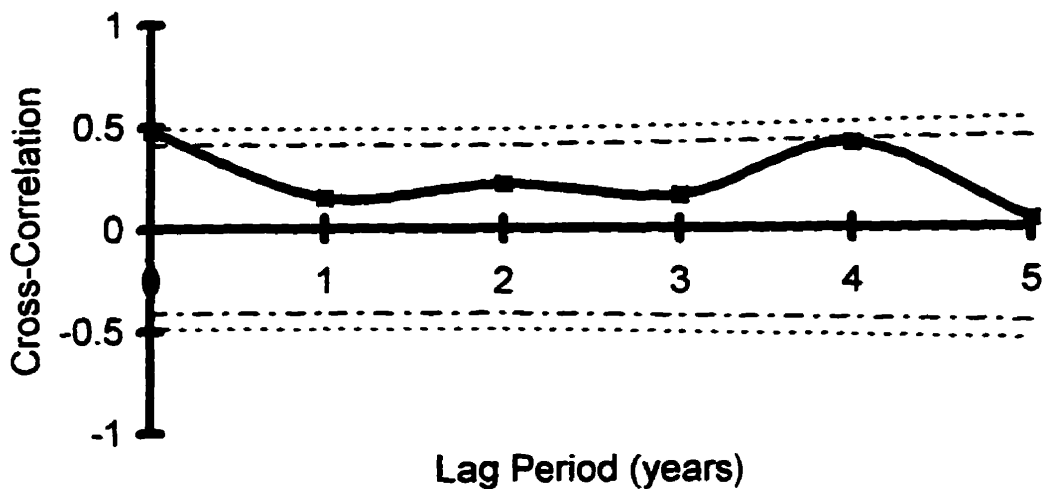


Elk were found to be statistically significant and positively correlated to the mean winter temperature index ( $r=0.5310$ ,  $n=17$ ,  $p<0.05$ )(Figure 30), the minimum winter temperature index ( $r=0.4800$ ,  $n=17$ ,  $p<0.10$ )(Figure 31), and the maximum winter temperature index ( $r=0.5481$ ,  $n=17$ ,  $p<0.05$ )(Figure 32).

**Figure 30. Correlogram- Elk vs. Mean Winter Temperature Index**

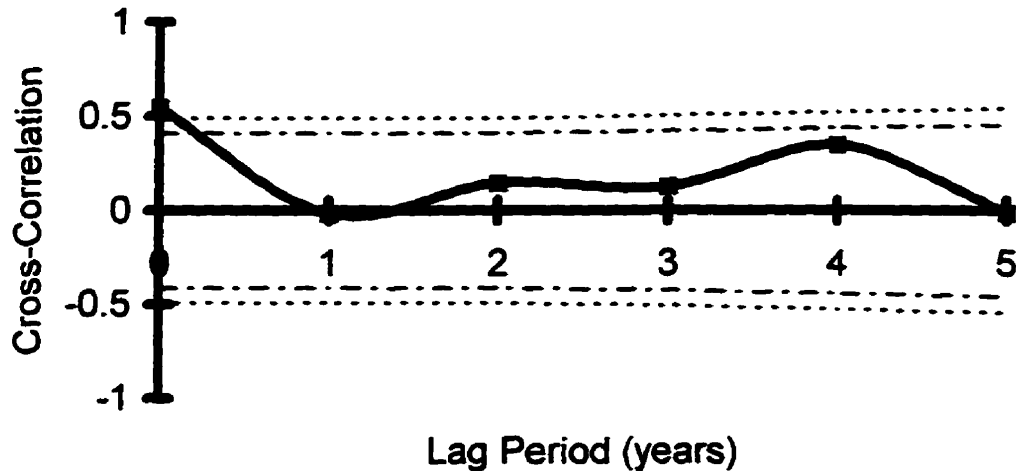


**Figure 31. Correlogram- Elk vs. Minimum Winter Temperature Index**





**Figure 32. Correlogram- Elk vs. Maximum Winter Temperature Index**



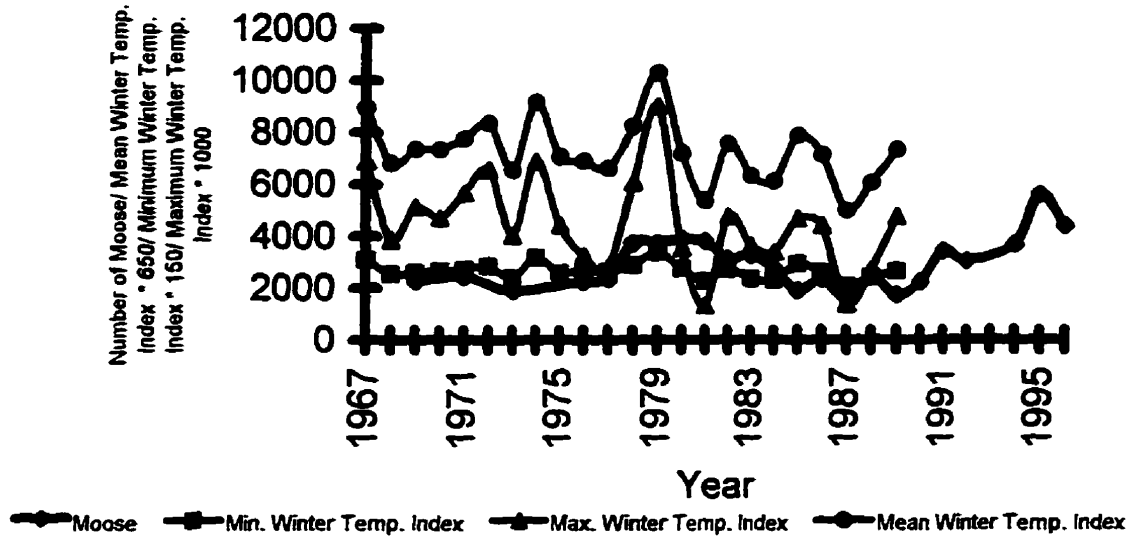
The significant positive correlation with no lag effect found in all three temperature parameters could have a possible relationship to the aerial survey itself. In years with severe winters, elk tend to leave the Park in high numbers (Rounds 1991). This would imply that in severe winters aerial surveyors would tend to see more elk as they were forced out of sheltered areas to seek food. (Aerial surveys also cover transects immediately adjacent to the Park- Figure 4).

Another theory is that elk are just responding immediately to a severely cold winter. For example, the severe winter of 1966-67 was preceded by a milder winter; similarly, it could be expected that, based on the theory that elk were dying immediately in a severely cold winter, the elk population would decrease.

The high positive correlation between elk and mean monthly minimum temperature with a four-year lag effect is interesting for a couple of reasons. First, it complies with the four-year lag effect found with elk and overall winter severity. Second, it suggests that if this four-year lag effect is valid, then mean monthly minimum temperature may be the temperature parameter that best predicts winter severity for ungulates, and, if so, should be incorporated into a modified winter severity index (mean

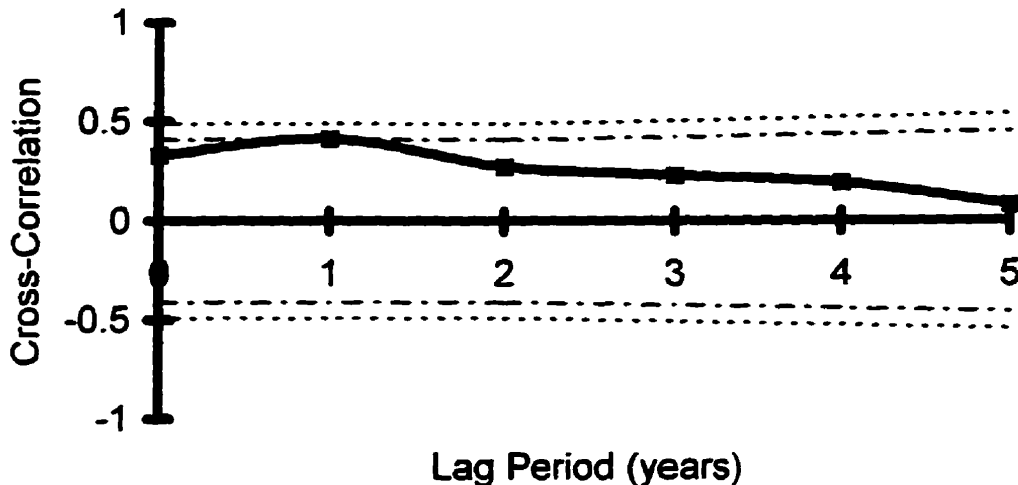
5.7.4 Moose and Winter Temperature (Figure 33)

Figure 33. Number of Moose vs. Winter Temperature Indices



There were no significant relationships found, except for a significant positive correlation with a one-year lag effect ( $r=0.4121$ ,  $n=18$ ,  $p<0.10$ ) between moose and the minimum winter temperature index (Figure 34).

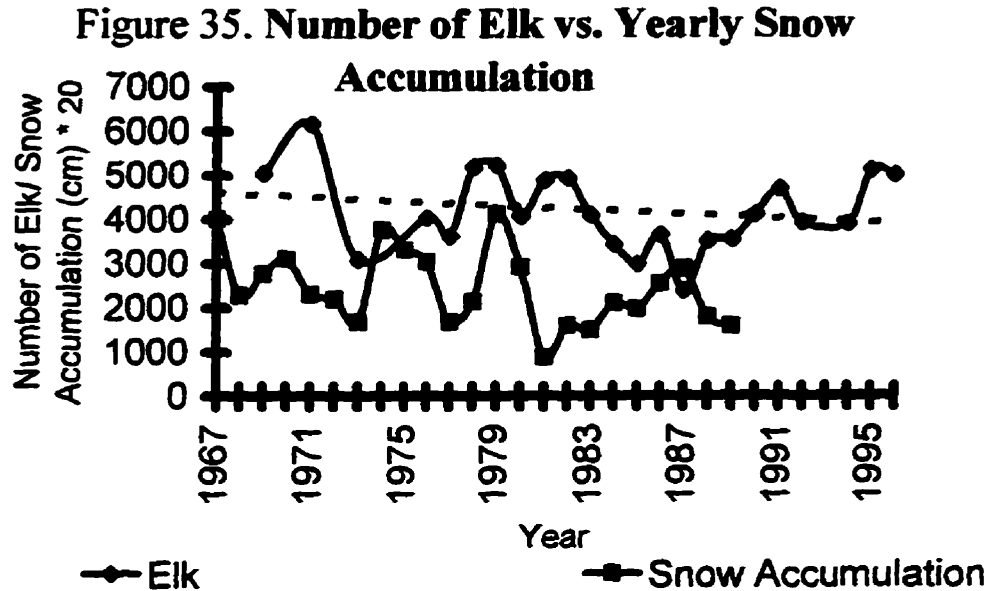
Figure 34. Correlogram- Moose vs. Minimum Winter Temperature Index



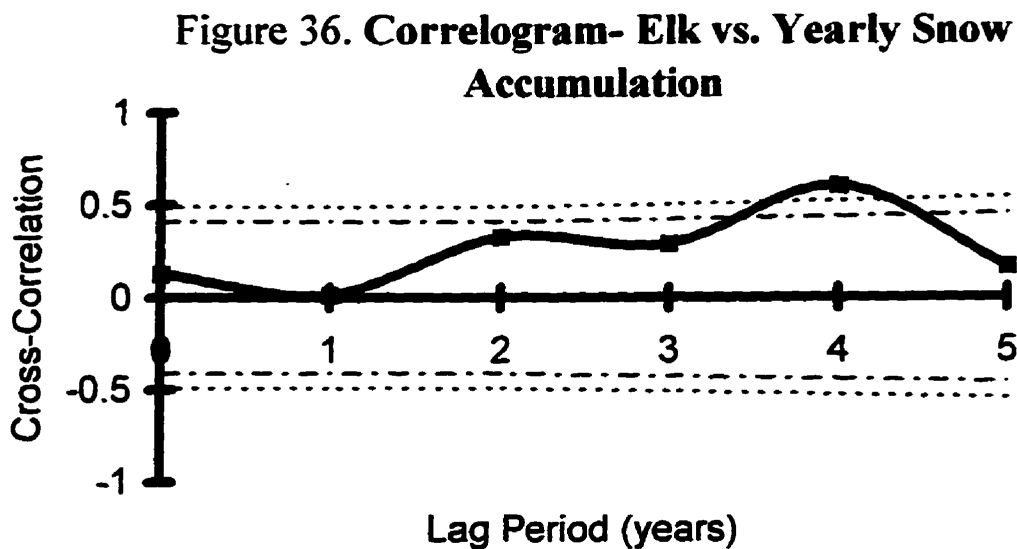
The relationship suggests that the moose responds to this severe winter by decreasing in number the following year (i.e. by the time the aerial survey was completed early in

The relationship suggests that the moose responds to this severe winter by decreasing in number the following year (i.e. by the time the aerial survey was completed early in 1968). Temperature may be influencing mortality of calves, recruitment rate and fecundity rate, leading to delays in these effects on the moose population.

5.7.5 Elk and Snow Accumulation (Figure 35)



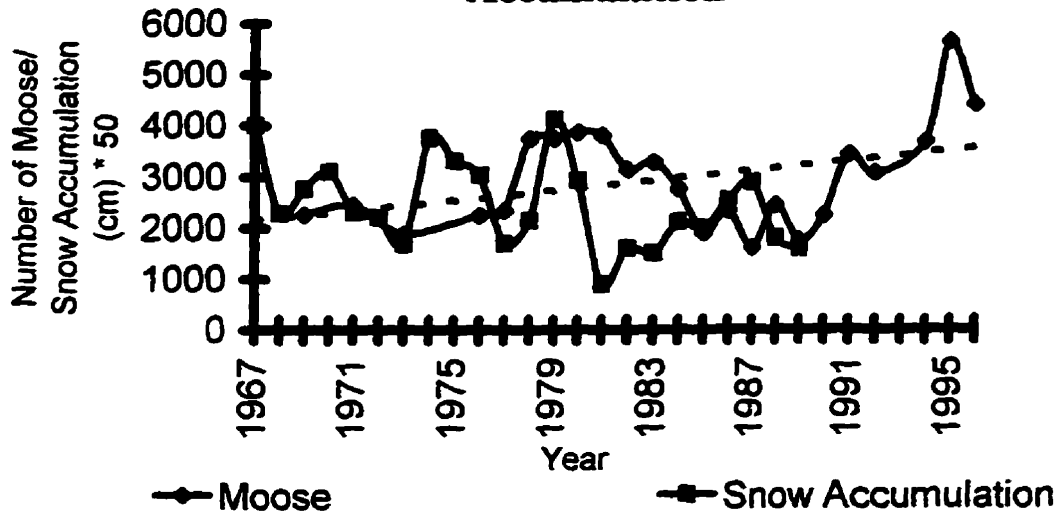
There is a statistically significant positive correlation between elk and yearly snow accumulation with a four-year lag ( $r=0.6047$ ,  $n=19$ ,  $p<0.05$ )(Figure 36).



The exact same pattern is evident here as with elk and the winter severity index. Assuming the index is valid, snow accumulation may be the most important winter parameter affecting ungulates. This finding complies with many other studies (Coady 1974, Mech *et al.* 1987, Messier 1991).

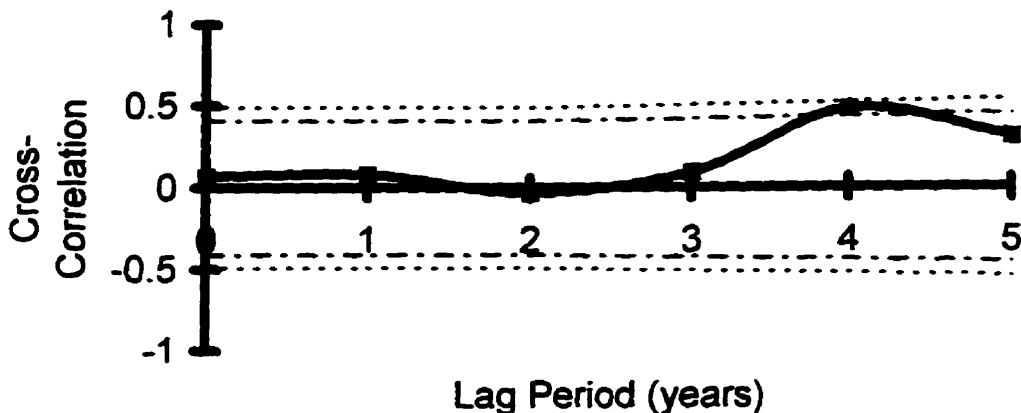
5.7.6 Moose and Snow Accumulation (Figure 37)

Figure 37. Number of Moose vs. Yearly Snow Accumulation



There is a significant positive correlation between moose and yearly snow accumulation with a four-year lag ( $r=0.4821$ ,  $n=19$ ,  $p<0.05$ ) (Figure 38).

Figure 38. Correlogram- Moose vs. Yearly Snow Accumulation



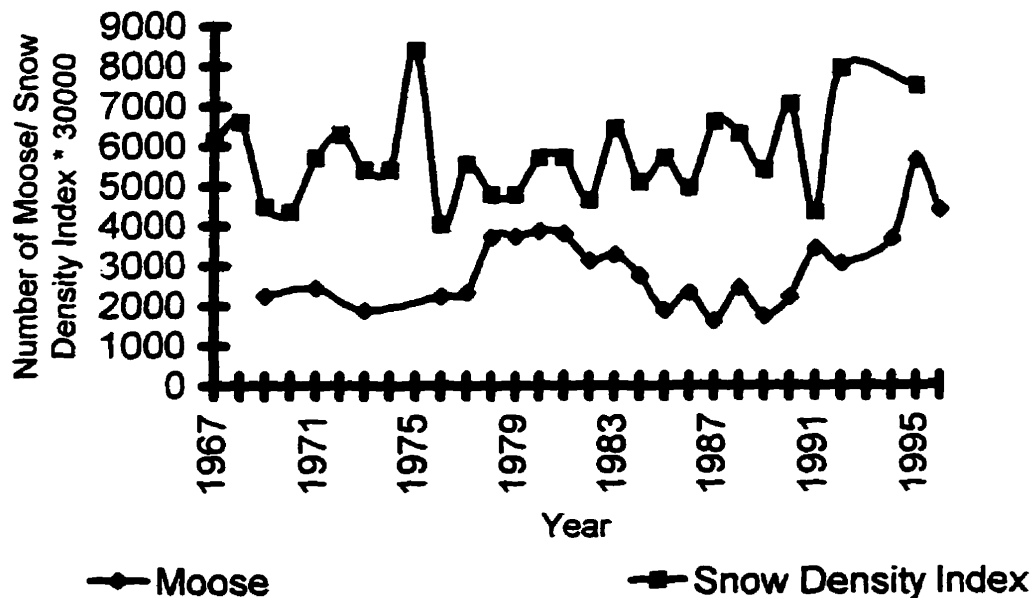
The four year lag is, again, less severe than that of the elk. A potential reason for snow to not impact moose as much as it may impact elk could relate the much higher chest height of moose. Snow cover exceeding two-thirds the chest height of wild cervids impedes movement (Telfer and Kelsall 1971, 1979). The fact that moose is significantly correlated to snow accumulation suggests that this might be the most important winter weather parameter affecting the population.

### 5.7.7 Elk and Snow Density

There were no significant correlations between elk and snow density (Appendix C).

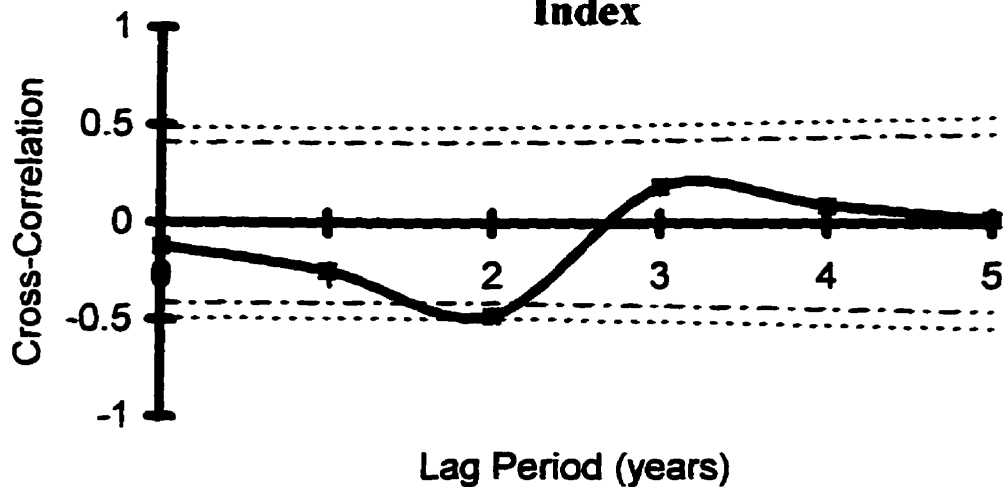
### 5.7.8 Moose and Snow Density (Figure 39)

Figure 39. Number of Moose vs. Snow Density Index



There was a significant negative correlation between moose and snow density with a two-year lag ( $r = -0.4756$ ,  $n = 19$ ) (Figure 40).

**Figure 40. Correlogram- Moose vs. Snow Density Index**



This correlation suggests that the snow density in a particular year affects the moose population two years later. Again, snow density might be causing delays in the response of the moose population to mortality of calves, low recruitment rate and reduced fecundity.

#### 5.7.9 Elk and Green-up Value

There were no significant positive or negative correlations found (Appendix C).

#### 5.7.10 Moose and Green-up Value

There were no significant positive or negative correlations found (Appendix C).

### 5.8 CONCEPTUAL MODELS

Conceptual models for elk and moose are portrayed in Figures 41 and 42, respectively. These models present an overview of the factors that are suspected to be influencing elk and moose populations, and are based on speculations presented in this chapter.

The suspected strength of a relationship was represented by the thickness of a line, and classified as either a “minor”, “moderate” or “high” influence on the elk or moose population. Arrows were also color-coded to represent either a positive or negative influence on the elk or moose population. The relationships that were purely inferred (i.e. were not found to be statistically significant) were represented by a dashed line. A complementary description of the models is presented throughout Chapter 6.

Figure 41. ELK MODEL

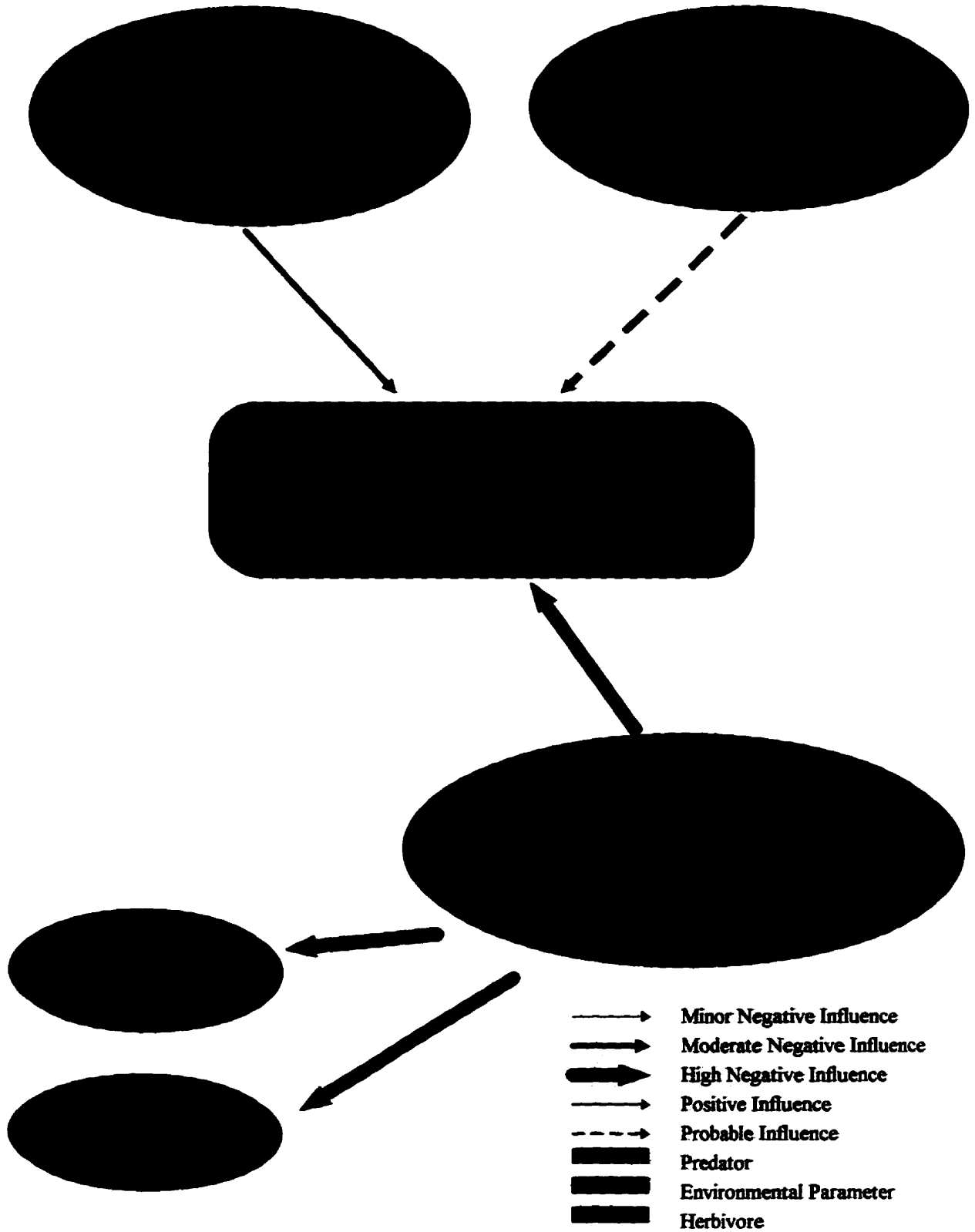
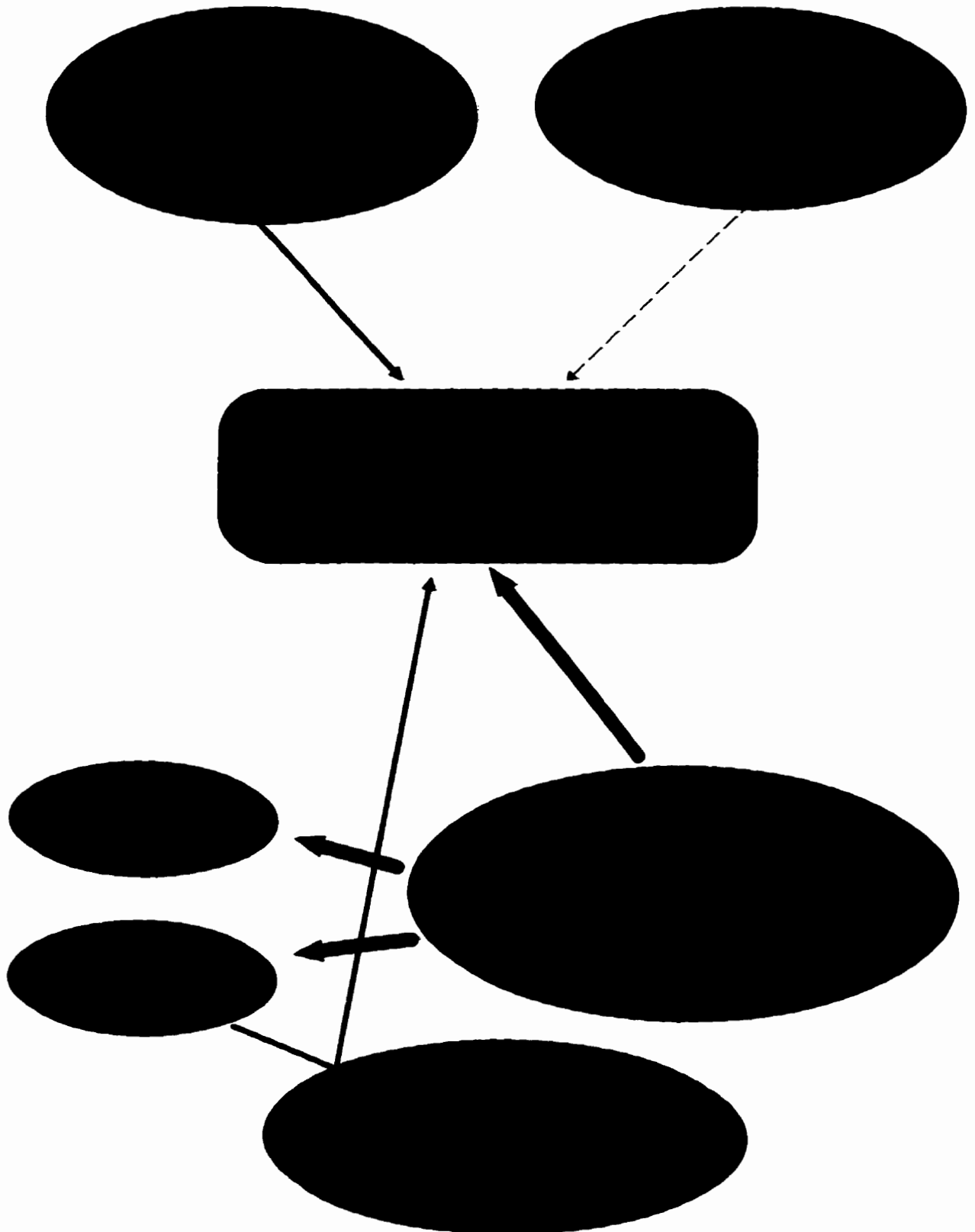


Figure 42. MOOSE MODEL





## **CHAPTER 6**

### **SUMMARY, CONCLUSIONS AND RECOMMENDATIONS**

#### **6.1 SUMMARY**

Since 1963, RMNP has conducted consistent yearly aerial surveys over the Park to estimate elk and moose numbers. Until this study, there had been no long-term analysis of the overall population trends in order to determine what factors might be responsible for causing the ungulate populations to fluctuate.

This study attempted to isolate and explore some of the quantifiable factors that may be influencing elk and moose population trends. These factors included hunter success around Park boundaries, beaver populations, wolf populations, snowshoe hare populations and winter severity. Through understanding these interactions, and their influence on ungulate populations, managers will be better able to predict the impact of human activities on ungulate populations.

Cross-correlation analysis was used to determine the relationship between both elk and moose populations, and each parameter. This type of analysis was essential to determine the lag effects of a particular parameter on the elk or moose population, if any. Line graphs and correlograms were used to explore the relationships.

Both elk and moose populations were found to be autocorrelated. However, moose were more strongly autocorrelated and a significant relationship existed for as long as two years, suggesting that the moose population changes much less dramatically than the elk population. The difference could relate to such age-specific events as age at maturity.

The relationship of elk and moose to elk and moose harvested, respectively, was suspected to be related to both the life history of each species and the heavy harvest of cows (due to no restriction in sex for the bag limit at any time in the season) in the RMNP region. Both relationships had a lag effect approximately equivalent to the age to reach maturity for each species. This could be a result of harvesting large numbers of cows that were therefore not able to produce female calves in the following years,

causing the populations to decline. The populations may recover two (elk) or four years (moose) later when those calves that survived the winter of the high harvest would have begun to produce offspring.

Both elk and moose populations, and the beaver population seem to be fluctuating somewhat in synchrony. This might be related to a common reaction of these species to variation in winter severity. As well, the beaver population was suspected to be affecting the moose population in the following year. This could be related to the fact that beaver tend to introduce favorable habitat for moose.

Although elk have been found to be the foremost prey item for wolves in RMNP, there was no statistically significant relationship found between the two species. Wolves were negatively correlated to moose population trends, though. These population trends may likely be independent of each other. Reasons could be that moose are gaining a competitive advantage over elk (since wolves prefer to prey on elk), therefore causing a steady population increase in moose. Wolves, on the other hand, tend to be steadily decreasing. The reasons for this may include little breeding stock, hunter harvest and mange.

As with beaver, both elk and moose populations seemed to be fluctuating somewhat in synchrony with the snowshoe hare population. Again, this is suspected to relate back to the animals' similar reaction to winter severity. As well, it was hypothesized that snowshoe hare may be competing with elk for browse in winter, especially in years when the hare population is at its peak. However, no relationship was found.

The elk population was found to be significantly correlated to the WSI with a four-year lag. The reason for the four-year lag could relate to winter calf mortality, reduced recruitment and reduced fecundity after severe winters. Moose did not show any significant correlation to the WSI, even though they exhibited essentially the same pattern in their correlogram (with the highest correlation at a four-year lag). Assuming that the WSI is valid, it would seem as if moose were not as affected by severe winters as elk were. In case the WSI was not valid, and to get more information as to which

parameters within the WSI were most important, each parameter was individually correlated to both the elk and moose populations.

The elk population was found to be significantly positively correlated to the mean winter temperature index, the maximum winter temperature index and the minimum winter temperature index. This could relate to the weather conditions at the time of the aerial survey (in years with severe winters, elk tend to leave the Park in high numbers to seek food and avoid snow accumulation, making them more visible) or could mean that the elk are immediately responding to a severely cold winter. Elk were also found to be strongly correlated to the minimum winter temperature index with a four-year lag effect, the same lag-effect as was found between the elk population and the WSI. Moose were found to be significantly correlated to the minimum winter temperature index with a one-year lag effect. The relationship suggests that minimum temperatures in winter may be causing delays in the response of moose populations to mortality of calves, low recruitment rate and reduced fecundity.

There was a significant positive correlation between both elk and moose, and snow accumulation with a four-year lag. Again, a four-year lag seems to be important in understanding the influence weather has on the ungulate population. The four-year lag for moose is less severe than that of the elk. A potential reason that snow accumulation may not impact moose as much as it may impact elk could be due to the much higher chest height of moose, thus less impedement.

The moose population was correlated to snow density with a two-year lag, suggesting similar time-delayed responses to effects of winter weather. Elk and moose were not significantly related to green-up value in any way.

## **6.2 CONCLUSIONS**

Of those examined, the most important factors found to be potentially influencing the elk population were hunter harvest and winter severity (specifically, snow accumulation and winter temperature). Both of these factors seem to be creating delays in population response by the effects of winter mortality of calves, reduced recruitment and reduced fecundity. As well, although no significant correlation was detected, it was suspected that

wolves are, at least, preventing the elk population from increasing dramatically. This relationship is potentially eliminating conditions suitable for a population irruption. The moose population was found to be influenced by hunter harvest, beaver populations and winter severity (specifically, winter temperature, snow accumulation and snow density). Again, hunter harvest and winter severity conditions may be creating time-delayed population responses. Although the wolf population was found to be significantly correlated to the moose population, the fact that there was no lag effect implied that the populations were acting independently of each other. It was presumed that there was a common response of the herbivores (elk, moose, beaver and snowshoe hare) to winter severity due to the significant positive correlations found between these species. This finding suggests that winter severity may ultimately control the mammal system of RMNP.

In an ecological study such as this, where individual factors are examined in an attempt to better understand an entire system, often we lose sight of the fact that we are dealing with nature- a complex system with many factors interacting in some manner, and resulting in synergistic effects. Further, knowing only what factor is the most influential in terms of population rate of increase restricts our understanding of population dynamics. For example, snow depth may be the best correlate of population decline of ungulates in RMNP, yet it may have no significance in terms of feedback within the system's dynamics, i.e. as a mechanism of population regulation. Therefore caution must be exercised in drawing any firm conclusions from these results. On the other hand, these results represent a depth of analysis into ungulate population dynamics that has not been previously undertaken by RMNP, and therefore can represent a basis for further research into elk and moose populations in the Park.

### **6.3 RECOMMENDATIONS**

1. Elk and moose populations should continue to be monitored, and further explorations into factors affecting their population trends should be examined once more data are collected. As well, a study of the accuracy/ precision of the ungulate aerial surveys should be undertaken, since models are only as good as the data going into them.

2. Given the importance of food supply shown in other studies, a browse survey methodology should be chosen and implemented in the Park as soon as possible, and the vegetation in the Park should be assessed yearly in order to determine if it is being extensively over-browsed, a sign of a possible population irruption.
3. The Park should urge the provincial government to set hunting seasons for a given year after aerial survey results are in. In this way, if the ungulate population seems to be dramatically decreasing (such as when or if a population irruption occurs), provincial resource managers can make appropriate amendments to harvest regulations for that year (rather than the next, as is current practice). If this is not possible, perhaps the provincial government can be persuaded to have alternate measures available if the elk and moose populations are threatened in any way. For example, DNR might postpone draws until mid-summer (and therefore be able to change the number of tags issued, if necessary). As well, a mechanism should be in place so that that DNR can close a season after the aerial survey results are in.
4. Further studies into the effect that the declining wolf population in RMNP is having on the ungulate populations should be undertaken.
5. Stelfox's winter severity index should be examined, considering the latest literature, and determining the appropriate weighting for the parameters within the index. Once the index is modified, the Park should undertake a program whereby necessary data are collected and indices are calculated on a yearly basis. This may give Park managers some predictive ability as to how and when the population will respond to severe winter conditions.
6. Before any conclusions are drawn about yearly ungulate population fluctuations, or management actions are taken at the federal or provincial level, management officials should examine all parameters found to be influencing the elk and moose populations. This will allow for a better understanding of the synergistic effects of ecological systems.

## LITERATURE CITED

- Anderson, C. C. 1958. The elk of Jackson Hole. Bull. 10. Laramie: Wyoming Game and Fish Comm. 184 pp.
- Bailey, R. H. 1968. Notes on the vegetation of Riding Mountain National Park, Manitoba. Nat. Parks For. Survey No. 2. Dep. For. and Rural Dev. For. Manage. Instit., Ottawa. 80 pp.
- Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildl. Monogr. 114. 49 pp.
- Banfield, A. W. F. 1949. An irruption of elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. 13(1): 127-134.
- Banfield, A. W. F. 1973. The mammals of Canada. University of Toronto Press.
- Barlow, J. L., B. W. Briscoe, and B. S. Lee. 1980. Riding Mountain National Park Conservation Plan. Unpubl. Parks Canada Rep., Winnipeg, Manitoba. 112 pp.
- Bayliss, P. 1985. The population dynamics of red and western grey kangaroos in arid New South Wales, Australia. I. Population trends and rainfall. J. Anim. Ecol. 54: 125-129.
- Bergerud, A. T. and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. 64: 1515-1529.
- Bergerud, A. T. and D. R. Miller. 1977. Population dynamics of Newfoundland beaver. Can. J. Zool. 55: 1480-1492.
- Bergerud, A. T. and J. B. Snider. 1988. Predation in the dynamics of moose populations: a reply. J. Wildl. Manage. 52: 559-564.
- Bergerud, A. T., W. Wyett, and J. B. Snider. 1983. The role of wolf predation in limiting a moose population. J. Wildl. Manage. 47: 977-988.
- Bider, J. R. 1961. An ecological study of the snowshoe hare, *Lepus americanus*. Can. J. Zool. 39: 81-103.
- Bird, R. D. 1961. Ecology of the aspen parkland of western Canada. Can. Dep. Agr. Pub. 1066. 155 pp.

*Literature Cited*

- Blood, D. A. 1966. Range relationships of elk and cattle in Riding Mountain National Park, Man. Can. Wildl. Ser. Wildl. Manage. Bull. Ser. 1, No. 19. 62 pp. & 2 maps.
- Blood, D. A. 1974. Variation in reproduction and productivity of an enclosed herd of moose (*Alces alces*). Trans. Int. Congr. Game Biol. 11: 59-66.
- Bobek, B. 1977. Summer food as the factor limiting roe deer population size. Nature (Lond.) 268: 47-49.
- Boutin, S. 1992. Predation and moose population dynamics: a critique. J. Wildl. Manage. 56(1): 116-127.
- Boyce, M. S. 1974. Beaver population ecology in interior Alaska. M.S. Thesis, Univ. Alaska, Fairbanks. 161 pp.
- Boyce, M. S. 1989. The Jackson elk herd. Cambridge University Press.
- Buechner, H. K. and C. V. Swanson. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. Trans. North Amer. Wildl. Conf. 20: 560-567.
- Canadian Parks Service. 1990. Canadian Parks Proposed Policy. Department of the Environment, Ottawa.
- Canadian Parks Service. 1994. Guiding Principles and Operational Policies. Canadian Heritage, Ottawa. 125 pp.
- Canadian Parks Service. 1997. Riding Mountain National Park Ecosystem Conservation Plan. Canadian Heritage, Ottawa. 111 pp.
- Carbyn, L. N. 1980. Ecology and management of wolves in Riding Mountain National Park, Manitoba. Final Report. Large Mammal System Studies Rep. No. 10. Can. Wildl. Ser., Edmonton, Alta. 184 pp.
- Carbyn, L. N. 1983. Wolf predation on elk in Riding Mountain National Park. J. Wildl. Manage. 47(4): 963-976.
- Caudill, S. J. 1976. Establishment of big game seasons in Colorado. Proc. West Assoc. State Game and Fish Comm. 56: 86-95.
- Caughley, G. 1970. Eruption of ungulate populations with emphasis on Himalayan tahr in New Zealand. Ecology 51: 53-72.

*Literature Cited*

- Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. *Appl. Biol.* 1: 183-246.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Toronto. 234 pp.
- Caughley, G. 1979. What is this "thing" called carrying capacity? Pages 2-8 in M. S. Boyce and L. D. Hayden-Wing, eds. North American elk: ecology, behaviour and management. University of Wyoming, Laramie, WY.
- Caughley, G., A. R. Sinclair, and D. Scott-Kemmis. 1976. Experiments in aerial survey. *J. Wildl. Manage.* 40: 290-300.
- Caughley, G. and C. J. Krebs. 1983. Are big mammals simply little mammals writ large? *Oecologia* 59: 7-17.
- Caughley, G. and A. Gunn. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. *Oikos* 67: 47-55.
- Chatfield, C. 1989. The analysis of time series. Fourth edition. Chapman and Hall, New York. 241 pp.
- Clutton-Brock, T. H. and S. D. Albon. 1982. Red deer in the highlands. BSP Professional Books.
- Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. *J. Anim. Ecol.* 54: 831-846.
- Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* 56: 53-67.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *J. Anim. Ecol.* 56: 857-871.
- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1991. Persistent instability and population regulation in Soay sheep. *J. Anim. Ecol.* 60: 593-608.
- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.* 61: 381-396.
- Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. *Am. Nat.* 149: 195-219.



*Literature Cited*

- Coady, J. W. 1974. Influence of snow on behaviour of moose. *Naturaliste canadien* 101: 417-436.
- Coblentz, B. E. 1970. Food habits of George Reserve deer. *J. Wildl. Manage.* 34(3): 535-540.
- Cody, M. L. 1974. Competition and the structure of bird communities. *Monographs in Population Biology No. 7*, Princeton University Press, Princeton. 318 pp.
- Cole, G. 1958. Big game-livestock competition on Montana's mountain rangelands. *Montana Wildl.*, April 1958: 24-30.
- Coughenour, M. B. and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecol. Appl.* 6(2): 573-593.
- Cowan, I. McT. 1950. Some vital statistics of big game on over-stocked mountain range. *Trans. N. Amer. Wildl. Conf.* 15: 581-588.
- Dickson, J. R. 1909. The Riding Mountain Forest Reserve. *Can. Dep. Int. For. Br. Bull.* No. 6. 42 pp.
- Dublin, H. T., A. R. E. Sinclair, S. Boutin, M. Anderson, and P. Arcese. 1990. Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. *Oecologia (Berl.)* 82: 283-288.
- Dunbar, D. 1991. The outdoor traveler's guide to Canada. Stewart, Tabori & Chang, New York. 400 pp.
- Dyck, A. P. and R. A. MacArthur. 1993. Daily energy requirements of beaver (*Castor canadensis*) in a simulated winter microhabitat. *Can. J. Zool.* 71: 2131-2135.
- Edmonds, E. J. 1988. Population status, distribution and movements of woodland caribou in west central Alberta. *Can. J. Zool.* 66: 817-826.
- Ehrlich, W. A., L. E. Pratt, and E. A. Poyser. 1956. Report of reconnaissance soil survey of Rosburn and Virden map sheet areas. *Can. Dep. Agr., Man. Dep. Agr. and Univ. of Man., Manitoba Soil Survey Soils Report No. 6.* 121 pp. and 2 maps.
- Environment Canada, Parks. 1987. Riding Mountain National Park management plan. Department of the Environment, Ottawa. 70 pp.
- Festa-Bianchet, M. M. Urquhart, and K. G. Smith. 1994. Mountain goat recruitment: kid production and survival to breeding age. *Can. J. Zool.* 72: 22-27.

*Literature Cited*

- Flook, D. R. 1970. A study of sex differential in the survival of wapiti. Can. Wildl. Ser. Rep. Ser. No. 11. Ottawa: Queens Printer. 71 pp.
- Fowler, C. W. 1987. A review of density-dependence in populations of large mammals. Pages 401-441 in H. H. Genoways, ed. Current Mammalogy Vol. 1. Plenum, New York.
- Franzmann, A. W. and C. C. Schwartz. 1985. Moose twinning rates: a possible population condition assessment. J. Wildl. Manage. 49: 394-396.
- Fryxell, J. A. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia (Berl.) 72: 83-91.
- Fryxell, J. M., D. J. T. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in white-tailed deer. J. Wildl. Manage. 55: 377-385.
- Fuller, W. A. 1953. Aerial surveys for beaver in the Mackenzie District, Northwest Territories. Trans. N. Amer. Wildl. Conf. 18: 329-336.
- Gaillard, J. M., A. J. Sempere, J. M. Boutin, G. Van Laere, and B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer. Can. J. Zool. 70: 1541-1545.
- Gates, C. C. and N. C. Larter. 1990. Growth and dispersal of an erupting large herbivore population in northern Canada: the Mackenzie wood bison (*Bison bison athabasca*). Arctic 43: 231-238.
- Goulet, G. 1995. Personal communication, Riding Mountain National Park.
- Green, H. U. 1933. The wapiti of the Riding Mountain, Manitoba. Can. Field Nat. 47(6): 105-11, 122-132, 150-157, 172-174.
- Greer, K. R. 1966. Fertility rates of northern Yellowstone elk populations. Proc. West Assoc. State Game and Fish Comm. 46: 123-128.
- Grenfell, B. T., O. F. Price, S. D. Albon, and T. H. Clutton-Brock. 1992. Overcompensation and population cycles in ungulates. Nature 355: 823-826.
- Gross, J. E. 1969. Optimum yield in deer and elk populations. Trans. N. Amer. Wildl. and Natur. Resour. Conf. 34: 372-387.
- Gunson, J. R. 1970. Dynamics of the beaver of Saskatchewan's northern forest. M.S. Thesis, Univ. Alberta, Edmonton. 122 pp.

*Literature Cited*

- Hakala, J. B. 1952. The life history and general ecology of the beaver (*Castor canadensis* Kuhl) in interior Alaska. M.S. Thesis, Univ. Alaska, Fairbanks. 161 pp.
- Hay, K. G. 1958. Beaver census methods in the Rocky Mountain region. *J. Wildl. Manage.* 22: 395-402.
- Hoggins, T. 1993. Timber wolf and other significant species report for Riding Mountain National Park, 1993. Parks Canada, Riding Mountain National Park, Wasagaming, Manitoba.
- Houston, D. B. 1982. The Northern Yellowstone Elk. Macmillan.
- Hummelt, C. A. 1990. 1989/90 Big Game Hunter Survey. Manitoba Department of Natural Resources.
- Jenkins, S. H. and P. E. Busher. 1979. *Castor canadensis*. *Mammal. Species* 120: 1-8.
- Jones, J. K., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1984. Mammals of the Northern Great Plains. University of Nebraska Press, Lincoln.
- Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. *Can. J. Zool.* 71: 2509-2517.
- Keck, A. J. 1975. The climate of Riding Mountain National Park. Unpubl. Proj. Rep. No. 19. Atmos. Environ. Serv., Toronto. 258 pp.
- Keith, L. B. 1974. Some features of population dynamics in mammals. *Int. Congr. Game Biol.* 11: 17-58.
- Keith, L. B. and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. *Wildlife Monographs* No. 58. 70 pp.
- Kittams, W. H. 1953. Reproduction of Yellowstone Elk. *J. Wildl. Manage.* 17(2): 177-184.
- Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, England. 343 pp.
- Lack, D. 1966. Population studies of birds. Clarendon Press.
- Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *J. Anim. Ecol.* 65: 653-670.

*Literature Cited*

- Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. *J. Wildl. Manage.* 53: 548-557.
- Legendre, L. and P. Legendre. 1983. Numerical ecology. Elsevier Scientific Publishing Company, New York.
- Leonard, R. D. 1980. The distribution and abundance, food habits, and interspecific relationships of the snowshoe hare during winter 1978-79 in Riding Mountain National Park. Large Mammal System Studies Rep. No. 9. Parks Canada, Riding Mountain National Park, Manitoba.
- Leopold, A. 1943. Deer irruptions. Pages 3-11 in Wisconsin's deer problems. Wisc. Cons. Dept. Pub. 321.
- LeResche, R. E. and R. A. Rausch. 1974. Accuracy and precision of aerial moose censusing. *J. Wildl. Manage.* 38: 175-182.
- Lindlof, B., E. Lindstrom, and A. Pherson. 1974. On activity, habitat selection and diet of mountain hare (*Lepus timidus* L.) in winter. *Viltrevy* 9(2): 27-43.
- Lothian, W. F. 1976. A history of Canada's National Parks: Volume I. Can. Dep. Indian North. Aff., Parks Canada. 123 pp.
- Lyon, L. J. 1980. Coordinating forestry and elk management. *Trans. Nor. Am. Wildl. and Nat. Res. Conf.* 45: 278-287.
- MacLennan, R. 1975. Use of forest cuts by big game in the Porcupine forest. *Trans. 11th North Amer. Moose Conf.* pp. 27-37.
- McCullough, D. R. 1979. The George Reserve deer herd. University of Michigan Press, Ann Arbor. 271 pp.
- McRoberts, R. E., L. D. Mech, and R. O. Peterson. 1995. The cumulative effect of consecutive winters' snow depth in moose and deer populations: a defence. *J. Anim. Ecol.* 64: 131-135.
- Madson, J. 1966. The elk. Conserv. Dep., Winchester-Western Div., Olin Corp. East Alton, Ill.: Olin Corporation. 125 pp.
- Manitoba Department of Natural Resources. 1997. Manitoba Hunting Guide.
- Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. *Wildl. Soc. Bull.* 6(2): 88-90.

*Literature Cited*

- May, R. M. 1981. Models for single populations. Pages 5-29 in R. M. May, ed. *Theoretical Ecology*. Blackwell Scientific, Oxford, U.K.
- Mech, L. D. 1966. The wolves of Isle Royale. *Fauna of the Nat'l Parks of the U.S. Ser. 7*. 210 pp.
- Mech, L. D. 1970. *The wolf*. Nat. Hist. Press, Garden City. 384 pp.
- Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. *J. Anim. Ecol.* 56: 615-627.
- Merrill, E. and M. S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263-274 in R. B. Keiter and M. S. Boyce, eds. *The Greater Yellowstone ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, Connecticut.
- Meslow, E. C. and L. B. Keith. 1971. A correlation analysis of weather versus snowshoe hare population parameters. *J. Wildl. Manage.* 35(1): 1-15.
- Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *J. Anim. Ecol.* 60: 377-393.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology* 75(2): 478-488.
- Messier, F. and M. Crete. 1984. Body condition and population regulation by food resources in moose. *Oecologia* 65: 44-50.
- Messier, F. and M. Crete. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* 65: 503-512.
- Milner-Gulland, E. J. 1994. A population model for the management of the saiga antelope. *J. Appl. Ecol.* 31: 25-39.
- Moen, A. N. 1968. Surface temperatures and radiant heat loss from white-tailed deer. *J. Wildl. Manage.* 32(2): 338-344.
- Moen, A. N. 1976. Energy conservation by white-tailed deer in the winter. *Ecology* 57: 192-198.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *J. Wildl. Manage.* 42(4): 715-738.

*Literature Cited*

- Mohler, L. L. and D. E. Toweill. 1982. Regulated elk population and hunter harvests. Pages 561-598 in J. W. Thomas and D. E. Toweill, eds. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pa.
- Murie, O. J. 1951. *The elk of North America*. Harrisburg, Pa.: Stackpole Co. 376 pp.
- Nasimovich, A. A. 1955. The role of the regime of snow cover in the life of ungulates in the USSR. (Translated from Russian). *Can. Wildl. Ser.*, Ottawa. 371 pp.
- Norton-Griffiths, M. 1976. Further aspects of bias in aerial census of large mammals. *J. Wildl. Manage.* 40: 368-371.
- Odum, E. P. 1971. *Fundamentals of ecology*. Third edition. W. B. Saunders Co., Philadelphia. 574 pp.
- Oldemeyer, J. L., A. W. Franzmann, A. L. Brundage, P. D. Arneson, and A. Flynn. 1977. Browse quality and the Kenai moose population. *J. Wildl. Manage.* 41: 533-542.
- Ozoga, J. J. 1968. Variations in microclimate in a conifer swamp deer yard in northern Michigan. *J. Wildl. Manage.* 32(1): 574-584.
- Ozoga, J. J. and L. J. Verme. 1970. Winter feeding patterns of penned white-tailed deer. *J. Wildl. Manage.* 34: 431-439.
- Ozoga, J. J. and L. W. Gysel. 1972. Response of white-tailed deer to winter weather. *J. Wildl. Manage.* 36: 892-896.
- Parks Canada. 1982. *Natural resource management process manual*. Parks Canada, Ottawa. Unpaginated.
- Peek, J. M. 1974. A review of moose food habits in North America. *Naturaliste canadien*, 101: 195-215.
- Peek, J. M. 1980. Natural regulation of ungulates (What constitutes a real wilderness?). *Wildl. Soc. Bull.* 8(3): 217-227.
- Peterson, R. L. 1955. *North American Moose*. University of Toronto Press, Toronto. 280 pp.
- Peterson, R. O. 1977. *Wolf ecology and prey relationship on Isle Royale*. U. S. National Park Service, Scientific Monographs, No. 11.
- Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose and the allometry of population cycles. *Science* 224: 1350-1352.

*Literature Cited*

- Pianka, E. R. 1976. Competition and niche theory. Pages 114-141 in R. M. May, ed. *Theoretical ecology: Principles and applications*. Blackwell Scientific Publications, Oxford.
- Picton, H. D. 1979. A climate index and mule deer fawn survival in Montana. *Int. J. Biometeorology* 23: 115-122.
- Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. *J. Appl. Ecol.* 21: 869-879.
- Pimlott, D. H., J. A. Shannon, and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Land and Forests, Toronto.
- Poll, D. M. 1981. Snowshoe hare population dynamics and interspecific relationships in Riding Mountain National Park during Winter 1979-1980. *Can. Wildl. Ser.*, Edmonton, Alberta.
- Potvin, F. 1988. Wolf movement and population dynamics in the Papineau-Labelle reserve, Quebec. *Can. J. Zool.* 66: 1266-1273.
- Pruitt, W. O., Jr. 1959. Snow as a factor in the winter ecology of the barren-ground caribou. *Arctic* 12: 158-180.
- Ransom, A. B. 1967. Reproductive biology of white-tailed deer in Manitoba. *J. Wildl. Manage.* 31(1): 114-123.
- Real, L. A. 1979. Ecological determinants of functional response. *Ecology* 60: 481-485.
- Riding Mountain National Park Round Table. 1996. Management Plan for Riding Mountain National Park.
- Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. I.U.C.N. Pub., New Series No. 4. pp. 261-273.
- Rounds, R. C. 1976. Selected ecological aspects of wapiti and moose of Riding Mountain National Park, Manitoba. Unpubl. Rep. Parks Canada, Winnipeg, Manitoba. 278 pp.
- Rounds, R. C. 1977. Population fluctuation of wapiti (*Cervus elaphus*) and moose (*Alces alces*) in Riding Mountain National Park, Manitoba 1950-1976. *Can. Field Nat.* 91(2): 130-133.
- Rounds, R. C. 1991. A brief analysis of the biological implications of hunting elk and moose around Riding Mountain National Park. Unpubl. Rep. 13 pp.

*Literature Cited*

- Royama, T. 1996. A fundamental problem in key factor analysis. *Ecology* 77: 87-93.
- Rusch, D. H., M. M. Gillespie and D. I. Makay. 1978. Decline of ruffed grouse population in Manitoba. *Can. Field Nat.* 92: 123-127.
- Saether, B. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* 12(4): 143-149.
- Saether, B. E. and M. Heim. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *J. Anim. Ecol.* 62: 482-489.
- Saether, B., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of a large herbivore, the moose *Alces alces*. *Ecology* 77(5): 1493-1500.
- Samoil, H. 1979. Aspects of snowshoe hare winter ecology in Riding Mountain National Park, 1977-78. Large Mammal System Study Rep. No. 8. Parks Canada, Riding Mountain National Park, Wasagaming, Manitoba. 71 pp.
- Seal, U. S., L. J. Verme, J. J. Ozoga, and A. W. Erickson. 1972. Nutritional effects of thyroid activity and blood of white-tailed deer. *J. Wildl. Manage.* 36: 1041-1052.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can. J. Zool.* 70: 1494-1503.
- Short, H. L., J. D. Newson, G. L. McCoy, and J. F. Fowler. 1969. Effects of nutrition and climate on southern deer. *Trans. N. Am. Wildl. Nat. Res. Conf.* 34: 137-145.
- Silver, H., N. F. Colovos, J. B. Holter, and H. H. Hayes. 1969. Fasting metabolism of white-tailed deer. *J. Wildl. Manage.* 33: 490-498.
- Sinclair, A. R. E. 1977. *The African buffalo*. University of Chicago Press, Chicago.
- Sinclair, A. R. E. 1989. Population dynamics of lemmings: temporal and spatial variation- an introduction. Pages 197-241 in J. M. Cherrett, ed. *Ecological Concepts*. Blackwell Scientific, Oxford, U.K.
- Sinclair, A. R. E., H. Dublin, and M. Borner. 1985. Population regulation of the Serengeti wildebeest: a test of food hypothesis. *Oecologia (Berl.)* 65: 266-268.



*Literature Cited*

- Skogland, T. 1978. Characteristic of the snow cover and its relationship to wild mountain reindeer (*Rangifer tarandus tarandus*) feeding strategies. *Arctic and Alpine Res.* 10(3): 569-580.
- Skogland, T. 1985. The effects of density-dependent resource limitation on the demography of wild reindeer. *J. Anim. Ecol.* 54: 359-374.
- Skogland, T. 1990. Density-dependence in a fluctuating wild reindeer herd; material vs. offspring effects. *Oecologia (Berl.)* 84: 442-450.
- Skuncke, F. 1949. *Algen, studier, jakt och vard.* P. A. Norstedt and Soners, Forlag, Stockholm. 400 pp.
- Sokal, R. R. and F. J. Rohlf. *Biometry.* Third edition. W. H. Freeman and Company, New York. 887 pp.
- Solberg, E. J. and B. E. Saether. 1994. Sexually selected characters as life history traits: annual variation in male body weight and antler size in moose (*Alces alces*). *J. Mammal.* 75: 1069-1079.
- Solomon, M. E. 1976. *Population dynamics.* Second edition. Edward Arnold (Publishers) Ltd., London.
- Soprovich, D. W. 1989. An assessment of the accuracy of the Manitoba general moose hunter questionnaire survey. Technical Report No. 89-02. Manitoba Natural Resources.
- Staines, B. W. 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). *J. Zool. (London)* 184: 403-419.
- Stelfox, J. G. 1976. Riding Mountain National Park- Guidelines for wildlife surveys and data recording. Unpubl. Can. Wildl. Ser. Rep., Edmonton. 12 pp.
- Stewart, R. R., R. R. MacLennan, and J. D. Kinnear. 1977. The relationships of plant phenology to moose. Sask. Dep. Tourism and Natur. Res. Tech. Bull. No. 3. 20 pp.
- Swenson, J. 1985. Compensatory reproduction in an introduced mountain goat population in Absaroka Mountains, Montana. *J. Wildl. Manage.* 49: 837-843.
- Taber, R. D., K. Raedeke, and D. A. McCaughran. 1982. Population characteristics. Pages 279-299 in J. W. Thomas and D. E. Toweill, eds. *Elk of North America: ecology and management.* Stackpole Books, Harrisburg, Pa.

*Literature Cited*

- Tarleton, P. 1992a. A plan for management of Cervidae in Riding Mountain National Park, Unpubl. Parks Canada Rep., Winnipeg, Manitoba. 60 pp.
- Tarleton, P. 1992b. Cervid monitoring and status report, Riding Mountain National Park, 1990-1991. Unpublished Canadian Parks Service Report. 33 pp.
- Telfer, E. S. 1978. Cervid distribution, browse and snow cover in Alberta. *J. Wildl. Manage.* 42(2): 352-361.
- Telfer, E. S. and J. P. Kelsall. 1971. Morphological parameters for mammal locomotion in snow. Paper presented at the 51st Ann. Meeting Am. Soc. Mamm., Vancouver, B.C. 6 pp., typescript.
- Telfer, E. S. and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. *Can. J. Zool.* 57(11): 2153-2159.
- Thompson, C. B., J. B. Holter, H. H. Hayes, H. Silver, and W. E. Urban, Jr. 1973. Nutrition of white-tailed deer. I. Energy requirements of fawns. *J. Wildl. Manage.* 37(3): 301-311.
- Trottier, G. C. 1980. Aerial beaver censuses in Riding Mountain National Park 1973-1980. Large Mammal System Study Rep. No. 11. *Can. Wildl. Ser.*, Edmonton. 53 pp.
- Trottier, G. C. and H. P. Samoil. 1978. Resource partitioning by ungulates and snowshoe hares in Riding Mountain National Park, Manitoba. Wildlife Society's (Central Mountains and Plains Section) meeting, Aug. 27-30, Riding Mountain National Park, Manitoba. 24 pp.
- Trottier, G. C. and R. C. Hutchison. 1980. Range, habitat and food relationships of ungulates in Riding Mountain National Park. Unpubl. *Can. Wildl. Ser. Rep.*, Edmonton. 102 pp.
- Trottier, G. C. and R. C. Hutchison. 1982. Ungulate- winter severity relationships in Riding Mountain National Park 1977-1980. Final Report. Large Mammal System Studies Rep. No. 12. *Can. Wildl. Ser.*, Edmonton. 36 pp.
- Trottier, G. C., S. R. Rollans and R. C. Hutchison. 1983. Range, habitat and foraging relationships of ungulates in Riding Mountain National Park. Large Mammal System Studies Rep. No. 14. *Can. Wildl. Ser.*, Edmonton. 224 pp.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19-40 in N. Cappuccino and P. W. Price, eds. *Population dynamics*. Academic Press.

*Literature Cited*

- Van Ballenberghe, V. 1987. Effects of predation on moose numbers: a review of recent North American studies. *Swedish Wildl. Res. Suppl.* 1: 431-460.
- Verme, L. J. 1968. An index of winter weather severity for northern deer. *J. Wildl. Manage.* 32(3): 566-574.
- Verme, L. J. and J. J. Ozoga. 1981. Appraisal of autumn-spring weather severity for northern deer. *Wildl. Bull.* 9: 292-295.
- Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. *J. Range Manage.* 30: 122-127.
- Watson, A. and R. Moss. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. Pages 167-220 *in* A. Watson, ed. *Animal populations in relation to their food supply*. Blackwell Scientific Publications, Oxford.
- Young, S. P. and H. T. Jackson. 1951. *The clever coyote*. Univ. Nebraska Press, Lincoln. 41 pp.

## APPENDIX A

### SAMPLE DBASE 4.1 CALCULATIONS: 1995 Ungulate Aerial Survey

Ungulate abundance survey 1995

RIDING MOUNTAIN NATIONAL PARK ELK ABUNDANCE SURVEY					
conducted January 26-30, 1995					
TRANSECT	TRANSECT AREA	COUNT	DENSITY	COUNT SQUARED	01-Feb-95 COUNT*AREA
1	3.862	3	0.777	9	11.586
2	10.298	49	4.758	2401	504.602
3	11.907	56	4.703	3136	666.792
4	13.355	8	0.599	64	106.84
5	13.998	15	1.072	225	209.97
6	14.803	7	0.473	49	103.621
7	14.964	16	1.069	256	239.424
8	13.837	20	1.445	400	276.74
9	13.837	26	1.879	676	359.762
10	13.194	20	1.516	400	263.88
11	13.355	15	1.123	225	200.325
12	13.516	7	0.518	49	94.612
13	13.516	9	0.666	81	121.644
14	13.194	5	0.379	25	65.97
15	13.033	15	1.151	225	195.495
16	14.32	15	1.047	225	214.8
17	14.964	10	0.668	100	149.64
18	14.803	10	0.676	100	148.03
19	15.446	9	0.583	81	139.014
20	16.412	7	0.427	49	114.884
21	16.573	14	0.845	196	232.022
22	16.573	6	0.362	36	99.438
23	15.768	10	0.634	100	157.68
24	14.964	5	0.334	25	74.82
25	13.516	18	1.332	324	243.288
26	13.355	28	2.097	784	373.94
27	13.516	27	1.998	729	364.932
28	12.872	46	3.574	2116	592.112
29	12.293	25	2.034	625	307.325
30	12.036	32	2.659	1024	385.12
31	11.849	15	1.288	225	174.735
32	12.293	45	3.661	2025	553.185
33	12.357	65	5.260	4225	803.205
34	12.711	32	2.518	1024	406.752
35	13.677	23	1.682	529	314.571
36	13.998	21	1.500	441	293.958
37	13.194	15	1.137	225	197.91
38	12.228	46	3.762	2116	562.488
39	12.228	37	3.026	1369	452.436
40	12.228	39	3.189	1521	476.892
41	12.228	19	1.554	361	232.332
42	12.228	34	2.781	1156	415.752
43	12.228	18	1.472	324	220.104
44	11.263	21	1.855	441	236.523
45	10.298	54	5.244	2916	556.092
46	10.619	28	2.637	784	297.332
47	10.941	78	7.129	6084	853.398

Appendix A- Sample dBase 4.1 Calculations

Ungulate abundance survey 1995

48	10.941	11	1.005	121	120.351
49	10.941	9	0.823	81	98.469
50	9.01	42	4.661	1764	378.42
51	6.436	14	2.175	196	90.104
52	5.792	12	2.072	144	69.504
53	5.792	12	2.072	144	69.504
54	5.792	0	0.000	0	0
55	5.792	0	0.000	0	0
56	5.792	5	0.863	25	28.96
57	5.792	3	0.518	9	17.376
58	5.792	3	0.518	9	17.376
59	5.792	4	0.691	16	23.168
60	5.792	5	0.863	25	28.96
61	5.792	2	0.345	4	11.584
62	5.792	4	0.691	16	23.168
63	5.792	1	0.173	1	5.792
64	5.792	3	0.518	9	17.376
65	5.792	22	3.798	484	127.424
66	5.792	2	0.345	4	11.584
67	5.792	1	0.173	1	5.792
68	3.218	6	1.865	36	19.308

Appendix A- Sample dBase 4.1 Calculations

Ungulate abundance survey 1995

<b>TOTALS</b>	<b>747.665</b>	<b>1284</b>	<b>1.717347</b>	<b>43590</b>	<b>15230.193</b>
Number of elk counted on transects:		1284			
Total area surveyed:		747.665 square kilometres			
Average density of elk per square kilometre (Jan. 95)		1.717346673			
Population estimate (Elk, January 1995)		5128.3			
Sum of squared observations		43590			
Sum of transect area x transect count:		15230.19			
Sum of squared areas:		9137.861			
Navigator/Recorder:	Gordon Pylypuik	Population variance:		1169923	
Left Observer:	Glenn Schmidt	Population standard error:		1089.672	
Right Observer:	Art Cochrane	Confidence 95%:		258.9934	
Left/Right Observer Jan. 26:	Ron Chotka	Covariance:		16.36057	
Flights:	January 26, 27, 28, 29, 30, 1995	Elk population estimate is:		5128.28	
N = the number of sample units in the population		269			
n = the number of sample units in the sample		68			
Z = the area of the census zone		2985			
z = the area of any one sample unit					
Y = the number of animals counted in that unit					
R = the ratio of animals counted to area searched =	SumY/Sumz =	density			
Szsq =	$1/n-1(Zsq-(Z)sq/n)$ = variance between the area of all sample units:	13.68999			
Where Z	is the individual transect area and n	is the number of transects surveyed.			
R estimated density = $y_i/z_i$ =		1.717347			
SYsq =	$1/n-1(Ysq-(Y)sq/n)$ = variance between elk counted in individual transects =	288.7322			
Szy =	$1/n-1(\sum(Z_i*Y_i)-(Z*Y)/n)$ =				
	covariance between elk counted and the area of each transect =	16.60476			
Where Z <sub>i</sub>	is the area of an individual transect and Y <sub>i</sub> is the count of elk on individual transects.				
Var (Y) =	$N(N-n)/n(SYsq-2RSzy+RsqSzsq)$ =	795.1323529	231.6999796	40.37561	
			216336.1036		
		216336.1	is the variance of Y		
square root of var Y is the standard error					
SE (Y) =	population standard error =	465.1195			
95% confidence limits of Y is:	465.119	t where t = 1.96 =		+/-	911.6341
Elk population upper confidence is:	6037.9				
	population estimate is:	5128.3	plus or minus	17.78%	
	lower confidence is:	4214.6			

Appendix A- Sample dBase 4.1 Calculations

Ungulate abundance survey 1995

RIDING MOUNTAIN NATIONAL PARK MOOSE ABUNDANCE SURVEY					
conducted January 26-30, 1995					
01-Feb-95					
TRANSECT	TRANSECT AREA	COUNT	DENSITY	COUNT SQUARED	COUNT*AREA
1	3.862	2	0.518	4	7.724
2	10.298	17	1.651	289	175.066
3	11.907	22	1.848	484	261.954
4	13.355	31	2.321	961	414.005
5	13.998	31	2.215	961	433.938
6	14.803	33	2.229	1089	488.499
7	14.964	19	1.270	361	284.316
8	13.837	9	0.650	81	124.533
9	13.837	23	1.662	529	318.251
10	13.194	21	1.592	441	277.074
11	13.355	12	0.899	144	160.26
12	13.516	19	1.406	361	256.804
13	13.516	16	1.184	256	216.256
14	13.194	5	0.379	25	65.97
15	13.033	24	1.841	576	312.792
16	14.32	22	1.536	484	315.04
17	14.964	15	1.002	225	224.46
18	14.803	28	1.892	784	414.484
19	15.446	30	1.942	900	463.38
20	16.412	15	0.914	225	246.18
21	16.573	11	0.664	121	182.303
22	16.573	17	1.025	289	281.741
23	15.763	27	1.712	729	425.736
24	14.964	15	1.002	225	224.46
25	13.516	27	1.998	729	364.932
26	13.355	24	1.797	576	320.52
27	13.516	25	1.850	625	337.9
28	12.872	27	2.098	729	347.544
29	12.293	10	0.813	100	122.93
30	12.035	22	1.828	484	264.77
31	11.649	23	1.974	529	267.927
32	12.293	25	2.034	625	307.325
33	12.357	63	5.098	3969	778.491
34	12.711	31	2.439	961	394.041
35	13.677	27	1.974	729	369.279
36	13.998	16	1.143	256	223.968
37	13.194	28	2.122	784	369.432
38	12.228	21	1.717	441	256.788
39	12.228	21	1.717	441	256.788
40	12.228	37	3.025	1369	452.436
41	12.228	30	2.453	900	366.84
42	12.228	30	2.453	900	366.84
43	12.228	49	4.007	2401	599.172
44	11.263	31	2.752	961	349.153
45	10.298	10	0.971	100	102.98
46	10.619	14	1.318	196	148.666
47	10.941	21	1.919	441	229.761

*Appendix A- Sample dBase 4.1 Calculations*

**Ungulate abundance survey 1995**

48	10.941	25	2.376	676	284.466
49	10.941	31	2.833	961	339.171
50	9.01	19	2.109	361	171.19
51	6.436	14	2.175	196	90.104
52	5.792	17	2.935	289	98.464
53	5.792	19	3.280	361	110.048
54	5.792	14	2.417	196	81.088
55	5.792	8	1.381	64	46.336
56	5.792	12	2.072	144	69.504
57	5.792	11	1.899	121	63.712
58	5.792	13	2.244	169	75.296
59	5.792	13	2.244	169	75.296
60	5.792	11	1.899	121	63.712
61	5.792	18	3.108	324	104.256
62	5.792	14	2.417	196	81.088
63	5.792	14	2.417	196	81.088
64	5.792	15	2.590	225	86.88
65	5.792	18	3.108	324	104.256
66	5.792	7	1.209	49	40.544
67	5.792	24	4.144	576	139.008
68	3.218	19	5.904	361	61.142



Appendix A- Sample dBase 4.1 Calculations

Ungulate abundance survey 1995

<b>TOTALS</b>	<b>747.665</b>	<b>1413</b>	<b>1.8899</b>	<b>35869</b>	<b>16440.358</b>	
Number of moose counted on transects:					<b>1413</b>	
Total area surveyed:					<b>747.665</b>	
Average density of moose per square kilometre (Jan. 1995)					<b>1.8899</b>	
Population estimate (Moose, January 1995)						<b>5641.3033</b>
Sum of squared observations					<b>35869</b>	
Sum of transect area x transect count:					<b>16440.358</b>	
Sum of squared areas:					<b>9137.861</b>	
Navigator/Recorder:	<b>Gordon Pylypuik</b>		Population variance:	<b>325706.93</b>		
Left Observer:	<b>Glenn Schmidt</b>		Population standard error:	<b>574.95063</b>		
Right Observer:	<b>Art Cochrane</b>		Confidence 95%:	<b>136.65437</b>		
Left/Right Observer Jan. 26:	<b>Ron Chotka</b>		Covariance:	<b>13.29881</b>		
Flights:	<b>January 26, 27, 28, 29, 30, 1995</b>		Moose population estimate is:	<b>5641.3</b>		
N = the number of sample units in the population				<b>269</b>		
n = the number of sample units in the sample				<b>68</b>		
Z = the area of the census zone				<b>2985</b>		
z = the area of any one sample unit						
Y = the number of animals counted in that unit						
R = the ratio of animals counted to area searched =	SumY/Sumz =					density
Szsq =	$1/n-1(Zsq-(Z)sq/n)$		variance between the area of all sample units:			<b>13.689991</b>
Where Z	is the individual transect area and n is the number of transects surveyed.					
R estimated density = y/zl =						<b>1.889984</b>
SYsq =	$1/n-1(Ysq-(Y)sq/n)$		variance between moose counted in individual transects =			<b>97.129719</b>
Szy =	$1/n-1(\sum(Zi*Yi)-(Z*Y)/n)$					
	covariance between moose counted and the area of each transect =					<b>13.4973</b>
Where Zi	is the area of an individual transect and Yi is the count of moose on individual transects.					
Var (Y) =	$N(N-n)/n(SYsq-2RSzy+RsqSzsqs)$			<b>795.1323529</b>	<b>46.11306062</b>	<b>48.896004</b>
	<b>75544.7814</b>				<b>75544.7814</b>	
the square root of var Y is the standard error						
SE (Y) =	population standard error =			<b>274.8541</b>		
95% confidence limits of Y is:		<b>274.8541</b>	*t where t = 1.96 =		<b>+/-</b>	<b>538.71405</b>
Moose population upper confidence is:		<b>6180.0</b>				
	population estimate is:	<b>5641.3</b>	plus or minus		<b>9.55%</b>	
	lower confidence is:	<b>5102.6</b>				

## **APPENDIX B**

### **METHODS OF WILDLIFE POPULATION ESTIMATION IN RMNP**

#### **1.0 Method for Elk/ Moose Harvest Estimation in GHAs 23 and 23A (Hummelt 1990)**

Each year, harvest statistics for various species of big game are estimated by a questionnaire method organized by the Department of Natural Resources (DNR). A sample questionnaire is presented in Figure 1. For draw seasons, names and addresses of successful applicants were received from Wildlife and Fisheries Licensing. Sampling was systematic and the sampling intensity was 100% of all tags. For those seasons where two licensees were allotted one tag (Firearm season), only one licensee per pair was sampled. It was attempted to send out questionnaires on the day prior to the end of the season. A second questionnaire was sent out to individuals who had not responded within 28 days after the first mailing. Questionnaires received after July 31st were not included in the data used to generate estimates. Similarly, license sales figures used in the estimates were those supplied by Wildlife and Fisheries Licensing at July 31st. After this time, harvest estimates for a particular GHA could be calculated with the following equation:

$$\text{Harvest (GHA)} = \frac{\text{Number of Licenses Sold} \times \text{Number of Kills (GHA)}}{\text{Number of Responses}}$$

The assumption necessary to making this estimate is that hunters from the GHA in question return questionnaires at the same rate as all hunters for the season (Hummelt 1990).

**Manitoba Elk Hunter:**

Each year we select a random sample of elk licences and request their assistance by completing a questionnaire. Please return the completed postcard as soon as possible; even if you did not hunt or kill an elk (or moose in G.H.A. 23/23A). Your reply will assist us in our management efforts and enable us to provide a sound population base for future years.

From our last year's survey we estimated that 3,133 elk hunters (2,746 tags) hunted for a total of 17,500 days, harvesting 1,022 elk and 242 moose.

NO POSTAGE OR ENVELOPE IS REQUIRED. YOUR SIGNATURE IS NOT NECESSARY.

SEPTEMBER							OCTOBER							NOVEMBER							DECEMBER							JANUARY																																																																
S	M	T	W	T	F	S	S	M	T	W	T	F	S	S	M	T	W	T	F	S	S	M	T	W	T	F	S	S	M	T	W	T	F	S																																																										
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31

NOTE: IF YOU DID NOT HUNT IN ANY 1985/86 ELK SEASON,  
PLEASE CHECK HERE  AND RETURN.

- In which 1985/86 elk season did you hunt? Landowner  Bowhunter  Firearm
- Did you use your game tag during the 1985/86 elk season? Yes  No   
*(If no, hunters: Do not mark yet unless your game tag was used.)*

If no, please go to question 5.

- In which game hunting area did you tag your animal? Game Hunting Area No.
- Was the animal you tagged an:
  - 1) adult male elk  3) immature male elk  5) adult male moose  7) immature male moose
  - 2) adult female elk  4) immature female elk  6) adult female moose  8) immature female moose
  - \*born in 1985* *\*born in 1985*

- Please list the number of days you hunted by Game Hunting Area:
 

Game Hunting Area Number	Number of Days Hunted
<i>(Please see map for reference)</i>	
G.H.A. <input type="text"/>	No. of Days <input type="text"/>
G.H.A. <input type="text"/>	No. of Days <input type="text"/>

339

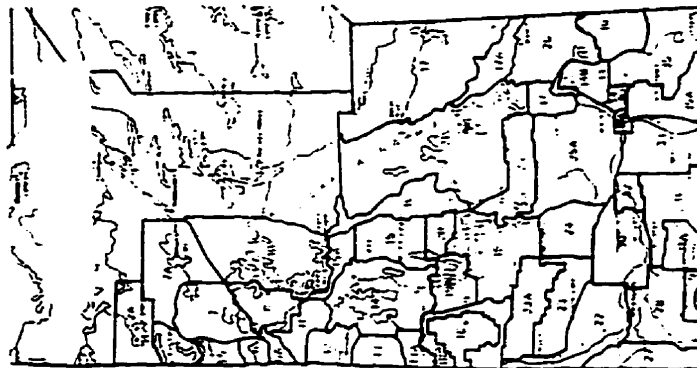


Figure 1. Sample Hunter Survey (Hummelt 1990).

### **1.1 Reliability of Harvest Statistics**

Harvest statistics, when generated by questionnaire are invariably inaccurate. This is true because of non-response bias (hunters who respond do not represent those who do not respond) and response bias (information is incorrectly recorded for a variety of reasons)(Hummelt 1990). For the Manitoba general moose season, Soprovich (1989) found that non-response bias resulted in harvest over-estimates of 43.0% for the late season, 23.7% for both seasons combined, and 64.4% for GHA 26. Soprovich (1989) also found several examples of response bias, including “brag” bias, inability of some hunters to correctly identify the age of their deer, mechanical error (checking the wrong box), the questionnaire having been answered by the wrong individual, and a case where two hunters who have tagged one moose between them will sometimes both indicate having tagged a moose.

It is to be expected that estimates for other seasons would exhibit similar levels of inaccuracy. For seasons with high response rate and negligible response bias (response bias is largely unknown for Manitoba estimates), estimates might be expected to be reasonably accurate. Because these harvest statistics are known to be inaccurate or it is reasonable to assume that they are inaccurate, they should be treated as indices to the statistics of interest. However, like the ungulate aerial surveys, managers should not ignore the indices principle value as indicators to change in harvest since the harvest statistics are collected with a consistent method.

### **2.0 Beaver Aerial Survey Technique (Trottier 1980)**

First, the Park was subdivided into 128 units (square quadrats each  $23.3 \text{ km}^2$ ) then 30 were chosen by beginning at a random starting point and selecting every fourth quadrat along east-west lines to sample colony density (Figure 2)(Trottier 1980). The 30 quadrats constituted 23.4% coverage of the Park. This random-start, systematic allocation of quadrats ensured homogenous coverage of the Park, yet maintained objectivity for statistical analysis. Stratification based on physiography identified local differences in

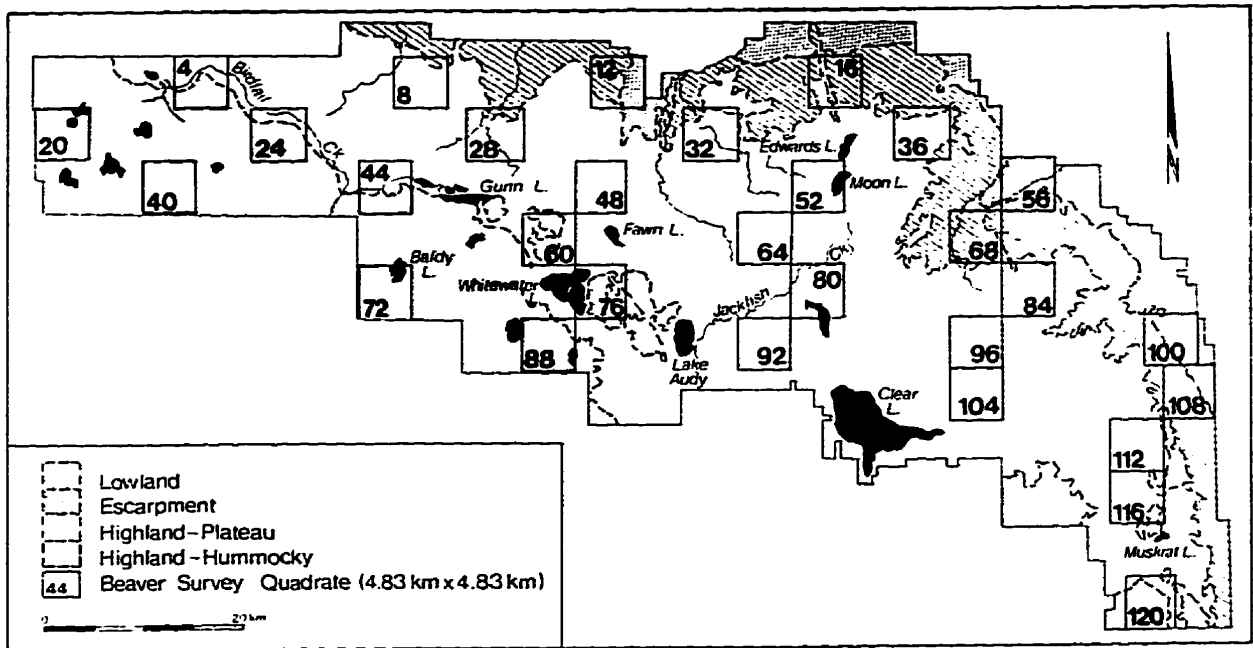


Figure 2. Distribution of Sample Quadrats for Aerial Beaver Censuses in Riding Mountain National Park (Trottier 1980).

population trends and densities which were not illustrated when data for all quadrats were pooled.

Each quadrat was systematically flown to obtain total coverage. Navigation was aided by use of an airphoto-mosaic (scale 1:1, 320) prepared for each quadrat. Each mosaic was scribed with 12 north-south flight-lines, spaced at 400 m intervals beginning 200 m inside the quadrat boundaries. All lines were flown approximately 122 m aboveground at 135 km/hr in a fixed-wing aircraft. Two observers occupied the rear seats of the aircraft and counted winter food caches (feed piles) seen on the observation strips. Window markers were used to limit the observation strip (approximately 200 m on either side of the aircraft).

The presence of a feed pile, which serves as a source of winter food for a colony, was the sole criterion used as proof of an active colony. Fuller (1953) and Hay (1958) report that the number of feed piles is the only sign of beaver activity that correlates directly with the number of colonies. These structures also happen to be very easy to detect during aerial surveys.

During the surveys for 1973, 1976 and 1977, the observers tallied feed piles on hand counters then reported totals for each flight line. Since 1979, the observers have used an intercom to report observations to an additional crew member who plotted sightings on the photo-mosaic. The survey crew consisted of a pilot, navigator, two right observers, two left observers and a recorder.

The beaver population, expressed as the number of colonies, was estimated by multiplying mean colony density of the 30 quadrats by the total number of quadrats in the Park (127.555). Confidence intervals were also calculated.

### **2.1 Reliability of Colony Estimates**

Since beaver feed piles are easy to see from the air at low altitudes (except those directly below the aircraft) and are stationary, the factors most responsible for errors are ability to accurately fly the transects and ability and performance of the observers (LeResche and Rausch 1974), which in turn are influenced by quality of navigation, altitude, air speed, winds, turbulence, light and vegetation cover. It is likely that navigation problems were

adequately controlled in the surveys by the navigator using detailed airphoto mosaics. Cross-winds, however, constantly push the aircraft off course and even with continual adjustments there is surely a source of error in maintaining the intended course. High winds and subsequent turbulence are equally important since they affect aircraft altitude and consequently, transect width. Turbulence nauseates the crew and affects their ability. Vegetation may not be an important factor except when ponds are very small and surrounded by coniferous cover (although this habitat would not be preferred by beaver) (Trottier 1980).

As with the hunter surveys and the ungulate aerial surveys, bias remains consistent in the beaver aerial surveys from year to year, and therefore provides a good index of the population.

### **3.0 Method for Wolf Ground Surveys (Hoggins 1993)**

All Park Wardens were responsible for submitting information on wolf sightings, wolf tracks, wolf mortalities and wolf prey data. When an actual sighting occurred, location, color of animal(s) and approximate age and condition of the animal(s) is recorded. Some excellent sighting information was collected during the ungulate and beaver aerial surveys. The respective survey coordinators recorded actual sightings and pass on this information to the Wolf Project Coordinator.

During the winter months, field wardens were continually looking for wolf tracks. When tracks were located, the animals were back-tracked to determine the number of animals in that pack and direction of travel. It was hoped, during the winter, wardens observed tracks in their areas on numerous occasions. From this data, the Project Coordinator established wolf pack territorial boundaries. During the month of February, a five-day wolf tracking blitz occurred (February is breeding season for wolves and they are very active during this time), and wardens were out covering their areas as often as possible.

#### **4.0 Method for Snowshoe Hare Track Surveys (Samoil 1979)**

Snowshoe hare track surveys were used to estimate 'hare activity units'. These surveys included track count transects in nine representative cover types (Table 1, Figure 3).

**Table 1. Names, Lengths and Locations of Snowshoe Hare Transects in Nine Cover Types within Riding Mountain National Park.**

NAME	LENGTH (m)	LOCATION
1. Poplar-Unburned	1022	Baldy Lake Road (South)
2. Poplar-Birch	866	Baldy Lake Fire Tower Trail and Baldy Lake Trail
3. Poplar-Spruce	885	Baldy Lake Road (North)
4. White Spruce	536	Gunn Lake Trail
5. Poplar-Burned	547	North of Gunn Lake
6. Black Spruce- Burned	552	North of Gunn Lake
7. Black Spruce- Unburned	331	North of Gunn Lake
8. Shrubland	351	North of Gunn Lake
9. Tamarack	449	East of Gunn Lake

The transect surveys commenced two days after a minimum snowfall of one centimeter (allowed for a standard period of activity), and were usually finished in the same day. Due to the low number of hare tracks after 1982, counts were conducted by snowmobile with only occasional travel by snowshoe. In years of high hare densities, counts were most often obtained on foot. All tracks intercepting the transect were identified to species; mammals smaller than red squirrels were not recorded. Tracks which followed a transect for the entire length were recorded as a single occurrence.

Hare tracks were weighted in the following manner: single track (1); 25% trampling of snow cover (1+(1)); 50% trampling of snow cover (1+(2)); 75% trampling of snow cover (1+(3)); or 100% trampling of snow cover (1+(4)). Hare activity units (HAUs) were calculated by dividing the summed weighted values of each transect by the length of the transect (m) and multiplying by 100 (divide the total by 9).



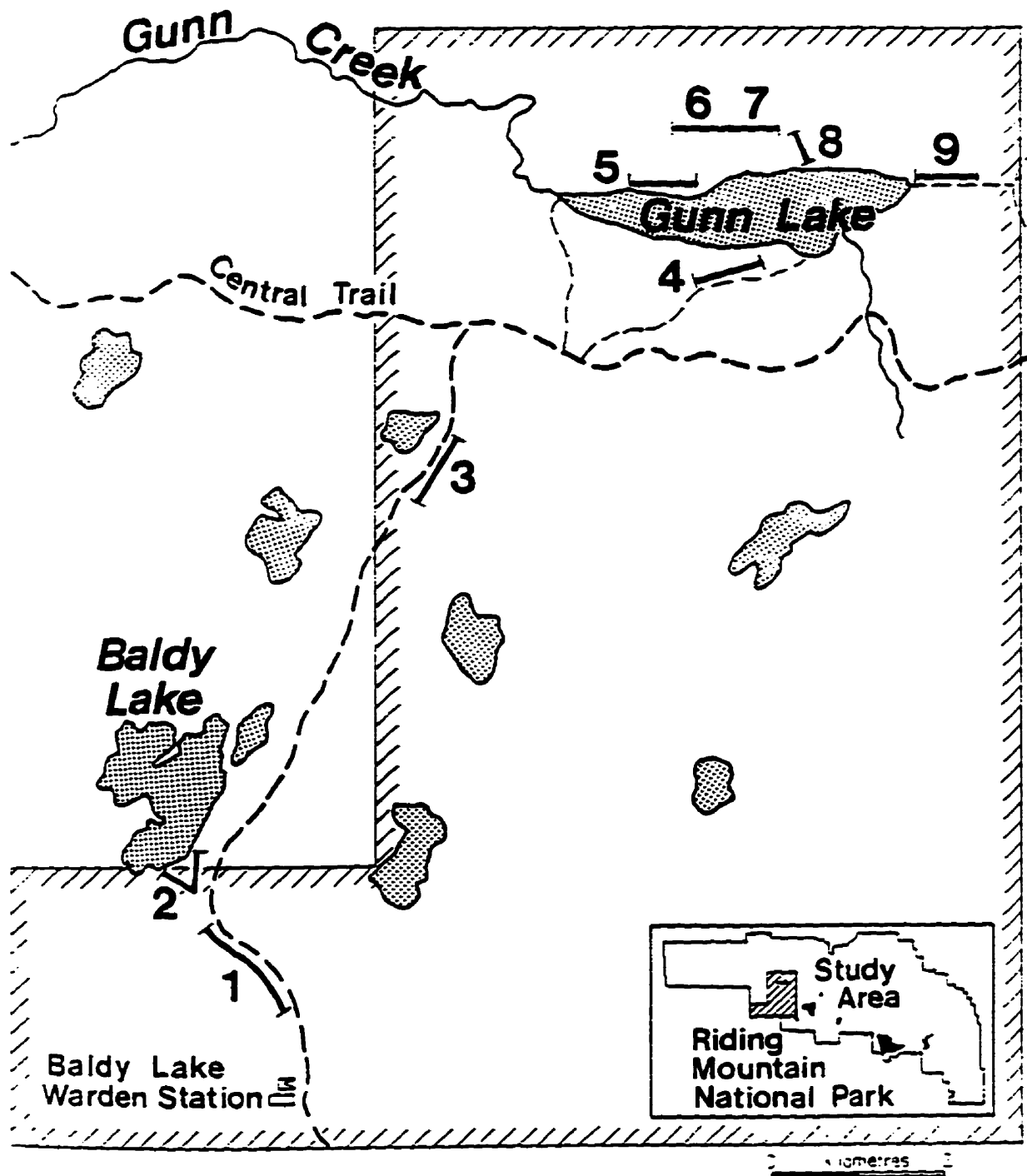


Figure 3. Location of the Study Area and Snowshoe Hare Activity Transects in Western Riding Mountain National Park (Samoil 1979).

## APPENDIX C

### NON-SIGNIFICANT RELATIONSHIPS

#### 1.0 Relationship Between Elk and Wolves

Figure 1. Number of Elk vs. Wolves

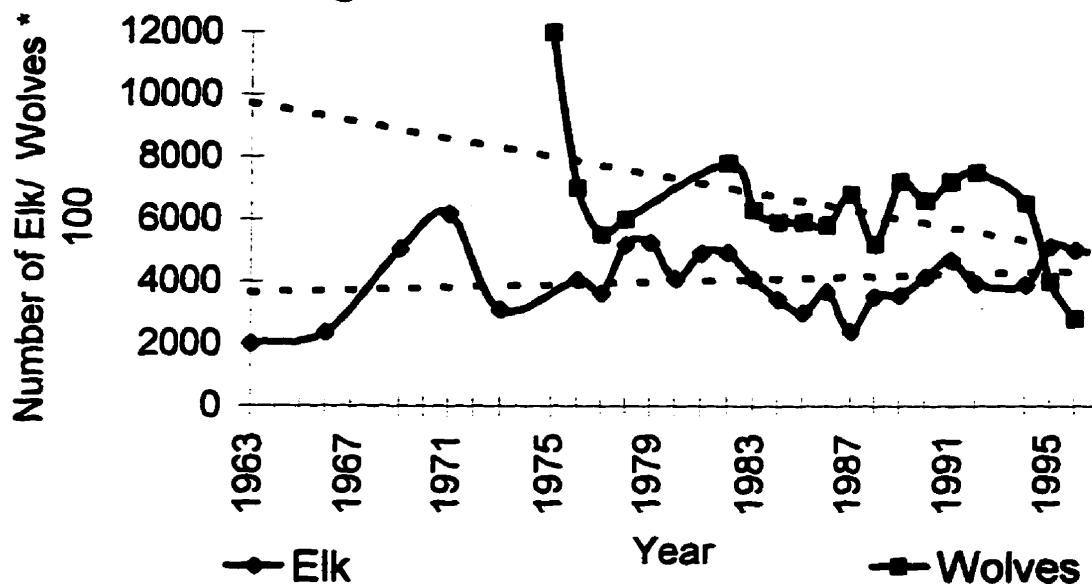
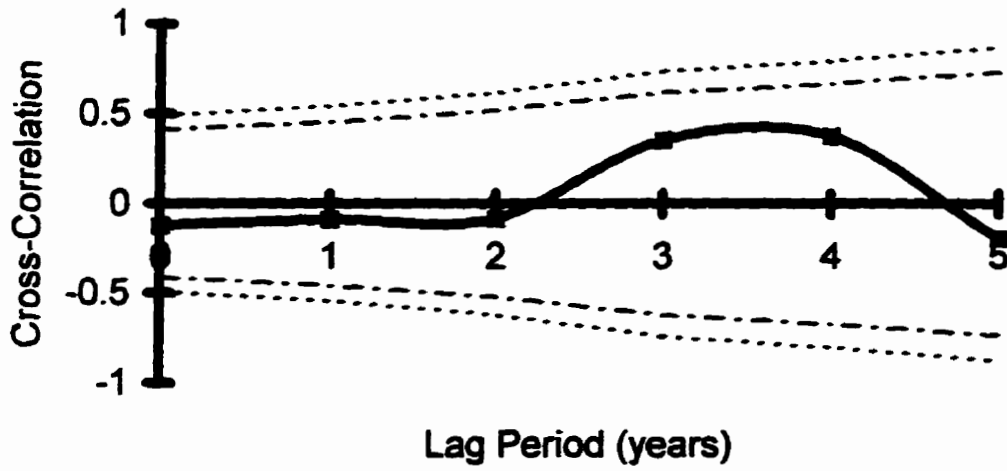


Table 1. Elk vs. Wolves

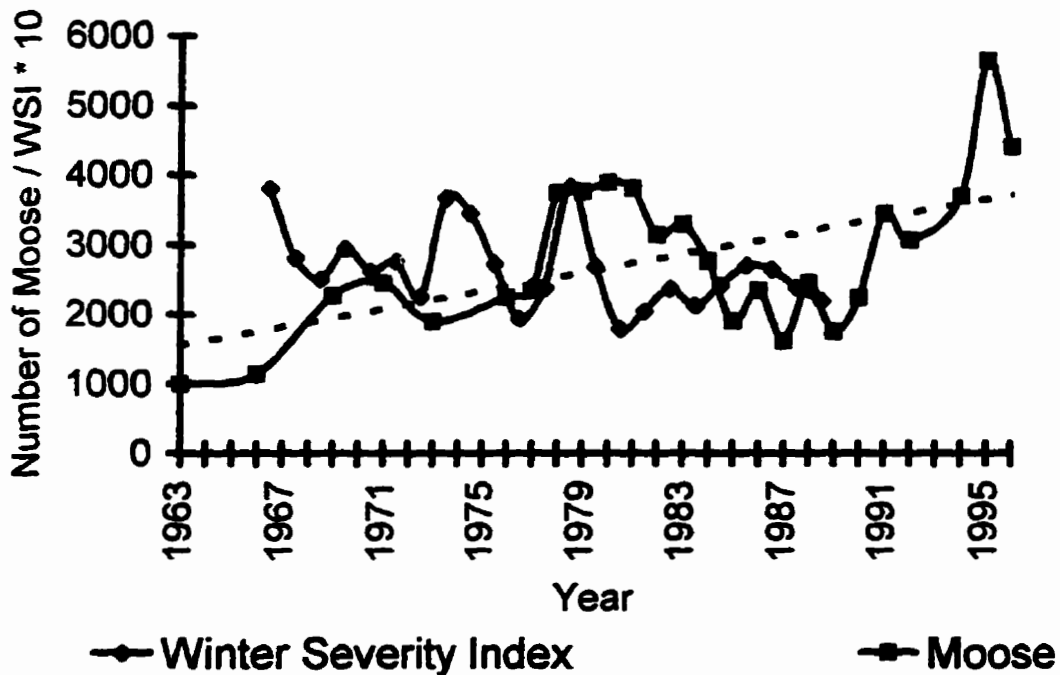
	<i>ELK</i>	<i>n</i>
No lag	-0.1207	17
1-yr. lag	-0.08914	15
2-yr. lag	-0.08311	13
3-yr. lag	0.3522	11
4-yr. lag	0.3771	11
5-yr. lag	-0.1945	11

Figure 2. Correlogram- Elk vs. Wolves



2.0 Relationship Between Moose and Winter Severity

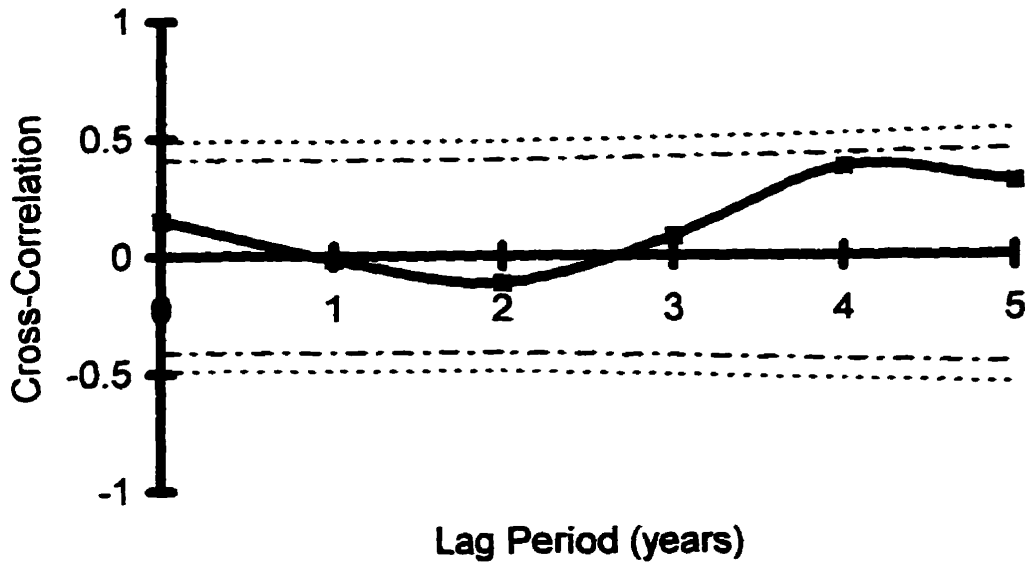
Figure 3. Number of Moose vs. Winter Severity



**Table 2. Moose vs. Winter Severity**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	0.1514	17
<b>1-yr. lag</b>	-0.01629	18
<b>2-yr. lag</b>	-0.1148	19
<b>3-yr. lag</b>	0.08390	19
<b>4-yr. lag</b>	0.3793	19
<b>5-yr. lag</b>	0.3141	19

**Figure 4. Correlogram- Moose vs. WSI**



### 3.0 Relationship Between Moose and Monthly Temperature

Figure 5. Number of Moose vs. Winter Temperature Indices

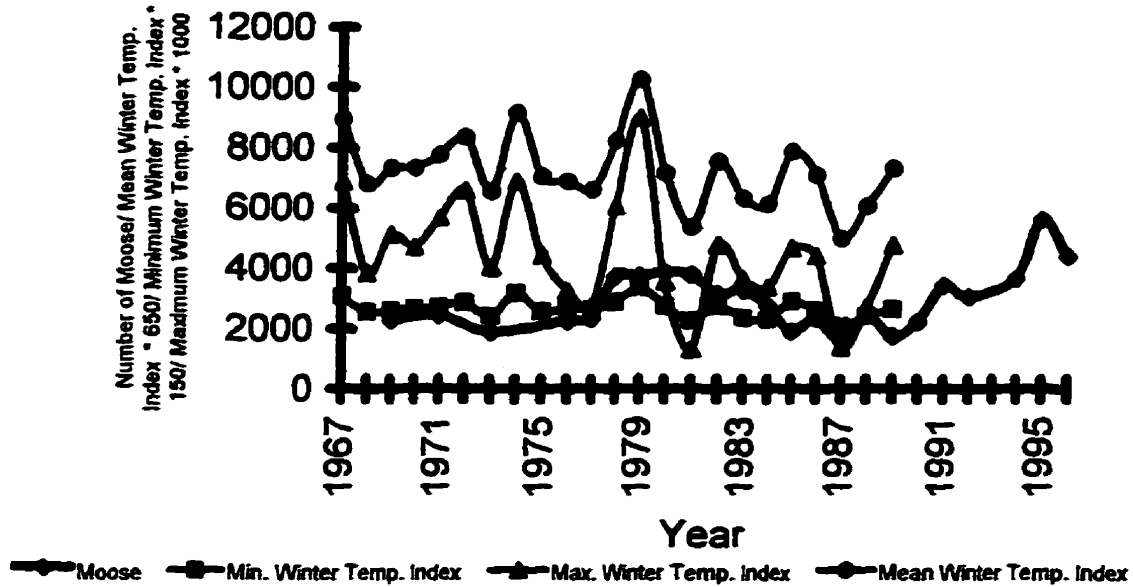
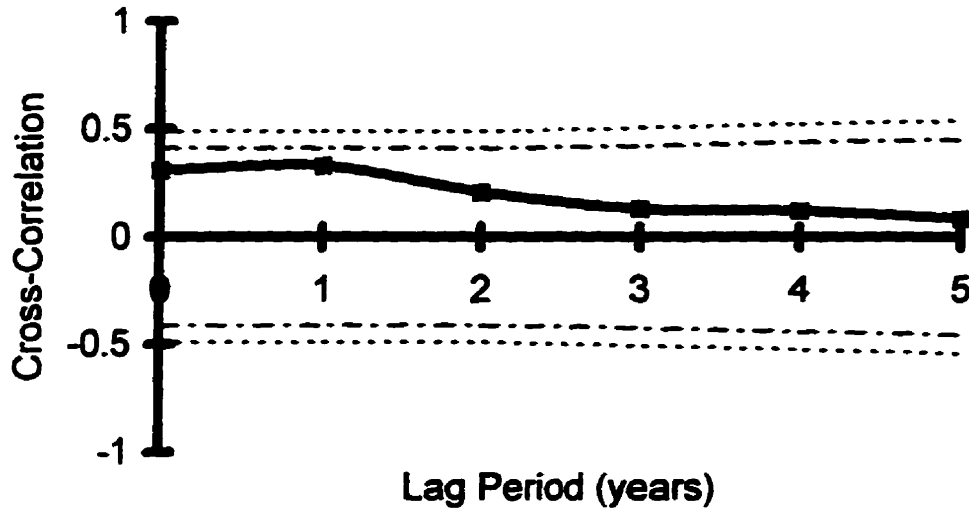


Table 3. Moose vs. Mean Winter Temperature Index

	<i>MOOSE</i>	<i>n</i>
No lag	0.3054	17
1-yr. lag	0.3275	18
2-yr. lag	0.2056	19
3-yr. lag	0.1312	19
4-yr. lag	0.1199	19
5-yr. lag	0.08463	19

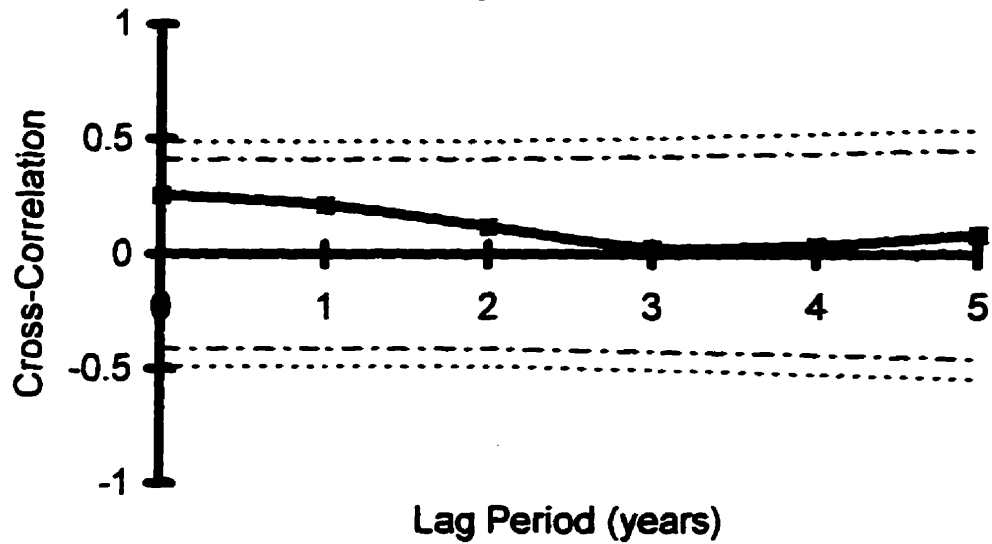
**Figure 6. Correlogram- Moose vs. Mean Winter Temperature Index**



**Table 4. Moose vs. Maximum Winter Temperature Index**

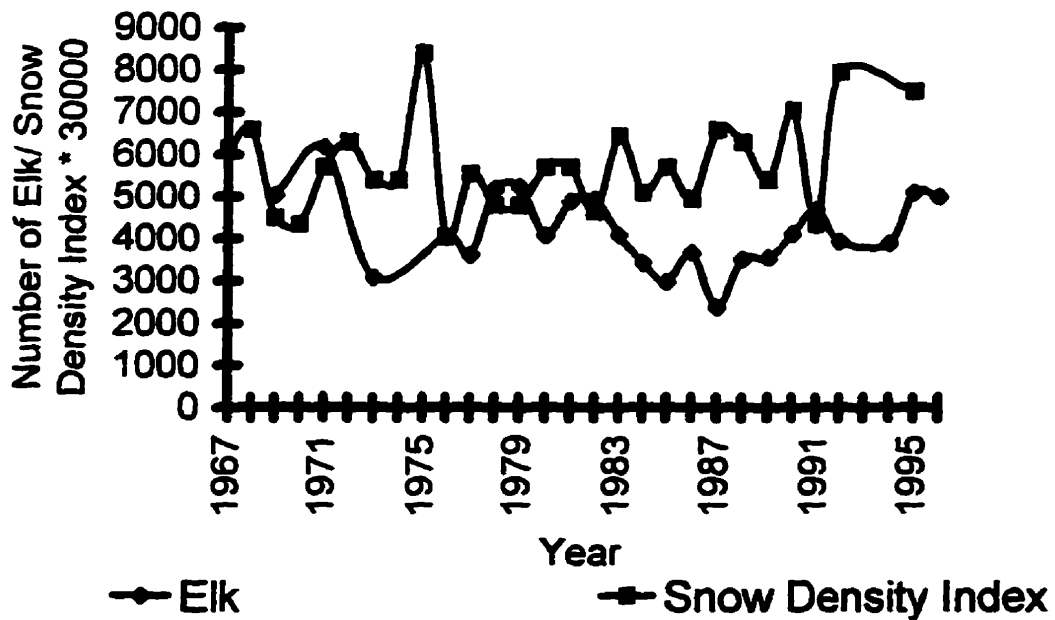
	<i>MOOSE</i>	<i>n</i>
No lag	0.2545	17
1-yr. lag	0.2127	18
2-yr. lag	0.1188	19
3-yr. lag	0.02745	19
4-yr. lag	0.03863	19
5-yr. lag	0.08593	19

**Figure 7. Correlogram- Moose vs. Maximum Temperature Index**



**4.0 Relationship Between Elk and Snow Density**

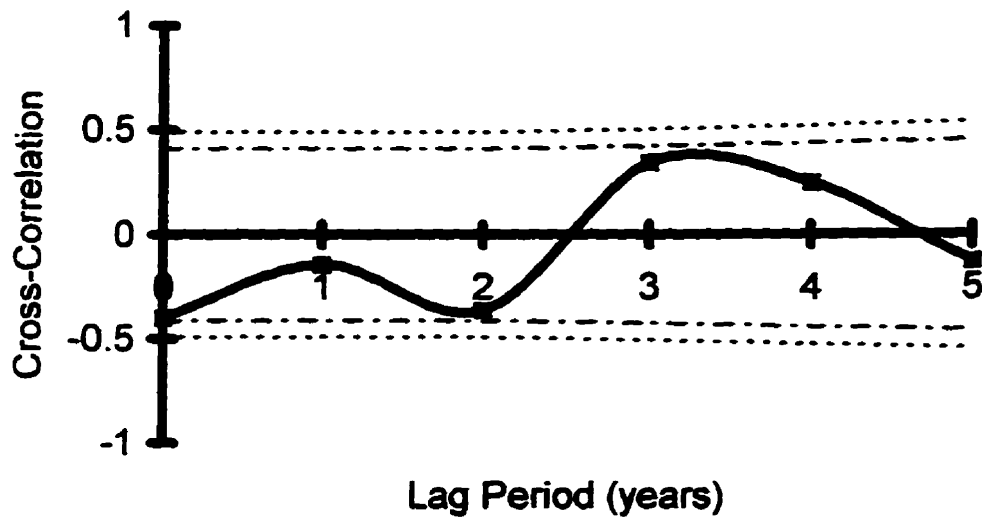
**Figure 8. Number of Elk vs. Snow Density Index**



**Table 5. Elk vs. Snow Density**

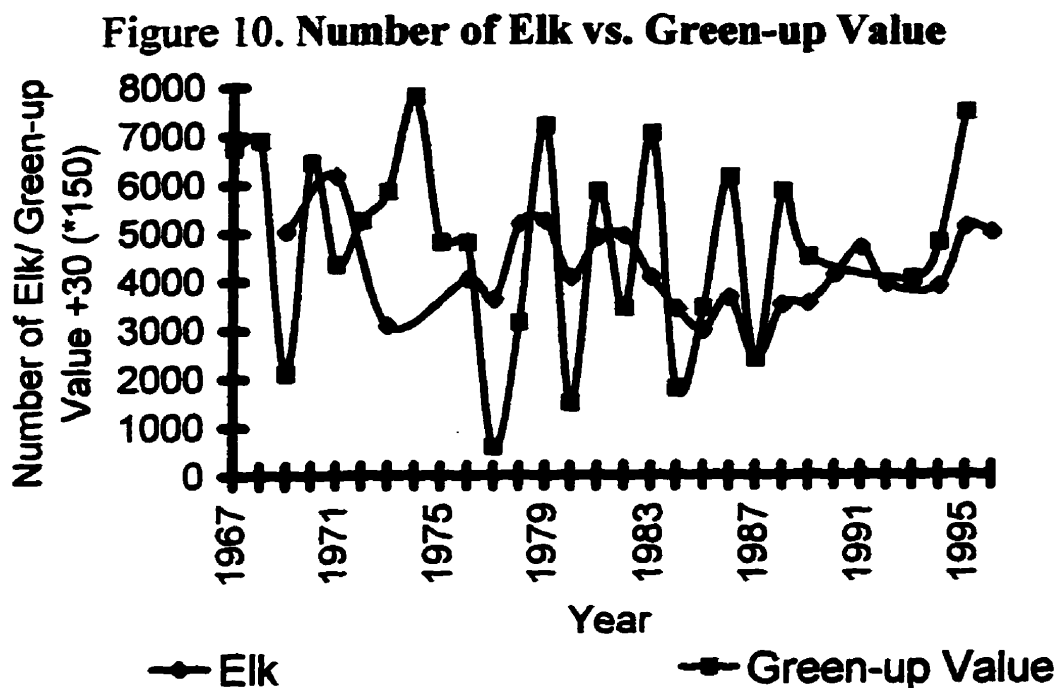
	<i>ELK</i>	<i>n</i>
<b>No lag</b>	-0.4005	17
<b>1-yr. lag</b>	-0.1448	18
<b>2-yr. lag</b>	-0.3642	19
<b>3-yr. lag</b>	0.3432	19
<b>4-yr. lag</b>	0.2496	19
<b>5-yr. lag</b>	-0.1310	19

**Figure 9. Correlogram- Elk vs. Snow Density Index**





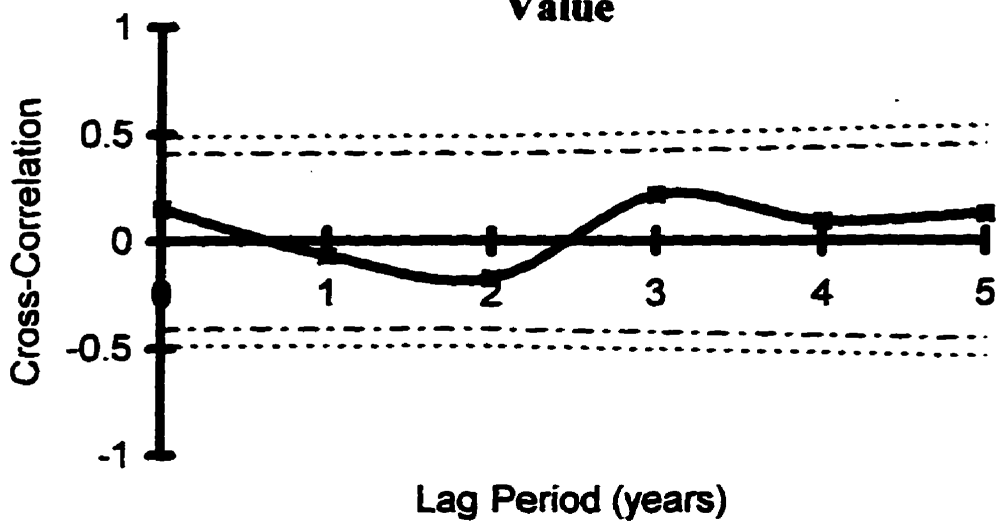
### 5.0 Relationship Between Elk and Green-Up Value



**Table 6. Elk vs. Green-up Value**

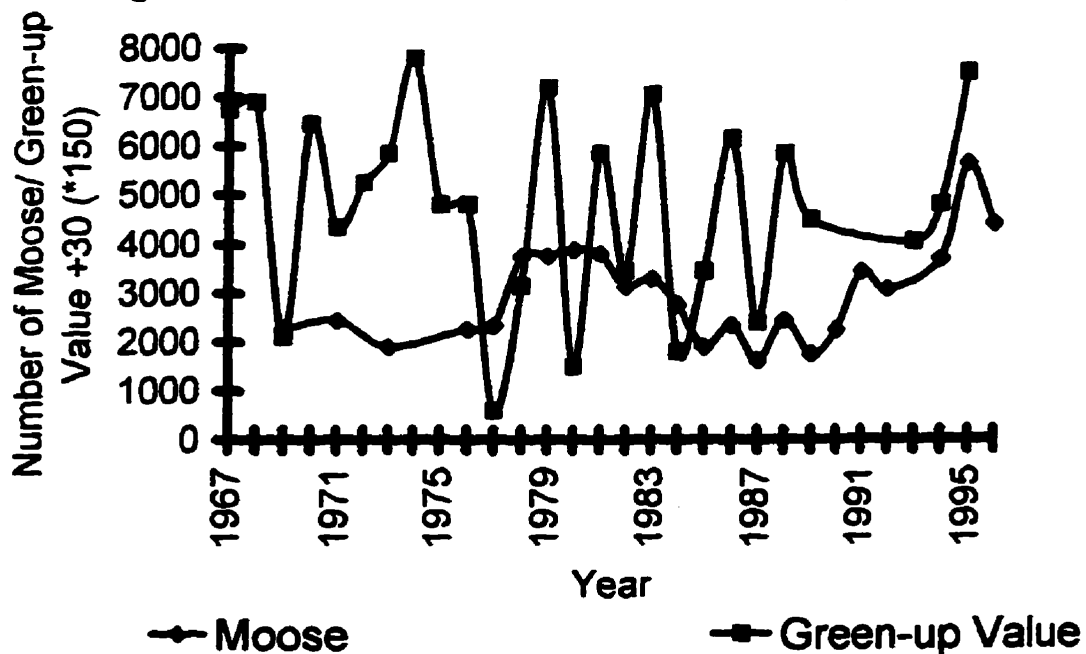
	<i>ELK</i>	<i>n</i>
No lag	0.1524	17
1-yr. lag	-0.06910	18
2-yr. lag	-0.1739	19
3-yr. lag	0.2155	19
4-yr. lag	0.09267	19
5-yr. lag	0.1282	19

**Figure 11. Correlogram- Elk vs. Green-up Value**



**6.0 Relationship Between Moose and Green-up Value**

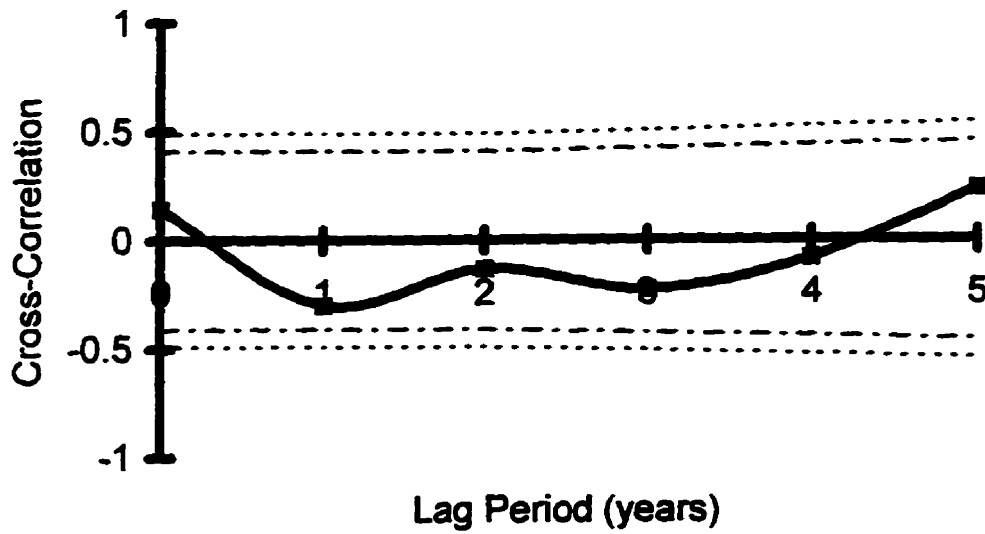
**Figure 12. Number of Moose vs. Green-up Value**



**Table 7. Moose vs. Green-up Value**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	0.1448	17
<b>1-yr. lag</b>	-0.3016	18
<b>2-yr. lag</b>	-0.1317	19
<b>3-yr. lag</b>	-0.2290	19
<b>4-yr. lag</b>	-0.08388	19
<b>5-yr. lag</b>	0.2370	19

**Figure 13. Correlogram- Moose vs. Green-up Value**



## APPENDIX D

### SCATTERPLOTS OF SIGNIFICANT RELATIONSHIPS

Figure 1. **NUMBER OF ELK VS. ELK (1-YR. LAG)**

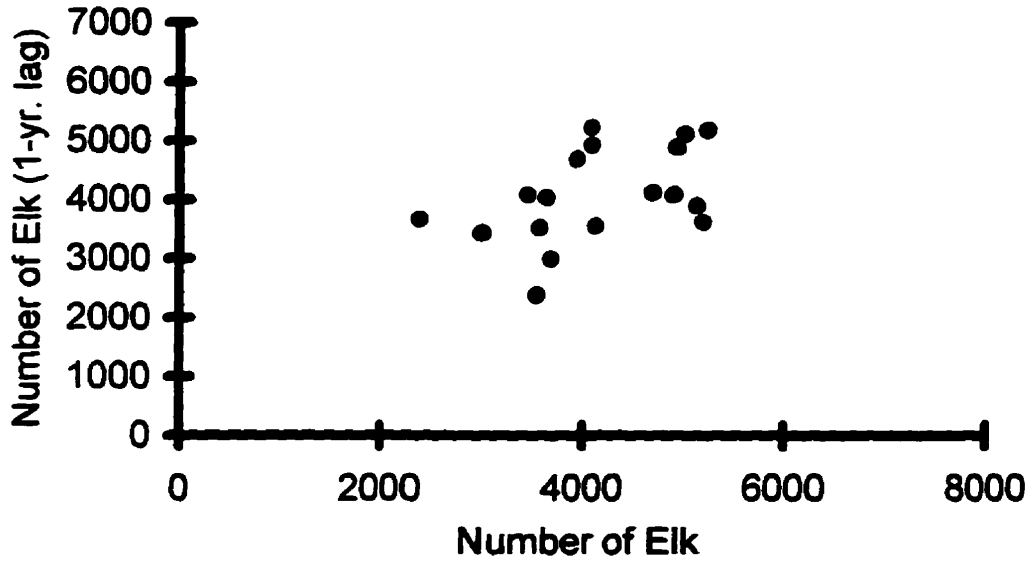
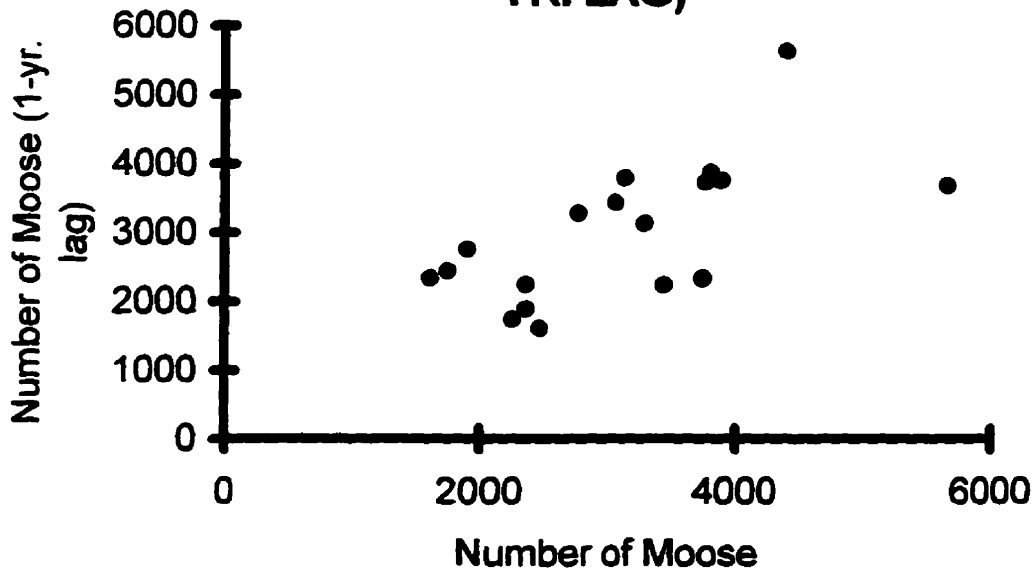
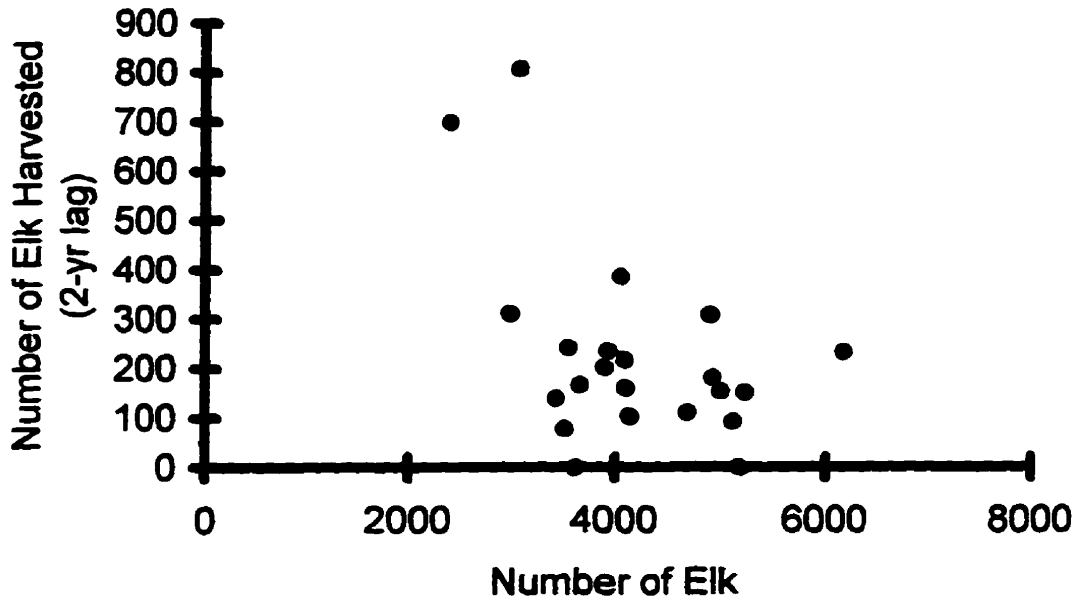


Figure 2. **NUMBER OF MOOSE VS. MOOSE (1-YR. LAG)**



**Figure 3. NUMBER OF ELK VS. ELK HARVESTED (2-YR LAG)**



**Figure 4. NUMBER OF MOOSE VS. MOOSE HARVESTED (4-YR. LAG)**

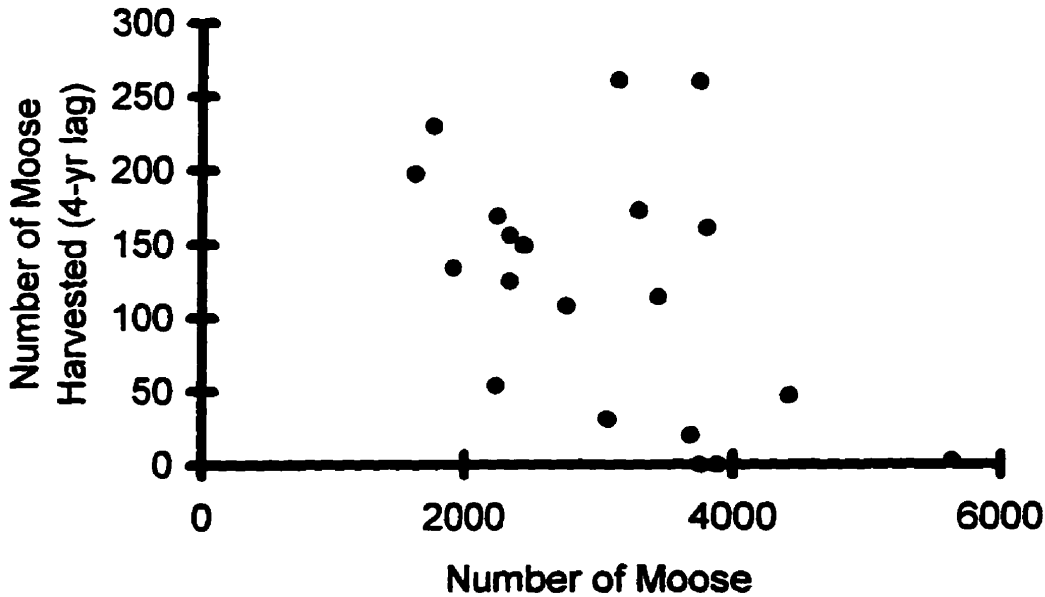


Figure 5. NUMBER OF ELK VS. BEAVERS

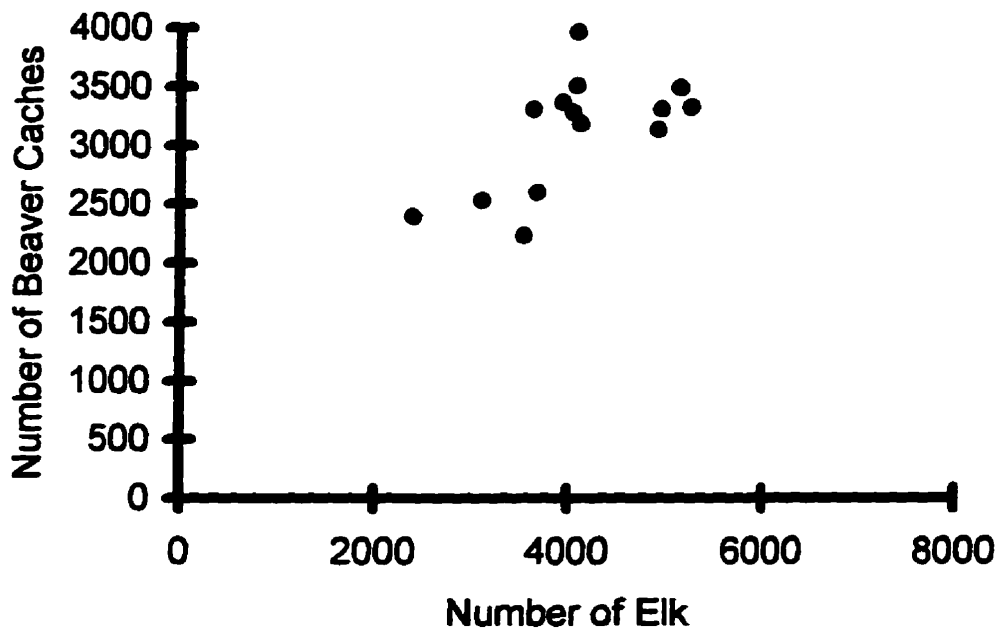


Figure 6. NUMBER OF MOOSE VS. BEAVERS  
(1-YR. LAG)

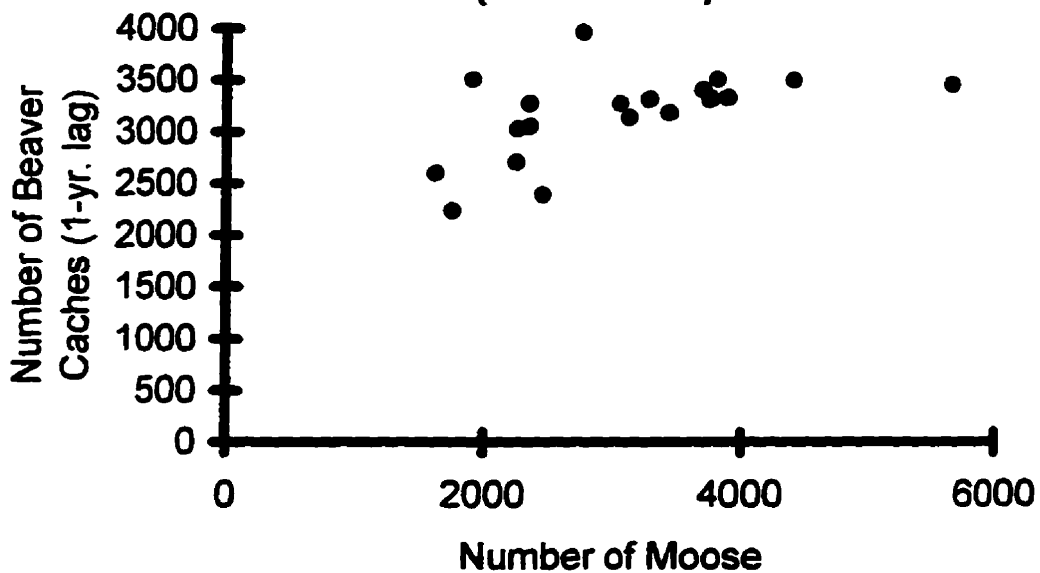


Figure 7. NUMBER OF MOOSE VS. WOLVES

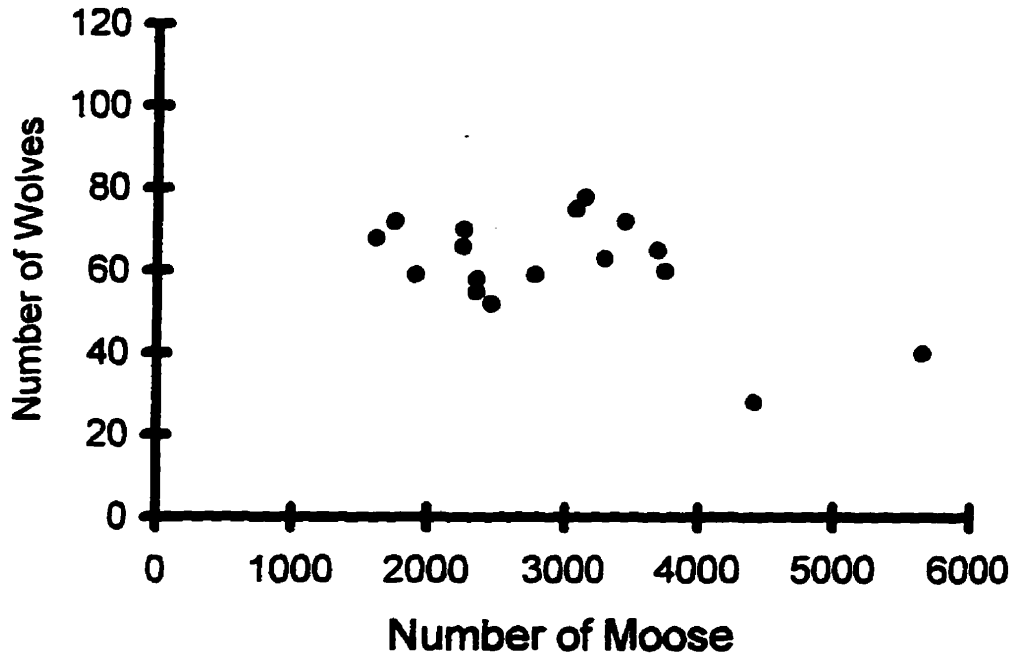


Figure 8. NUMBER OF ELK VS. SNOWSHOE HARE

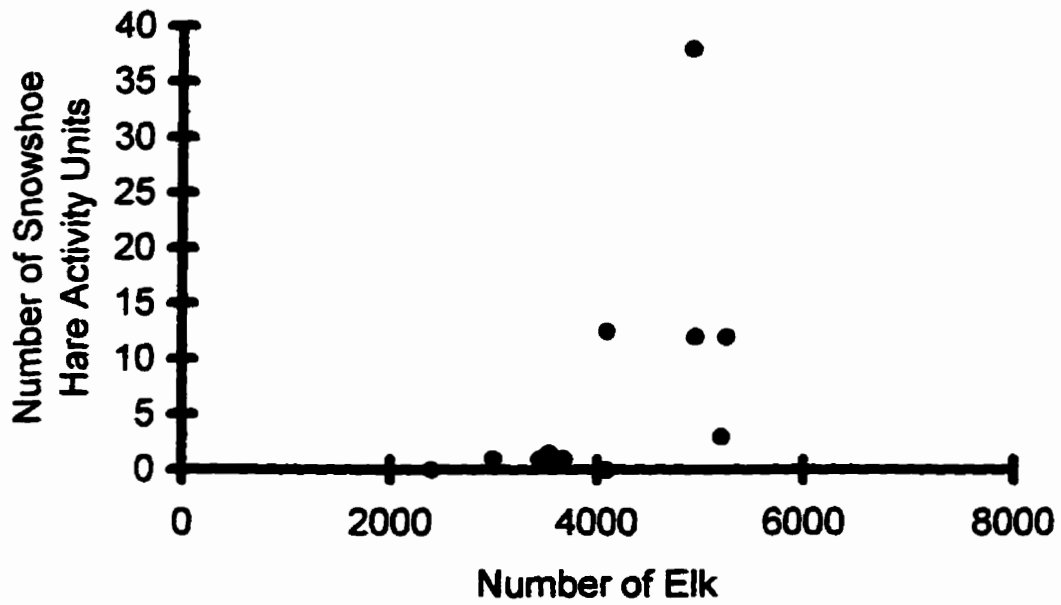


Figure 9. NUMBER OF MOOSE VS. SNOWSHOE HARE

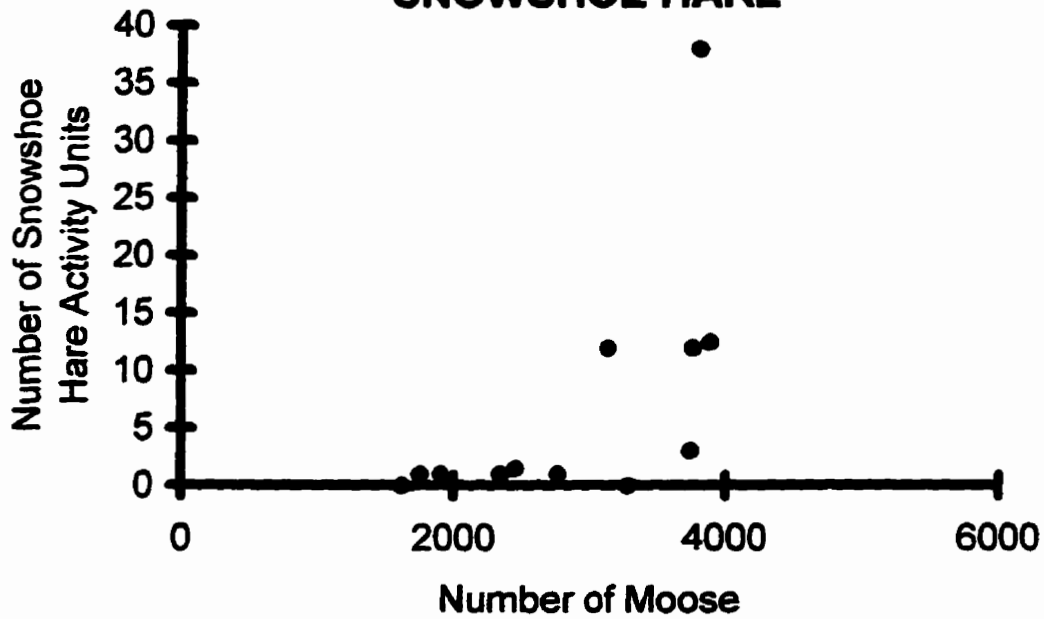




Figure 10. **NUMBER OF ELK VS. WSI (4-YR. LAG)**

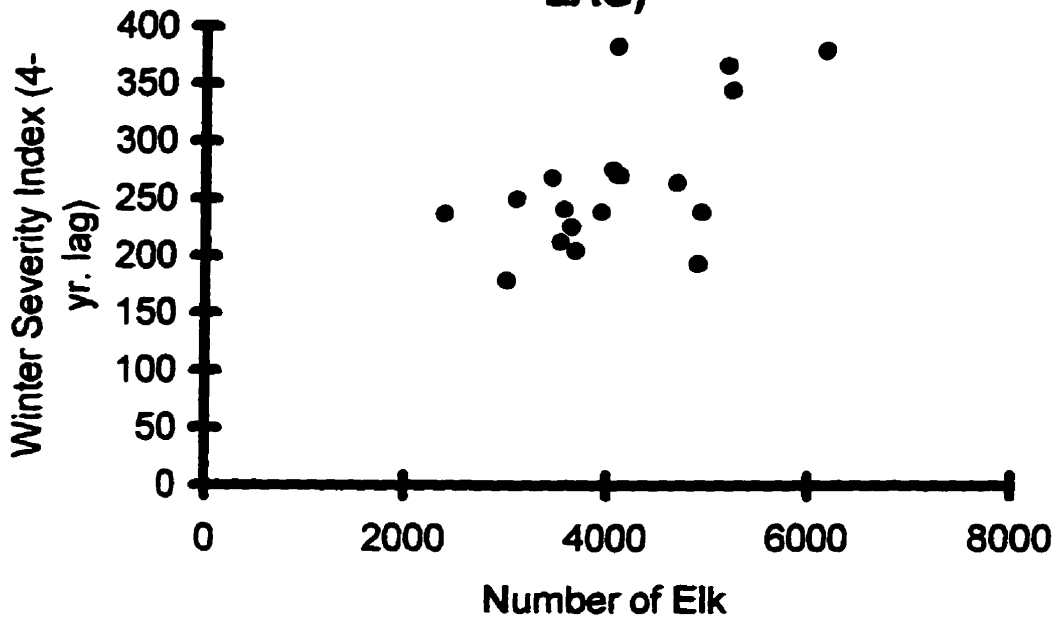


Figure 11. **NUMBER OF MOOSE VS. WSI (4-YR. LAG)**

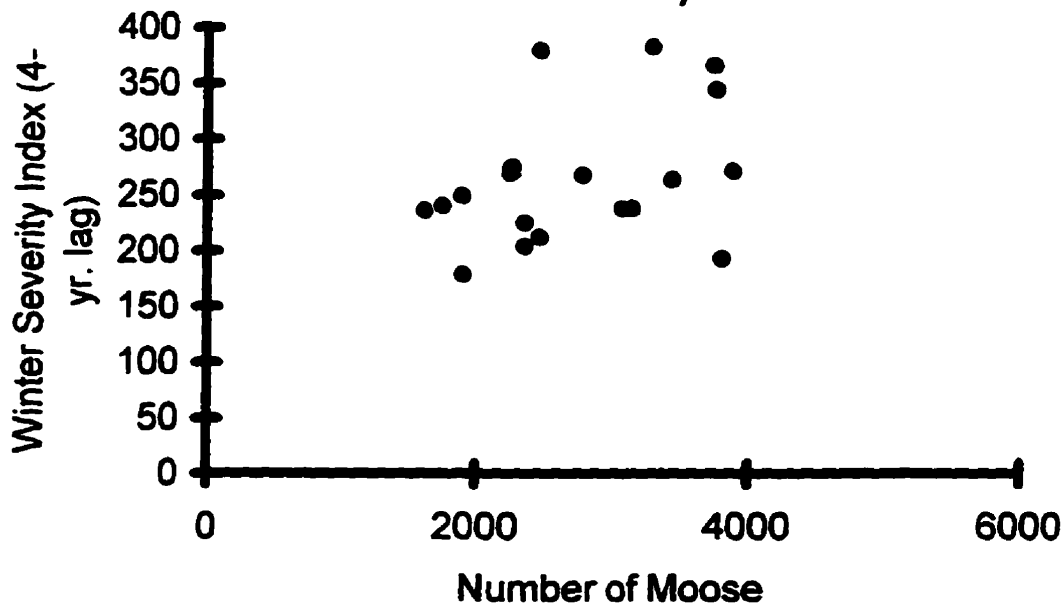


Figure 12. NUMBER OF ELK VS. MEAN WINTER TEMPERATURE INDEX

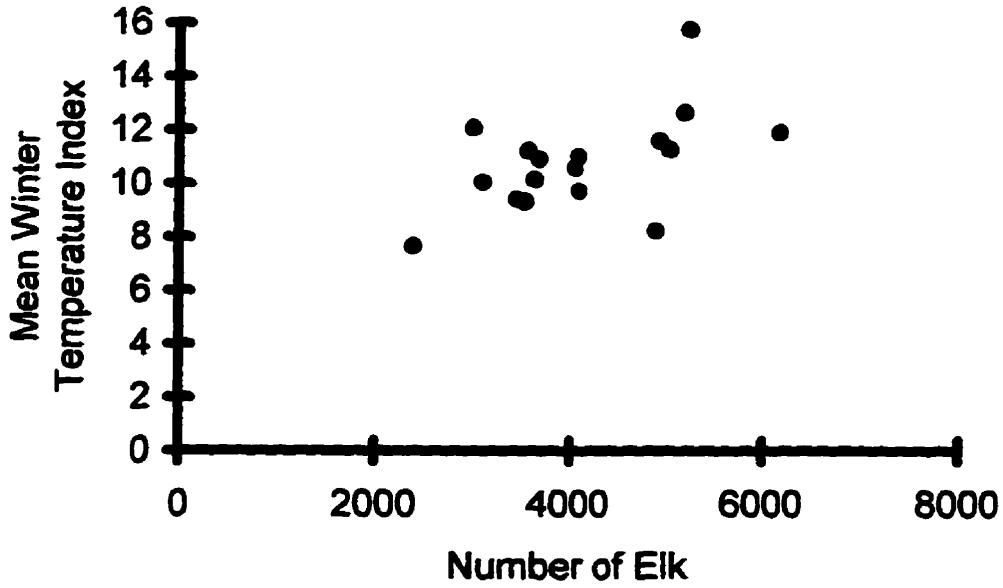


Figure 13. NUMBER OF ELK VS. MINIMUM WINTER TEMPERATURE INDEX

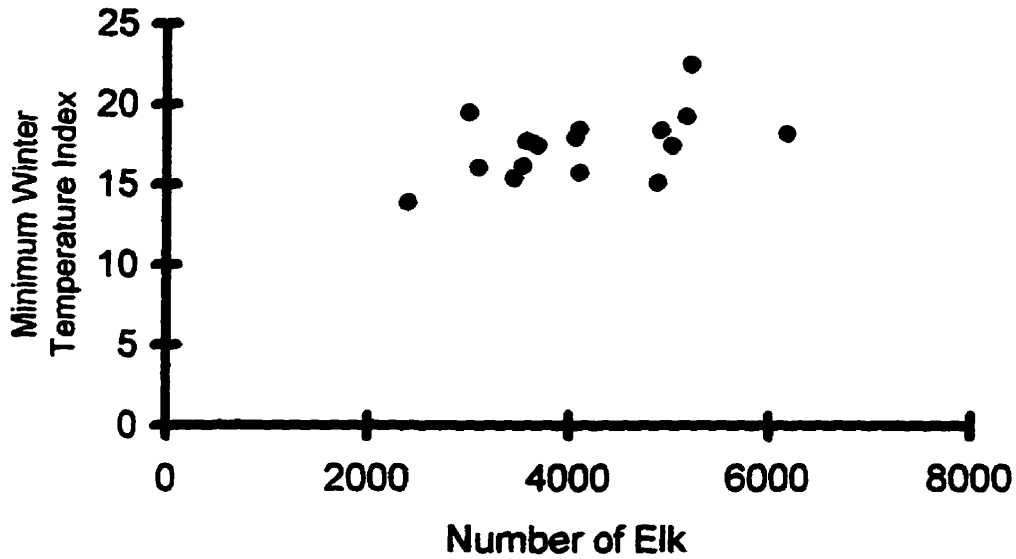


Figure 14. NUMBER OF ELK VS. MAXIMUM WINTER TEMPERATURE INDEX

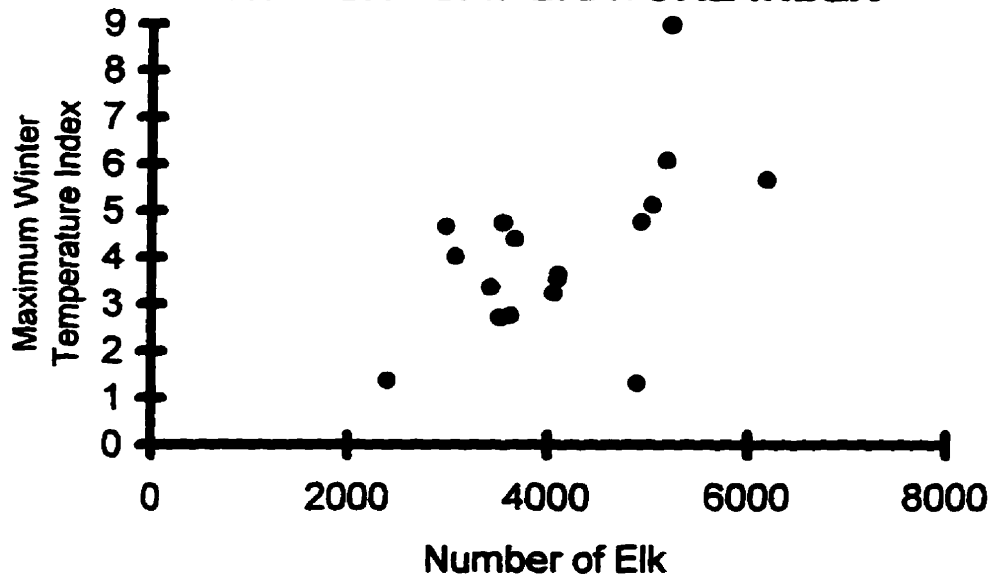


Figure 15. NUMBER OF MOOSE VS. MINIMUM WINTER TEMP. INDEX (1-YR. LAG)

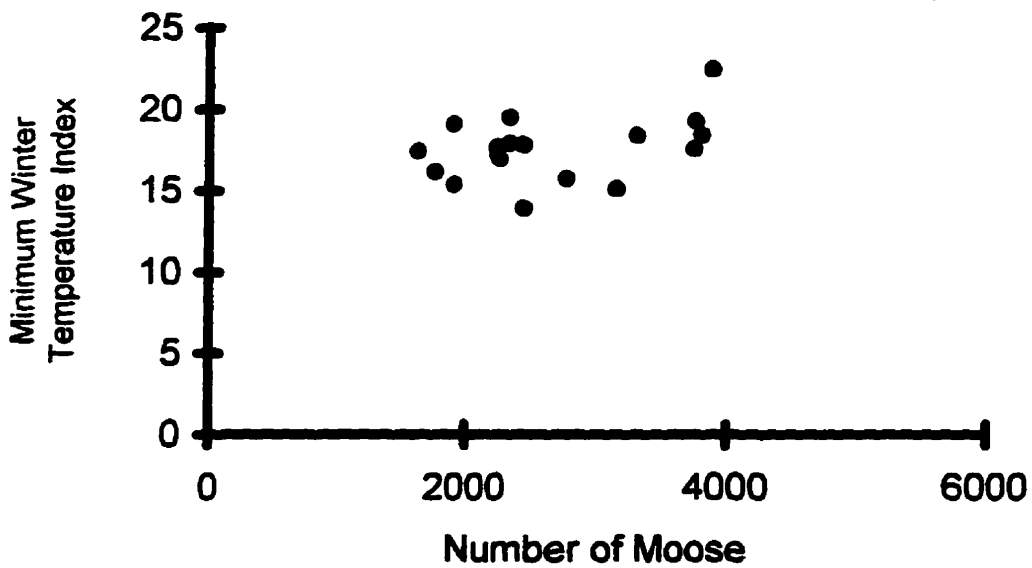


Figure 16. NUMBER OF ELK VS. SNOW ACCUMULATION (4-YR. LAG)

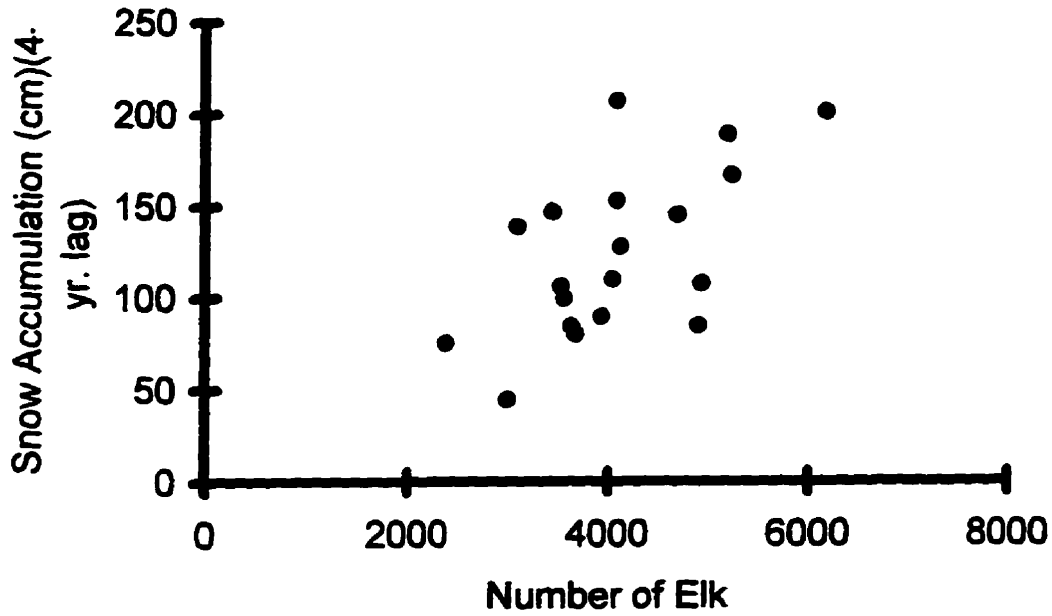
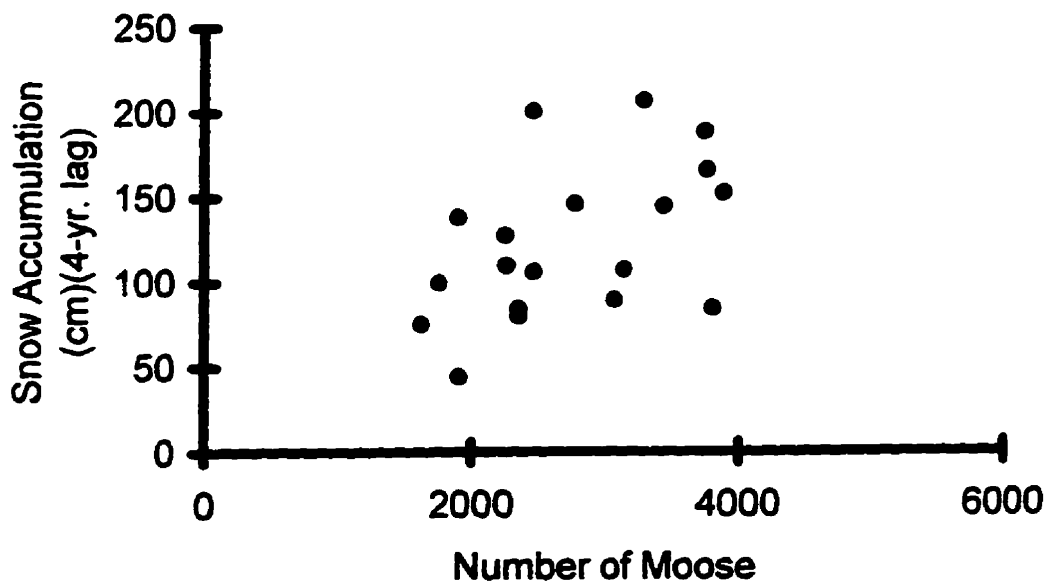
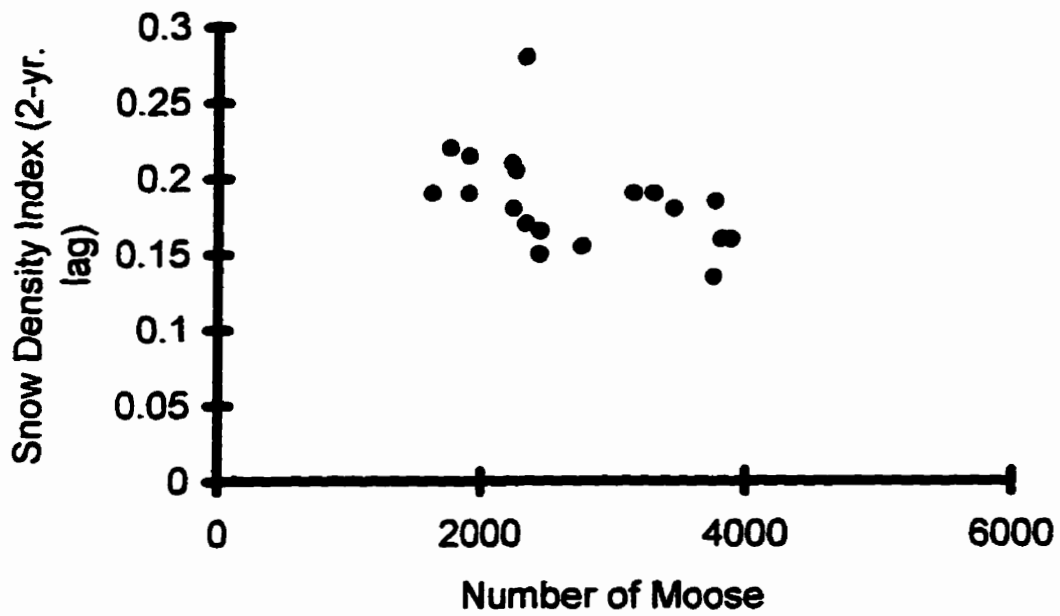


Figure 17. NUMBER OF MOOSE VS. SNOW ACCUMULATION (4 YR. LAG)



**Figure 18. NUMBER OF MOOSE VS. SNOW DENSITY INDEX (2-YR. LAG)**



## APPENDIX E

### TABLES CORRESPONDING TO CORRELOGRAMS

Table 1. Elk Autocorrelations

	<i>ELK</i>	<i>n</i>
No lag	1*	25
1-yr. lag	0.4668 <sup>+</sup>	18
2-yr. lag	0.1588	19
3-yr. lag	0.2173	19
4-yr. lag	-0.07527	18
5-yr. lag	-0.4140	18

\* = statistically significant,  $\alpha = 0.05$  (Legendre and Legendre 1983)

<sup>+</sup> = statistically significant,  $\alpha = 0.10$  (Legendre and Legendre 1983)

Table 2. Moose Autocorrelations

	<i>MOOSE</i>	<i>n</i>
No lag	1*	25
1-yr. lag	0.6497*	18
2-yr. lag	0.4865 <sup>+</sup>	19
3-yr. lag	0.4112	19
4-yr. lag	0.08310	18
5-yr. lag	-0.2279	18

**Table 3. Elk vs. Hunter Harvest**

	<i>ELK</i>	<i>n</i>
<b>No lag</b>	0.2306	23
<b>1-yr. lag</b>	-0.03093	22
<b>2-yr. lag</b>	-0.4812*	22
<b>3-yr. lag</b>	-0.2974	22
<b>4-yr. lag</b>	-0.1861	21
<b>5-yr. lag</b>	-0.05547	20

**Table 4. Moose vs. Hunter Harvest**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	0.01549	22
<b>1-yr. lag</b>	0.05506	22
<b>2-yr. lag</b>	-0.1771	21
<b>3-yr. lag</b>	-0.3610	20
<b>4-yr. lag</b>	-0.4628 <sup>+</sup>	20
<b>5-yr. lag</b>	-0.3258	20

**Table 5. Elk vs. Beavers**

	<i>ELK</i>	<i>n</i>
<b>No lag</b>	0.6271*	14
<b>1-yr. lag</b>	0.4008	12
<b>2-yr. lag</b>	0.1034	12
<b>3-yr. lag</b>	-0.04841	12
<b>4-yr. lag</b>	-0.4852	13
<b>5-yr. lag</b>	-0.4216	11

**Table 6. Moose vs. Beavers**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	0.5908*	14
<b>1-yr. lag</b>	0.6566*	12
<b>2-yr. lag</b>	0.3899	12
<b>3-yr. lag</b>	0.2517	12
<b>4-yr. lag</b>	-0.05420	13
<b>5-yr. lag</b>	-0.3174	11

**Table 7. Moose vs. Wolves**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	-0.5839*	17
<b>1-yr. lag</b>	-0.3259	15
<b>2-yr. lag</b>	-0.04943	13
<b>3-yr. lag</b>	0.2396	11
<b>4-yr. lag</b>	0.2764	11
<b>5-yr. lag</b>	0.1975	11

**Table 8. Elk vs. Snowshoe Hare**

	<i>ELK</i>	<i>n</i>
<b>No lag</b>	0.5628 <sup>+</sup>	10
<b>1-yr. lag</b>	0.5616	10
<b>2-yr. lag</b>	0.3124	10
<b>3-yr. lag</b>	-0.08527	10
<b>4-yr. lag</b>	-0.3232	9
<b>5-yr. lag</b>	-0.3349	9



**Table 9. Moose vs. Snowshoe Hare**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	0.5967 <sup>+</sup>	10
<b>1-yr. lag</b>	0.4754	10
<b>2-yr. lag</b>	0.4443	10
<b>3-yr. lag</b>	0.1412	10
<b>4-yr. lag</b>	-0.1905	9
<b>5-yr. lag</b>	-0.3126	9

**Table 10. Elk vs. Winter Severity Index**

	<i>ELK</i>	<i>n</i>
<b>No lag</b>	0.2018	17
<b>1-yr. lag</b>	-0.03255	18
<b>2-yr. lag</b>	0.1604	19
<b>3-yr. lag</b>	0.3865	19
<b>4-yr. lag</b>	0.5998*	19
<b>5-yr. lag</b>	0.1288	19

**Table 11. Elk vs. Mean Winter Temperature Index**

	<i>ELK</i>	<i>n</i>
<b>No lag</b>	0.5310*	17
<b>1-yr. lag</b>	0.07234	18
<b>2-yr. lag</b>	0.1862	19
<b>3-yr. lag</b>	0.1459	19
<b>4-yr. lag</b>	0.3926	19
<b>5-yr. lag</b>	0.01461	19

**Table 12. Elk vs. Minimum Winter Temperature Index**

	<i>ELK</i>	<i>n</i>
No lag	0.4800 <sup>+</sup>	17
1-yr. lag	0.1501	18
2-yr. lag	0.2186	19
3-yr. lag	0.1630	19
4-yr. lag	0.4175	19
5-yr. lag	0.04343	19

**Table 13. Elk vs. Maximum Winter Temperature Index**

	<i>ELK</i>	<i>n</i>
No lag	0.5481*	17
1-yr. lag	-0.01710	18
2-yr. lag	0.1429	19
3-yr. lag	0.1242	19
4-yr. lag	0.3486	19
5-yr. lag	-0.01160	19

**Table 14. Moose vs. Minimum Winter Temperature Index**

	<i>MOOSE</i>	<i>n</i>
No lag	0.3299	17
1-yr. lag	0.4121 <sup>+</sup>	18
2-yr. lag	0.2722	19
3-yr. lag	0.2292	19
4-yr. lag	0.1913	19
5-yr. lag	0.08082	19

**Table 15. Elk vs. Snow Accumulation**

	<i>ELK</i>	<i>n</i>
<b>No lag</b>	0.1266	17
<b>1-yr. lag</b>	0.01227	18
<b>2-yr. lag</b>	0.3265	19
<b>3-yr. lag</b>	0.2894	19
<b>4-yr. lag</b>	0.6047*	19
<b>5-yr. lag</b>	0.1658	19

**Table 16. Moose vs. Snow Accumulation**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	0.06763	17
<b>1-yr. lag</b>	0.07757	18
<b>2-yr. lag</b>	-0.03299	19
<b>3-yr. lag</b>	0.09206	19
<b>4-yr. lag</b>	0.4821 <sup>+</sup>	19
<b>5-yr. lag</b>	0.3116	19

**Table 17. Moose vs. Snow Density**

	<i>MOOSE</i>	<i>n</i>
<b>No lag</b>	-0.1207	17
<b>1-yr. lag</b>	-0.2482	18
<b>2-yr. lag</b>	-0.4756 <sup>+</sup>	19
<b>3-yr. lag</b>	0.1894	19
<b>4-yr. lag</b>	0.09082	19
<b>5-yr. lag</b>	0.01975	19