

**DEVELOPMENT OF AN ECOLOGICAL MODEL FOR THE RIDING
MOUNTAIN NATIONAL PARK ELK POPULATION**

BY

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**Development of an Ecological Model for the Riding
Mountain National Park Elk Population**

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Christina Patterson

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
of
MASTER OF NATURAL RESOURCES MANAGEMENT**

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ABSTRACT

The state of ecological integrity can be determined by assessing the viability of a species that is considered vital to the ecosystem (Woodley 1993). This study involved modeling the Riding Mountain National Park elk population and components, which influenced and impacted the viability of the elk population, thereby indicating the state of ecological integrity within RMNP. Main components included in the model were wolves, human harvest, bear predation and winter severity.

The development of the model utilized the STELLA software. As well, data were gathered from RMNP, the Manitoba Department of Conservation and various studies. The data was used to build the formulae that were placed in the model and then run. Sensitivity runs were conducted by varying the values of human harvest rate on elk, bear predation rate of elk calves, the adult and yearling birth rate of elk, and the wolf population. As well, additional runs were also carried out to test the elk population.

The results of the run with the initial values showed an elk population that is beginning to decline. As well, the sensitivity runs indicated that the elk population was sensitive to changes in the human harvest rate on elk, the bear predation rate on calves and the adult birth rate. The model results also indicated that elk population was not that sensitive to changes in the wolf population. As well, the effect of winter severity on the elk population was minimal.

The sensitivity of the elk population to the human harvest rate component indicates that the viability of the elk population could be significantly influenced by increases in the harvest rate. Because this is the a component of the model that RMNP managers can influence because RMNP managers are involved in setting the regulated

harvest rates outside RMNP, the results of the model runs are beneficial for developing management practices that will help manage this component to prevent it from compromising the viability of the elk and possibly the ecological integrity of RMNP.

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CHAPTER 1

1.0 INTRODUCTION

The *Canada National Parks Act* (2001) states, “The maintenance of ecological integrity through the protection of natural resources shall be the Government’s first priority”. The definition of ecological integrity defined in the *Canada National Parks Act* (2001) and applied to Canada’s National Parks is:

“An ecosystem has integrity when it is deemed characteristic for its natural region, including the composition and abundance of native species and biological communities, rates of change and supporting processes. Ecosystems have integrity when their native components, plants, animals and other organisms and processes such as growth and reproduction are intact”

By striving for the maintenance of ecological integrity, Parks Canada is attempting to minimize human-caused impacts and stresses from both external and internal sources on the ecosystems of Canada’s National Parks. Riding Mountain National Park (RMNP) is attempting to address the maintenance of ecological integrity within its boundaries, while still trying to function holistically with the land surrounding it.

This chapter presented a basic history of RMNP and highlighted an essential component of the Park to indicate the state of ecological integrity in RMNP. As well, this chapter defined the objectives of this thesis.

1.1 RIDING MOUNTAIN NATIONAL PARK

Riding Mountain National Park (RMNP) was established in 1929 by order-in-council and officially opened in 1933 (Fay 1981). RMNP is 2976 square kilometers of diverse landscape located roughly in the geographical center of North America, approximately 225 km northwest of Winnipeg in southwestern Manitoba (Figure 1). RMNP is surrounded on all sides by agricultural landscape (Figure 2).

Despite the creation of political and geographical boundaries that separate the Park from the surrounding agricultural land, RMNP does not function in isolation. Wildlife movement, water drainage, human activities and many other natural processes freely move back and forth from the Park to land surrounding it.

1.2 REGIONS OF RMNP

RMNP is where the eastern, western and northern Canadian regions come together (Applebaum and Trueman 1996). Each region contributes a different life zone to the Park's ecosystem. The life zone of the western region is the grasslands. Roughly 2.5% of the Park consists of grassland of which about one-third is native Rough Fescue (*Festuca hallii*) and the remainder is upland meadow of Slender Wheat-Kentucky Bluegrass (*Agropyron trachcaulum-Poa pratensis*) and lowland meadow of pure sedge (*Carex* spp.) or mixtures of slough grasses (*Glyceria* sp., *Calamagrostis* spp.) and sedges (Trottier 1986).

The life zone of the northern region is the boreal forests of spruce, jackpine, aspen and birch. The life zone of the eastern region is the eastern deciduous plant life consisting of oak, Manitoba Maple (*Acer negundo*) and white elm (*Ulmus americana*) (Applebaum and Trueman 1986).

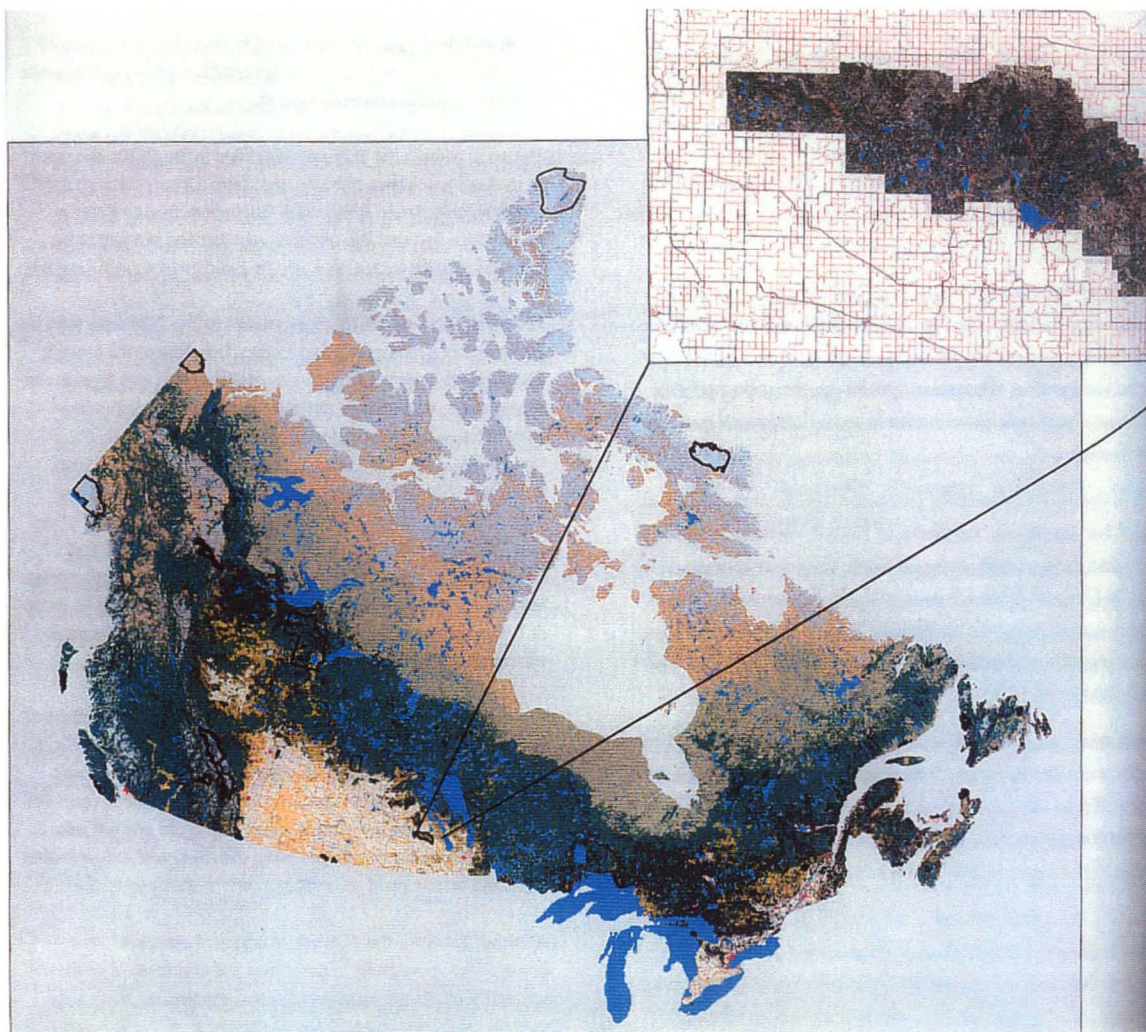


Figure 1. Satellite Image of Canada and Riding Mountain National Park

Source: Parks Canada (1998a)

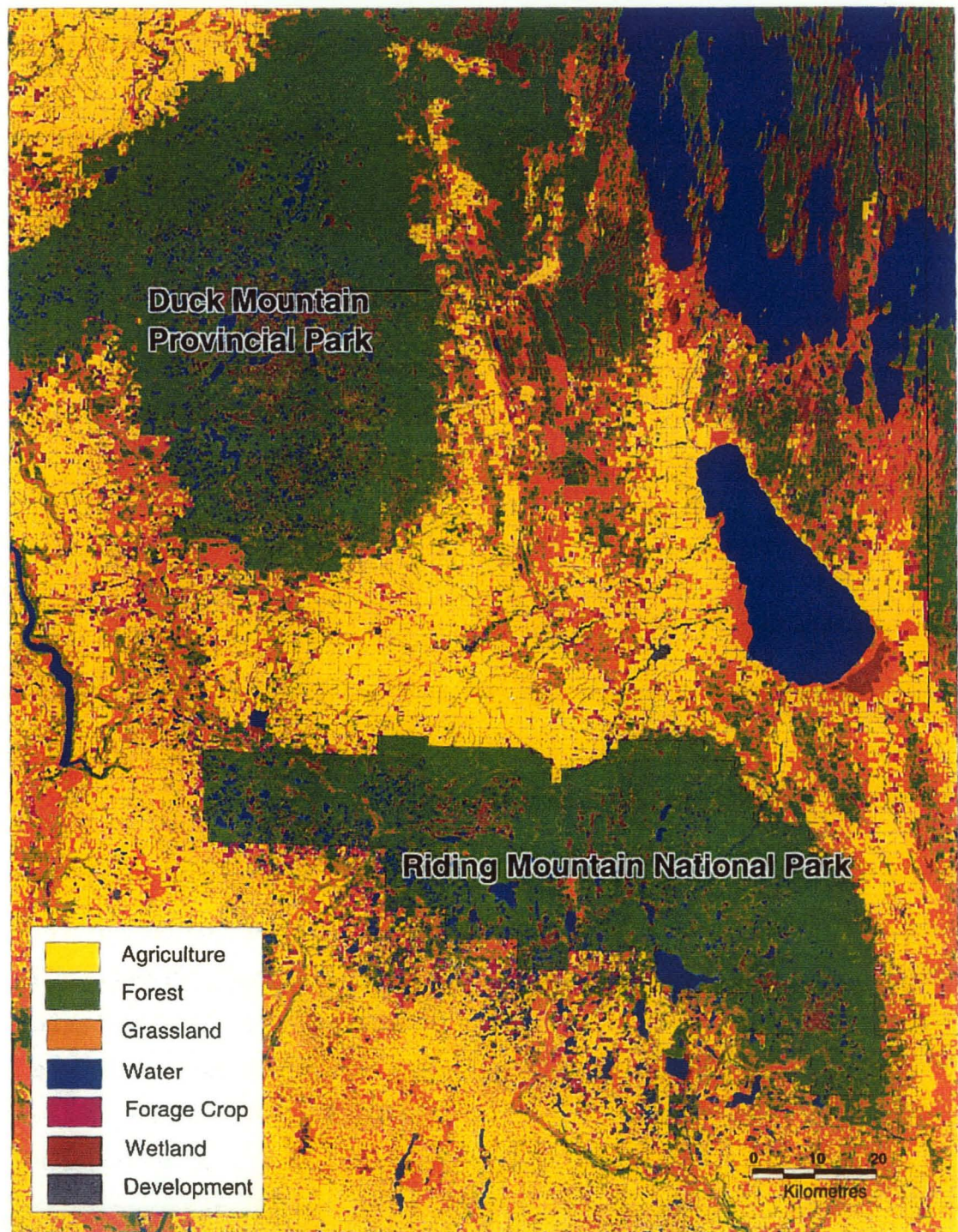


Figure 2. A Classified Landsat Image of Riding Mountain National Park, Manitoba (1993)

Source: Prairie Farm Rehabilitation Administration (PFRA) and Manitoba Remote Sensing. (Nylen-Nemetchek, 1999).

1.3 LANDSCAPE OF RMNP

Approximately 70% of the Park area is occupied by aspen and mixed aspen-white spruce forests in various stages of succession. Grasslands, shrublands and several coniferous formations account for most of the remaining vegetation (Rounds 1977). The landscape is also made up of an interspersed of ponds, marshes and lakes within the upland areas, as well as the Manitoba Escarpment, which rises 475 metres above the farmland below (Trottier 1986).

1.4 ANIMAL LIFE OF RMNP

The varying landscape of RMNP is home to many species. The Park is home to top carnivores such as wolf (*Canis lupus*), lynx (*Lynx canadensis*), coyote (*Canis latrans*) and black bear (*Ursus americanus*). In addition to elk (*Cervus elaphus*), there are a number of ungulate species such as white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and bison (*Bison bison*). Smaller mammals such as beaver (*Castor canadensis*) and snowshoe hare (*Lepus americanus*) also inhabit the Park. Scavengers, invertebrates and bacterial agents of decomposition and nutrients recycling are also a part of the Park's ecosystem (Riding Mountain National Park Round Table 1996).

1.5 HUMAN INTERACTION WITH RMNP

Throughout the history of RMNP, human activities such as hunting, livestock grazing, logging, and settlement have greatly altered the regional landscape (Tabulenas 1983; Jamieson 1974). Vegetation succession, as a result of various human and natural disturbances, has altered Park habitats, causing corresponding changes in the relative distribution and abundance of ungulate species. Wildlife populations have also been

impacted by extensive hunting and trapping that occurred in the late 1800's and early 1900's. Previous fire suppression policies, increased park visitation and ongoing land use changes adjacent to the park boundary increasingly isolated the Park and compromised its ecological integrity (Trottier *et al.* 1983).

1.6 ECOLOGICAL INTEGRITY AND RMNP

The state of ecological integrity within an ecosystem can be addressed by either observing the state of the entire ecosystem, or observing the state of the vital components within the ecosystem. Woodley (1993) presents the viability of species as part of his definition of ecological integrity.

The RMNP elk population is one of the most recognizable and vital components of the RMNP ecosystem. Elk are powerful modifiers of habitat through their foraging activities, they are potential prey for wolves and hunters outside the Park boundaries and they are in competition with other species for browse in winter (Carbyn 1980). Because of the important role, which elk play in the ecosystem, their presence (or lack there of) would evoke critical changes in both the biotic community and the physical environment (Parks Canada 1998a).

1.7 OBJECTIVES

Riding Mountain National Park is attempting to address the maintenance of the ecological integrity of the natural ecosystem by striving to ensure management decisions affecting the Park and its resources are based on sound resource and ecosystem-based management practices (Parks Canada 1998b). To aid in meeting this objective, a tool that will help enhance the understanding of the ecosystem, its components and their

interactions was required. The development of a system dynamics model was appropriate to help identify key components and interactions within the Park's ecosystem.

Due to the extensiveness of the RMNP ecosystem, the time frame of the project, and the available data, the model focused on one component of the RMNP ecosystem. The viability and trends of elk abundance in RMNP were considered reflective of the integrity of the Riding Mountain region (Parks Canada 1998a). Therefore, the objective of this study was to build a model, utilizing the viability of the RMNP elk population as an indicator of the state of ecological integrity in RMNP. The model allowed for testing hypotheses of various management strategies, to determine their effects on the elk population. As well, the model determined the effects of changes to major components of the ecosystem on the elk population and how those components may influence the viability of the elk population in RMNP. This in turn would help provide an indication of the state of ecological integrity in RMNP. In order to accomplish this objective, this study:

- 1). Developed a working model of the RMNP elk population. The model focused on the interactions of the elk with major components of the ecosystem such as wolves, humans, climate and others in RMNP. The model attempted to highlight those components that have the greatest impact on the viability of elk in RMNP and thereby aided in the development of management strategies that will be beneficial to the RMNP elk population and in turn to the maintenance of ecological integrity in RMNP.

- 2). Identified areas in which there were data gaps in the RMNP data sources.
- 3). Transferred knowledge of system dynamics modeling to RMNP, for use in additional modeling projects.

1.8 THESIS STRUCTURE

The thesis is presented in seven chapters. Chapter two consisted of a literature review of System Dynamics and Modeling. Chapter three consisted of the history of elk in RMNP and the components (variables) of the ecosystem that interact with the elk population. Chapter four described the model development. Chapter five addressed the model run and the trials used to test the model. Chapter six contained the results and discussion of the model runs. Chapter seven provided the conclusions as a result of the model and recommendations for the maintenance of ecological integrity of RMNP.

CHAPTER 2

2.0 INTRODUCTION

A system can be defined as any phenomenon, either structural or functional having at least two separate components, and some interaction between these components. A model is any abstraction or simplification of a system (Hall and Day 1977). Models are used in order to promote a greater understanding of the systems they represent. The following section reviewed the history of system dynamics, the benefits and drawbacks of modeling, the use of models with wildlife populations and examples of how model could be used with wildlife populations.

2.1 SYSTEMS DYNAMICS AND MODELING HISTORY

The field of system dynamics originated in the 1960's with the work of Jay Forrester and his colleagues at the Sloan School of Management at the Massachusetts Institute of Technology. They developed the initial ideas for system dynamics by applying concepts from feedback control theory to the study of industrial systems (Ford 1999). Forrester (1969) applied the new ideas in his well-known publication *Urban Dynamics*, which explained the pattern of rapid population growth and subsequent decline in major cities such as Manhattan. The model Forrester developed was used to portray a city as a system of interacting industries, housing and people (Ford 1999). *Urban Dynamics* acted as a stepping-stone for the expansion of the field outside of the industrial area, paving the way for the increase in application of the system dynamics concept. Today system dynamics and modeling are being applied to a variety of situations, including modeling various components of ecosystems (Starfield 1997, Medin and Anderson 1979, Hobbs 1989).

2.2 MODELING APPROACH

The system dynamics approach to modeling is the active development of a model from the knowledge of a system in order to simulate the dynamic behaviour of a system. The modeling process attempts to map out a model in such a manner that it is precise and consistent with the physical system it represents (Barth 1998). Development of models involved utilizing the interrelationships, variability, linkages and feedbacks that occur between the many components of a particular ecosystem (National Oceanic & Atmospheric Administration & Resources for the Future 1975).

The first step in modeling involved identifying the model components. One of the most important components of systems were state variables. State variables were the variables on which all other calculations in the model were based and were considered the indicators of the current status of the system (Hannon and Ruth 1997). In modeling a population such as snowshoe hare, their population number would be considered a state variable.

The next step was to identify the system elements that were responsible for changes to the state variables, which were flows. They added and subtracted from the state variables (Medin and Anderson 1979). An example of flows was either the births or the deaths in a population. Identification of state variables and flows allowed for the development of feedback loops. With development of feedback loops, the basic structure of a model was created. The next step was to implement the formulae and the other interactions that were a part of the system.

2.3 MODEL VALIDATION

The most important step at the end of the modeling process was the validation of the model's results and the determination of whether or not the model built represented the system it was modeling. In regards to validity of a model, Forrester (1968) presented two statements.

“First, a model cannot be expected to have absolute validity. A model is constructed for a purpose. It should be valid for the purpose but may be irrelevant or wrong for some other purpose...”

“A second essential point in clarifying a discussion of validity was to realize the impossibility of positive proof. The difficulty starts in selecting criteria of validity. There is no absolute proof but only a degree of hope and confidence that a particular measure was pertinent in linking together the model, the real system and the purpose.”

One way to validate model results was to compare them to already existing published results and data. The greater the number of instances in which model results and reality coincide under a variety of different scenarios, the more probable it was that the model captured the essential features of the real system it attempted to portray (Hannon and Ruth 1997). One of the most common and important tests was to set the inputs of a model at their historical values and see if outputs matched history (Ford 1999). Medin and Anderson (1979) in their model of Colorado mule deer found that there was general compatibility between the already existing database and the results generated by the model in regards to the deer population. They believed that precision

fitting past data and predicting correctly basic patterns of response generated confidence in the model (Medin and Anderson 1979).

2.4 BENEFITS OF MODELING

Dynamic models allowed for the ability to see how a system changes over time and may have helped in the understanding of why some systems oscillate over time (Ford 1999). Growth, decay and oscillations were the fundamental dynamic patterns of systems (Ford 1999). Models were constructed to help in the understanding of why certain patterns occur. Models aided in the understanding of the dynamics of real-world processes by mimicking the actual but simplified forces that were assumed to result in a system's behaviour (Hannon and Ruth 1997).

Models allowed for the testing of management strategies and the determination of the validity of the strategies through changes within the formulas used in the models. By varying the intensity of disturbances in the ecosystem, managers could gain an understanding of the sensitivity of the model and by extension of the real world in that particular time frame (National Oceanic & Atmospheric Administration & Resources for the Future 1975). But models were not useful in a management context unless they accept inputs in the form of human-induced changes and disturbances. As well, models also allowed for testing of different assumptions and relationships within an ecosystem, thereby helping in detecting critical weaknesses in hypotheses and assumptions made about the ecosystem in the creation of the models (National Oceanic & Atmospheric Administration & Resource for the Future 1975).

Modeling helped identify the data gaps in the system that was being studied as well as indicating normal or abnormal fluctuations in a complex system (Hannon and

Ruth 1997). As well, models aided in identifying unanticipated factors and interactions that occur within an ecosystem. Identifying these factors allows for adjustment of management procedures to include new factors and interactions (Jeffers 1978). The models must also provide information that was relevant and meaningful for making policy decisions on the level of use of a given resource (National Oceanic & Atmospheric Administration & Resources for the Future 1975).

Modeling was done to aid conceptualization and measurement of complex systems and sometimes to predict consequences of an action that would be expensive, difficult or destructive to do with the real system (Hall and Day 1977).

Modeling provided a storage area for data and ideas, which was collected and learned over time. An ever-developing model should capture the knowledge of the lessons learned through the years about how the system actually works (Hannon and Ruth 1997).

2.5 DRAWBACKS TO MODELING

Despite all the benefits that models provided, there were drawbacks. Dynamic modeling was attempting to represent a system that was dynamic and sometimes unpredictable. Unfortunately, the tools that were being used to represent these systems were themselves not completely dynamic. Modeling attempted to represent a system by enclosing a selected number of system components and determining the model-system's behaviour over time in response to the forces found only inside the model. The model was therefore seen as a closed system (Hannon and Ruth 1997). Real systems in contrast were not closed but open, allowing for new, even unprecedented development in response to highly infrequent but dramatic changes in their environment. This lead to another

drawback of the modeling, which was that it was not possible to completely verify a model by comparing model results to the behaviour of the real system as mentioned previously in the chapter. There may have been extenuating circumstances that led the real system to behave differently from the model (Hannon and Ruth 1997). Such circumstances will always be present, precisely due to the fact that it was the modeler's goal to capture only the essentials of the real system and to abstract away from other factors. Consequently, complete verification of a model can only be done with regard to the consistency or logical accuracy, of its internal structure (Hannon and Ruth 1997).

Another drawback to the modeling process was the attempt by many modelers to encompass every aspect of a system, thereby making the model far too complicated and in the end unrepresentative of the system that was being modeled. As well, this type of model becomes as complicated as the system that was being modeled, therefore removing the objective of building a model. Smith (1974) provided two reasons as to why she believed that a model should be as simple as possible. The first reason was that if a model was too complicated it was difficult to discover the behaviour of the model and the second reason was that it was important when comparing the behaviour of two model ecosystems to be sure that it was the multiplicity of species interactions and not some other fact which was the relevant difference (Smith 1974).

2.6 USE OF MODELS WITH WILDLIFE POPULATIONS

Ecosystems are complex in nature. One of the best ways to break them down was to develop a model that will help create an understanding. In his arguments for the use of modeling for wildlife management, Starfield (1997) stated:

“The management of wildlife populations is no longer restricted to the collection of data and the creation of charts. The most effective way to manage populations is to utilize the data collected and create models of the populations which one is managing.”

The collection of wildlife population data is expensive and time consuming. In wildlife management, models could be used in circumstances where data was missing in order to see how much difference the missing data might make or to see if the missing data could swing the decision one way or another (Starfield 1997).

Models were not restricted to only modeling populations. Models were being used for such things as modeling energy balance in mule deer over the winter (Hobbs 1989). As well, models could be used on different aspects of a wildlife population. For example, a model could be used to determine the long-term effect of certain management strategies on a population, or a model could focus on the age and sex structure of the population. In considering the use of a contraceptive dart on elephants, Cochrane *et al.* (1997) utilized a model to determine the number of cows that would have to be darted each year, how quickly the population would grow if fewer cows were darted and what changes in the age structure of the herds could be expected.

A model for wildlife management could be constructed as an experiment, a hypothesis or a problem-solving tool (Starfield 1997). Models could be constantly modified and adapted to the environment they represent. A model for wildlife management could be developed to represent and test many different circumstances, which arise in the management of wildlife populations (Starfield 1997).

In many circumstances, the management of wildlife not only involves the managers, but an increasing number of stakeholders, with various and often conflicting objectives. The use of certain types of models could provide the stakeholder with the probability of success of their objective, which then returns the onus on the stakeholder to weigh out the cost against the success (Starfield 1997).

The use of modeling in wildlife management is beneficial; therefore “the question is not whether to model, but rather how to model usefully and efficiently” (Starfield 1997).

2.7 EXAMPLES OF THE USE OF MODELS

There are many different types of models available for use in a variety of situations. Models were being used in many real life situations regarding ecosystems and the environment in determining the impact the activities of man were having on species of plants and animals.

Medin and Anderson (1979) attempted to capture the dynamics of a Colorado mule deer population through the modeling process. In the development of the model, Medin and Anderson (1979) recognized that the model was not a complete representation of the mule deer-environment system; therefore they included the basic structural and functional elements required for the study of the dynamics of any exploited deer population (Medin and Anderson 1979). A majority of the input variables for the model were collected directly by Medin and Anderson from the mule deer environment. The development of the equations and relationships were based on observations as well as references from other studies. The model was tested with initial values, as well as variables in the values to determine the sensitivity of some of the variables. Hypothetical

simulations were also run on the model. The model-generated estimates of population attributes generally appeared to mimic data based estimates (Medin and Anderson 1979). After studying the results of the models, Medin and Anderson (1979) concluded that fragments of knowledge and assumptions about a system could be developed into a useful simulation model. As well, ill-defined relationships of a system could also be incorporated into a model (Medin and Anderson 1979).

Hobbs (1989) developed a model of energy balance in mule deer. The model was utilized to predict the changes in body size and fatness of the average doe and fawn and predict the rates of mortality due to starvation in populations of does and fawns. Unlike the previous example, the state variables in this model were the calories of metabolizable energy in the forage standing crop, the labile energy pool in the animal and the animal's endogenous energy reserves (Hobbs 1989). Rates of flow from these variables responded to changes in operative temperature, snow depth and animal density (Hobbs 1989). In order to enhance the understanding of winter ecology of mule deer, Hobbs utilized planned manipulations of model variables. Hobbs (1989) found that the model predictions of overwinter mortality in does and fawns closely resembled trends in field measurements of mortality during 14 different years in 2 different habitats. As well, model predictions of fat reserves did not differ from measured values during early and midwinter, but diverged from measurements at winter's end. Overall Hobbs (1989) found that by organizing results of nutritional research in a form that is accessible and interactive, the model can facilitate decisions on managing mule deer populations and their habitat.

Models are now being used extensively to provide a greater understanding of the systems, which they represent. By using models, one can symbolically explore ecological relationships and gain a feeling for the way the system probably would react to a particular disturbance (National Oceanic & Atmospheric Administration & Resources for the Future 1975). Models are now acting as tools to help learn more about the structure and behaviour of nature, both now and in the future (Hall and Day 1977).

CHAPTER 3

ELK IN RIDING MOUNTAIN NATIONAL PARK

3.0 INTRODUCTION

The viability of indigenous species is woven into the core of ecological integrity and therefore studying species viability is important to help assess the level of ecological integrity of a region (Nylen-Nemetchek 1999). Elk are indigenous to the RMNP region and are considered an integral part of the RMNP ecosystem (Riding Mountain National Park Ecosystem Conservation Plan 1997). This chapter provides the history of elk in the RMNP area and some of the interactions and influences that impact the elk.

3.1 ELK HISTORY IN RIDING MOUNTAIN NATIONAL PARK

Prior to European settlement, elk herds roamed extensively throughout North America. The arrival of European settlers resulted in extensive hunting and habitat loss of elk, thereby dramatically reducing their distribution and numbers throughout Canada and the United States. This resulted in smaller isolated populations scattered throughout the regions. Today, elk can be found in 7 provinces and 24 states (Rocky Mountain Elk Foundation 2001). There have been successful reintroductions of elk in Canada, with the species spreading into the most suitable ranges available to them in Western Canada (Carbyn 1983).

The Riding Mountain region is home to the Manitoban elk (*C. e. manitobensis*), one of the six subspecies of North American elk (Polziehn *et al.* 1998). This subspecies' former range covered the Prairie Provinces of Canada, the Great Plains of the United States and a western portion of Ontario (Figure 3). Intensification of settlement during the late 1800's and early 1900's resulted in the dramatic reduction of the Manitoban elk

population, leaving only small, scattered herds. The largest remaining concentration of this subspecies was found in the Riding Mountain region (Polziehn *et al.* 1998). In attempts to preserve this elk population, a 13 x 39 km game reserve was established in 1900 in the already existing Riding Mountain Dominion Forest Reserve (Richards 1997). Hunting was still permitted within the forest reserve, but not in the game reserve. The impacts due to hunting and local use on the elk population remained high despite the lack of hunting within the game reserve. By 1914, an estimated 500 elk remained (Blood 1966). By 1917, the entire forest reserve was closed to hunting by legislative decree, enabling the elk population to rebound (Green 1933). By 1925, park officials estimated the number of elk to be between 2000 and 2500 animals (Banfield 1949). The elk population continued to grow, benefiting from the establishment of Riding Mountain National Park in 1933. During the 1940's extensive logging for the war effort, habitat fragmentation, a consequence of logging and other natural and human-induced activities, and lack of predators resulted in an irruption of the elk population (Tabulenus 1983). The population peaked at 16,800 animals in the fall of 1946. Severe winter weather in 1946-47 and habitat deterioration due to over-browsing dramatically reduced the population in the last half of the decade (Rounds 1977). The number of elk stabilized in the early 1950's at roughly 4500 animals. Hunter harvest of elk during the time period 1951-53 further aided in decreasing elk numbers to approximately 2500 animals in 1954. For the last half of the 20th century, the elk population in RMNP has fluctuated; with highs ranging from 4500 to 6000 animals to lows of around 2000 animals (Figure 4).

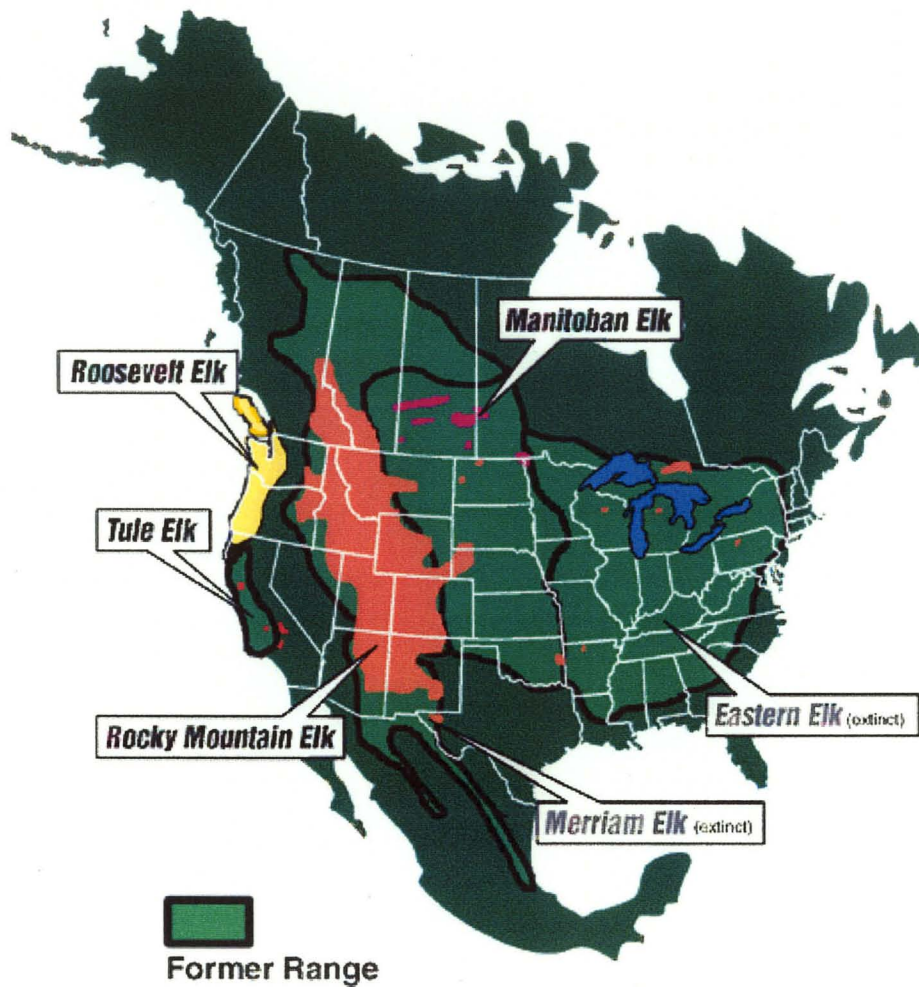


Figure 3. Present and Former Range of the Elk of North America

Source: Rocky Mountain Elk Foundation 2001

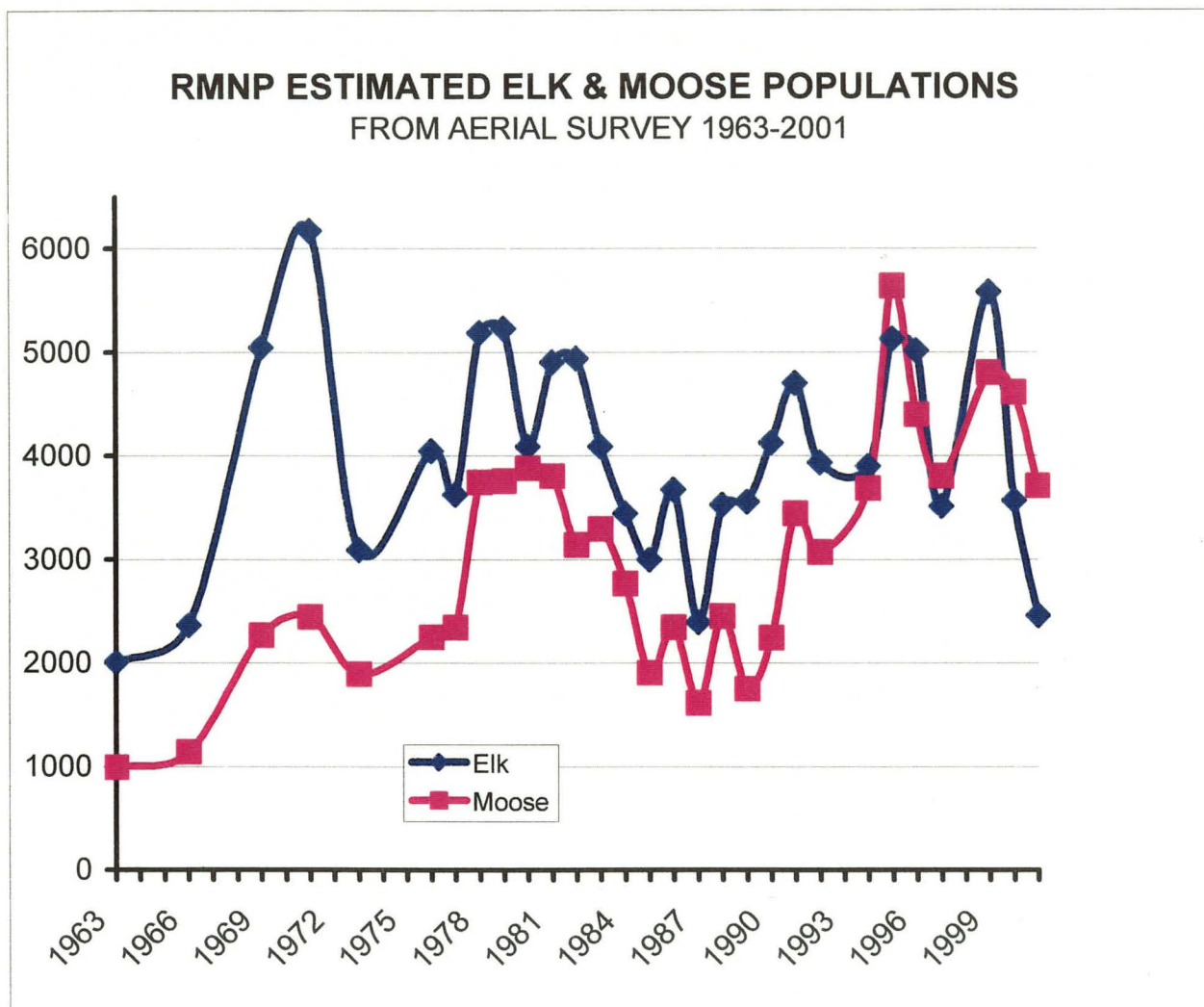


Figure 4. Riding Mountain National Park Elk and Moose Populations Based on Aerial Surveys.

Source: RMNP 2001a.

3.2 INFLUENCES AND INTERACTIONS WITH ELK IN RMNP

Elk like many other species in an ecosystem are influenced by direct management through harvest, or by indirect human effects such as predator extirpation, introduced and controlled parasites, alterations in landscape structure and food supplementation by agricultural practices (Augustine and McNaughton 1998). The following sections address the components that influence and interact with the elk population of RMNP.

Climate

The climate of the Riding Mountain area 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 persists for about five months (mean = 152 days) (Keck 1975). Total precipitation is about 50 cm per year, with the levels varying based on elevation (Richards 1997).

The longest and most dominant season in the Riding Mountain area is winter; therefore one of the greatest influences on the elk population in RMNP is winter severity. Winter severity includes factors such as snow cover characteristics and temperature. Turner *et al.* (1994) found that winter severity played a dominant role in ungulate survival and that winter range conditions were the primary determinant of ungulate survival and reproduction within Yellowstone. As well, Mech *et al.* (1987) stated that length and severity of winter are two factors that determine the extent of the annual weight loss and the ability of the animals to recover during the rest of the year. Richards (1997) found a negative correlation between winter severity and the elk population, which agreed with similar findings of Edwards (1956) who had shown a negative

relationship between ungulate population levels and snow depth. High winter severity resulted in the eventual decline of the elk population. Reasons for the decline could be related to winter calf mortality, reduced recruitment and reduced fecundity after severe winters. Singer *et al.* (1997) found that severe winter weather negatively influenced elk calf survival. Severe winters could lead to higher deaths in the calf population, possibly eliminating an entire age class population. Lack of quality and quantity in the food supply could negatively affect the fecundity rate in elk, delaying sexual maturity (Lack 1954). Trottier *et al.* (1983) found that foraging and winter severity can be used to predict short term population trends because of strong correlations between diet quality and animal conditions in terms of frequency of conception, birth weight and survival of calves. Because ungulates are pregnant during winter and spring, winter and spring weather potentially has a great effect on fetal development, weight, and survivability of offspring and thus on population change (Mech *et al.* 1987).

Snow cover is an integral factor in the environment of ungulates and an integral component of winter severity (Pruitt 1979). Pruitt (1959) showed that the distribution of caribou on their winter range was correlated with and predicted by certain characteristics of snow cover, such as depth, hardness and density. Depth indicates the thickness of the snow through which an animal must move if not supported by the snow; density, the water equivalent of the snow, inhibits locomotion by increasing drag on legs or body; hardness is defined as the physical bonds between crystals of snow cover and therefore will determine the force which must be exerted to move through the snow and the capacity of snow to support the animal (Coady 1974). Snow cover can hinder movement, influence cratering and hence availability of food, and limit habitat (Pruitt 1990). Trottier

and Hutchison (1980,1982) observed in conditions of large amounts of snow cover, elk avoided meadowlands and deciduous forests and moved into mixedwood and coniferous habitat, thereby limiting their available food supply.

The maximum snow depth that elk will crater is approximately 60 cm, but elk will usually not crater in snow deeper than 30 cm (Palidwor 1990). Therefore in years in which the snow is significantly deep, the quality and quantity of the food consumed is lower, affecting the condition of the elk. Increased hardness will impede an ungulate's ability to crater for food, in spite of the snow depth. Increased snow thickness and hardness has been found to coincide with reduced intake of grass, sedge and forbs by elk. The impact on the elk population is more dramatic than with other ungulate populations because from October to May, 60 to 70% of the elk diet may be obtained from grazing sedges and grasses if snow is absent, patchy or less than 30 cm thick and of low density (Trottier and Hutchinson 1982).

Snow cover not only leads to decreased food supply, it also hinders elk locomotion, making them more susceptible to wolf predation. Huggard (1993) found that the kill rate for wolf packs on ungulates increased from 1 ungulate/5.4 days in conditions where there is no snow, to 1 ungulate/1.1 days in snow 60 cm deep. Deep snow hinders the movements of elk and other ungulates, as well as wolves, but due to the lighter foot load of the wolves in comparison to most ungulates, the hunting success of the wolves is increased. Carbyn (1981) observed increased kill rates and surplus killing by wolves during winters with a high winter severity in RMNP. Huggard (1993) concluded that because the kill rate of wolves is correlated with snow depth, unpredictable variation in yearly snowfall may add substantial, density-independent variation to wolf-prey

interactions. Mech *et al.* (1992) found in their study of prey selection by wolves in Denali National Park, deep snow had a direct effect on reducing prey condition and mobility and thus increasing predation by wolves. As well, they also found an indirect effect of snow depth on caribou calves that had been in-utero and thus were predisposed to wolf predation during the next summer and winter (Mech *et al.* 1992).

Temperature is another component of winter severity. Large ungulates possess considerable thermal inertia, aiding in thermoregulation (Hudson and Frank 1987). Despite the ability to thermoregulate, 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). Trottier and Hutchison (1982) found that ungulates exhibited physiological, reproductive and behavioural reactions to severe winter temperature.

Wolves

The wolf population within and outside RMNP has fluctuated throughout the last century (Figure 5). In the early 1900's, virtually no wolves were present in the RMNP area as a result of extensive hunting, trapping, land clearing and poisoning by European settlers (Carbyn 1980). Not only were wolves considered a predator of livestock, but also a competitor with human hunters for the ungulates in the area. Therefore, wolves continued to be absent from RMNP during the 1920's and 1930's. There was the odd sighting of wolves around the Park, but the absence of this particular predator in the Park continued into the 1940's. Slowly the population began to increase in numbers and by the 1950's it was estimated that there were approximately 20-25 wolves in the Park (Carbyn 1980). The wolf population peaked in 1975 at 120 animals, but over the last 25

years there has been a decline in the wolf numbers. Only in the last year or two has the population increased slightly.

Elk are the primary food source of wolves in Riding Mountain National Park (RMNP) (Paquet 1989). The relationship between the elk population and the wolf population in RMNP is significantly influenced by many factors. Despite the fact that the wolf population is so heavily influenced by external sources, it continues to impact the elk population to a certain extent. The number of elk taken by wolves in comparison to the number of moose is higher (Carbyn 1983). Carbyn (1983) determined the maximum number of elk killed per wolf in RMNP from 1 October to 30 April was approximately 15 and a pack of 5 would theoretically kill about 75 elk, but due to the abundance of alternate prey, the harvest number of elk by wolves is buffered. Wolf predation on elk in RMNP at the present reduces the rate of increase and possibly prevents an irruption like that documented in 1947 by Banfield (1949), at which time presence of wolves within RMNP was rare, but increasing (Banfield 1947).

In the predator-prey relationship, weather could be a contributing factor to the success of the predator. Severe winters could benefit predators by increasing the possibility of malnutrition and impeding locomotion of elk and other ungulates, resulting in a higher wolf predation rate. But mild winters could be considered more favourable for elk and other ungulates due to lack of snow and easier access to food (Peek 1980). Adams *et al.* (1992) found in their research on wolf predation on caribou calves, there was an increase in calf mortality during the summer following a winter of above average snowfall. They believe this was due to lighter birth weights of the calves due to increased nutritional and physical stress on the cows during the winter. Adams *et al.* (1992) found that the

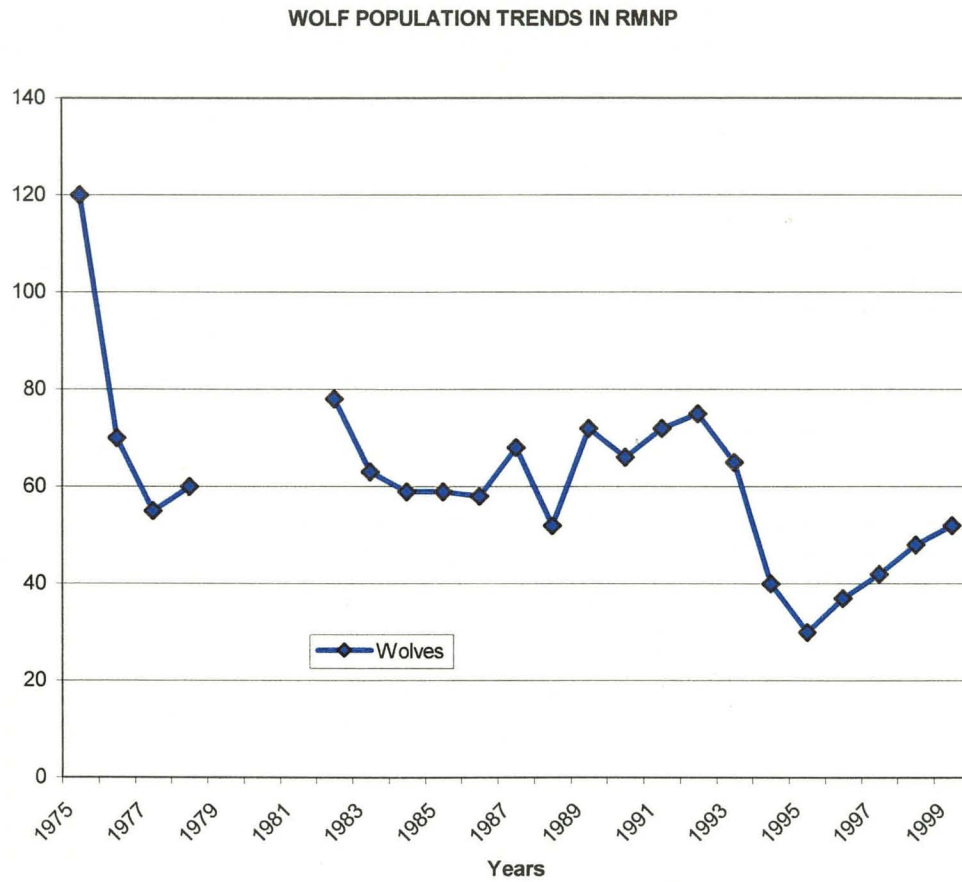


Figure 5. Riding Mountain National Park Wolf Population.

Source: RMNP 2001b.

increase in the death of calves was more strongly correlated to birth weight than to wolf density.

Human Harvest

Although hunting is not permitted in RMNP, the human harvest of elk by hunting outside Park boundaries impacts the elk population inside the Park. Every year a hunting season is permitted in Game Hunting Zones 23 and 23A that surround the Park (Figure 6). The hunt is regulated by the provincial Department of Conservation. RMNP staff supplies the provincial government with the ungulate population trend based upon the aerial surveys of the population done that year. Richards (1997) found that there was a negative correlation between hunter harvest and the elk population levels, resulting in a decline in the elk population within the Park following a large harvest year. Richards (1997) suggested both the life history (i.e. that the females do not produce offspring until they are two years of age) and lack of restrictions on the sex of animals taken for bag limits in these two hunting zones, which can lead to an over harvest of cows, were two possible reasons for the decline. Cows of the population that are 4-12 years old are the experienced breeders and are the ones that ensure population survival (Flook 1970). A large harvest of females would most likely consist of the cows that fall within the 4-12 year age range, leading to less cows for production over the following years. Carbyn (1983) found that hunters around the RMNP took a larger proportion of middle-aged elk (i.e. 2yrs plus), in comparison to the wolves, which focused on the young, old or sick. In a year of heavy harvest, a higher number of breeding females could be taken, thereby possibly influencing the population.

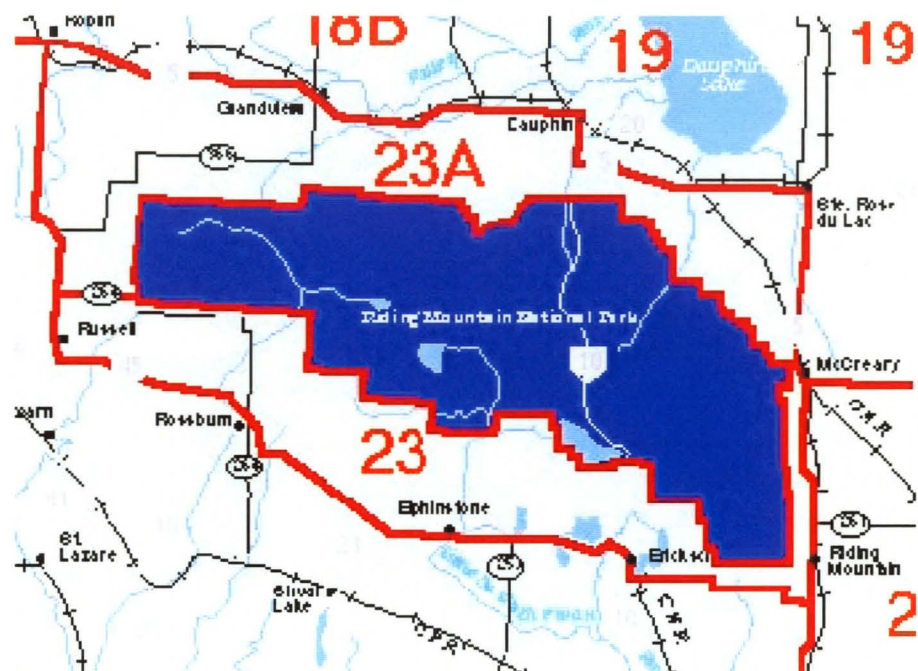


Figure 6. Game Hunting Areas Surrounding Riding Mountain National Park.

Source: Manitoba Department of Conservation 2001

Fire

Fire is a major component of the RMNP ecosystem and has an influence on elk populations. Fire and fire suppression have both influenced the Riding Mountain elk population. Burning and suppression of fire both alter the landscape and plant species composition of the environment, upon which elk rely. Aboriginal peoples used fire to control the grasses and browse, inaugurating the first growth or stimulating the second, thereby dictating the pattern of feeding by wildlife such as bison, deer, elk and moose. This in turn affected the annual migration of these grazer and browsers, as well as hunters (Pyne 1993). European settlers tried to suppress and control fire, which altered the plant species composition within the Park and surrounding area, thereby influencing ungulate populations.

Fire not only alters the vegetative composition of the burned area, but the effects of fire also tie into the effects of winter severity on elk. Turner *et al.* (1994) found in Yellowstone that fire size and pattern had no appreciable effect on ungulate survival during mild winters, but resources were limited when winter conditions were severe. During severe winters, fire decreased ungulate survival during the initial postfire winter but could enhance survival during later postfire winters (Turner *et al.* 1994). Turner *et al.* (1994) also found that the spatial pattern of the fire influenced ungulate survival. Ungulate survival was greater with clumped than fragmented fire patterns during more severe winters, but only for the small to moderate fires. During the initial postfire winter, survival could be 100% greater in the single-patch burn than in the random burn when 15% or 30% of the landscape was affected. When 60% of the landscape was burned, there was no ungulate survival during the severe winter (Turner *et al.* 1994).

Hobbs (1996) found that ungulates influenced fire regimes by altering the quality and quantity of fuels available for combustion. In grasslands, ungulates often reduced the extent, frequency, and intensity of fires through the reduction of standing biomass of plants available (Frost and Robertson 1987, Stronach and McNaughton 1989). In shrublands and forests, ungulate effects can increase the likelihood of crown fires, while reducing the likelihood of surface fires (Hobbs 1996). Some plants species in shrublands and forest contain volatile compounds that increase the flammability of the trees and shrubs. These volatile compounds also act as an important deterrent to herbivory (Christensen 1985). Therefore, due to lack of browsing on the shrubs and trees containing volatile compounds, ungulates may offer a competitive advantage to those particular plants. This favours the development of woody plant communities that are more flammable, more resistant to decomposition, and less palatable. Therefore, ungulates increase likelihood of crown fires by accelerating succession toward plant communities that are more likely to support such fires (Hobbs 1996).

Alteration of the habitat following fires has been found to correspond with increase in calf predation. Singer *et al.* (1997) found that fire increased the vulnerability of elk calves to predation. The theory for the increase in predation rate was that due to burning of tall shrub and conifer cover, elk calves might have been less well hidden.

Forage

Ungulates not only depend on plant communities but also generate strong direct and indirect feedbacks on plant community composition and structure. This in turn would affect long-term ungulate population growth (Augustine and McNaughton 1998).

Trottier *et al.* (1983) found the most important components of the elk diet in RMNP were shrubs and sedges. Grasses ranked third and forbs were considered to be the least important component of the elk diet, due to their lower nutritional quality. The availability and quality of the elk's food sources is influenced by other factors within the ecosystem. Weather conditions, the season and fire were factors that greatly influenced the quantity and quality of available forage. Trottier *et al.* (1983) found that in winter if the snow came late, wetland sedges were the primary component of the diet, whereas if the snow came early, shrubs were consumed in the greatest quantity. Mild winters led to an exploitation of sedges and grasses, but increasing snow severity limited access to these forages and twigs of shrubs became the dominant food source (Trottier *et al.* 1983). The elk's food source was not limited by the boundaries of the Park. Trottier *et al.* (1983) observed frequent movement of elk in and out of the Park and onto the adjacent farmland.

Alfalfa hay is readily available and provides an external food source, especially during times of severe winter conditions. Trant (1992) found that within a 10km zone surrounding RMNP, agriculture is intensifying, with over 92% of that land under production. Within that zone, crops consisting mainly of grains and cereals or close-row type crops have increased. Planted forage type crops such as tame hay and improved pastureland have also increased, providing a substantial alternative food sources for the elk from RMNP (Trant 1992).

During periods of cold weather, ungulates were forced to seek cover in areas where little forage is available, thus food intake was often reduced (Ozoga and Verme 1970). Prolonged snow cover or abnormally low temperatures in the spring could delay the green-up time of forage, requiring ungulates to remain in a negative energy balance.

The timing of spring green-up and the length of the growing season affect the condition of ungulates and ultimately, their reproductive potential (Trottier and Hutchison 1982). Trottier and Hutchison (1982) observed a very low calf:cow ratio of elk following a late green-up. As well, the winter elk count was also reduced. Reduction of forage intake or intake of poor quality forage due to high winter severity, could lead to weight loss in pregnant elk, which could result in decreased birth weights of calves, leading to decreased survivability. Under captive conditions at the Sybille Big Game Research Unit in Wyoming, Thorne *et al.* (1976) showed that weight loss in pregnant elk was significantly correlated with calf weights at birth and growth to four weeks. Under these conditions, elk calves that weighed 16 kg at birth stood a 90 percent chance of surviving to the fourth week; while those that weighed 11.4 kg a 50 percent chance. Pregnant cows, which lost more than 3 percent of their body weight between January and just prior to calving, did not produce 16 kg calves (Thorne *et al.* 1976). Singer *et al.* (1997) concluded in their study of radiocollared elk calves in Yellowstone National Park that summer survival of the calves was positively correlated with estimated birth weight. Calves that were lighter at birth had a lower survival rate than those that were heavier at birth. As well, Singer *et al.* (1997) also found that the calves dying from predation weighed less at birth than those surviving from predation.

Forage availability both in quality and quantity was also important throughout the summer and early fall. Flook (1967) found that the most important factor determining pregnancy rates in elk was female weight at the time of breeding. Cook *et al.* (2001) in attempts to determine the nutritional influences on breeding dynamics of elk, nutritionally restricted female elk of a captive herd during the summer and early autumn and found

that the elk which were nutritionally restricted prior to the breeding season delayed breeding or failed to breed, thereby reducing pregnancy rates.

Other Influences

Beaver is one component of the RMNP ecosystem that is seen as possibly influencing the elk population. Trottier *et al.* (1983) believed that the increasing beaver population might be having an effect on the density of the elk within the Park, as a result of increased flooding of elk habitat. As well, beaver are considered an important food source in the summer diet of wolves, thereby reducing the possible summer predation on elk (Carbyn 1980, Meleshko 1986). Carbyn (1980) found that there was an inverse relationship between elk and beaver in regards to wolf predation in the summer. The highest incidence of elk in the summer diet occurred when the incidence of beaver was the lowest (Carbyn 1980).

Black bear predation on calves could influence the calf crop of a particular year. The harvest of calves by bears is heaviest in the calves' first three weeks of life (Singer *et al.* 1997). The predation level can be as low as a few to upwards of 50 per cent of the calf crop, thereby dramatically influencing the population.

Moose and deer are the two other major ungulate species found in RMNP. Both populations are generally increasing in numbers. Trottier *et al.* (1983) found overlapping use of range, habitat preferences and diets between elk, deer and moose. In situations such as severe winters, competition could arise. Trottier *et al.* (1983) found that high winter severity hindered the movement of elk and deer. Both tended to move into similar habitats with limited food supply. Trottier *et al.* (1983) also found that moose were much less impeded by deep winter snow and were able to remain in more open areas.

Carbyn (1980) found that harvest by wolves on moose was significantly lower than that of elk and combined with changing habitat and effects of winter severity, moose could possibly have a competitive advantage over elk.

CHAPTER 4

MODEL DEVELOPMENT

4.0 INTRODUCTION

This chapter describes the steps used to develop the model based upon the elk population in RMNP. There were three major steps in the development of the model. The first step was the development of causal loop diagrams, the second was the development of feedback loops and the third was implementation of data into the sectors of the model and subsequent running of the model. Data were gathered from RMNP records, the Provincial Department of Conservation and other studies. The data were utilized to develop formulas for the model. Previous studies aided in the development of the model by providing the important factors that affect the elk populations within RMNP.

4.1 STELLA

The elk model was developed using the STELLA research software, version 5.1.1 by High Performance Systems Incorporated. The STELLA software is equipped with numerous mathematical functions for use in formula development. Some examples of the functions were RANDOM, INTEGER (INT), SUM, and SINWAVE, to name a few. As well, STELLA was equipped with the ability to graph components of the model against one another. The STELLA program provided run results, and allowed for variations to be made and hypotheses to be tested in different runs without causing harm to the environment. The STELLA model was only as good as the data that was inputted and the formulae created.

In future the model created in STELLA can be changed and manipulated by the managers of the Park to reflect situations, which are occurring in different aspects of the Park's ecosystem, allowing for different management strategies to be tested. As well, STELLA can be utilized to create other models for other aspects of the Park's management program.

4.2 CAUSAL LOOP DIAGRAMS

The purpose of causal loop diagrams was to portray how information feedback works in a system (Ford 1999). The diagram identified the positive and negative results of the major interactions of the components of the model (Figure 7). The diagram indicated the positive relationship between elk and elk births, as well as identified the negative relationship between the elk population and elk deaths. The diagram identified an overall negative relationship between elk and wolves. An increase in the wolf population will most likely lead to an increase in predation and an increase in elk deaths. This may result in a decrease in the elk population through a slowdown in population growth, thereby identifying this relationship between wolves and elk as a negative one.

The diagram also identified other relationships within the model. There was a negative relationship between elk and winter severity and elk and human harvest. A majority of the relationships were negative between elk and many components within the model, which indicated a feedback system, leading to the development of the feedback loops.

4.3 FEEDBACK LOOPS

Causal loop diagrams identified the major positive and negative relationships within the model, and were used to develop the feedback loops of the model. The

feedback loops highlighted the major interrelationships of the model (Figure 8). Some of the major interrelationships identified within this model were between the elk and wolves, the elk and winter severity, and elk and hunters.

The feedback loops consisted of the stocks and flows of the system. Stocks of systems were the represented accumulations or reductions in the base population. The elk sector of the model contained two stocks (state variables), which were the adult elk and calves. The wolf and moose sectors contained one stock each, which were the initial wolf and moose populations. The flows of a system represented inflows and outflows from the stocks. The flows utilized in the model for the elk sector were birth of calves, deaths of calves and adults, and human harvest deaths of the adult stock. The wolf sector contained flows for the births and the deaths of wolves. The moose sector consisted of flows for the births, deaths and human harvest deaths of the moose stocks.

Further development of the system required the addition of converters. Within the model, the converter component was utilized to influence the stocks and flows. Winter severity, human harvest rate, birth rate and death rate were examples of converters.

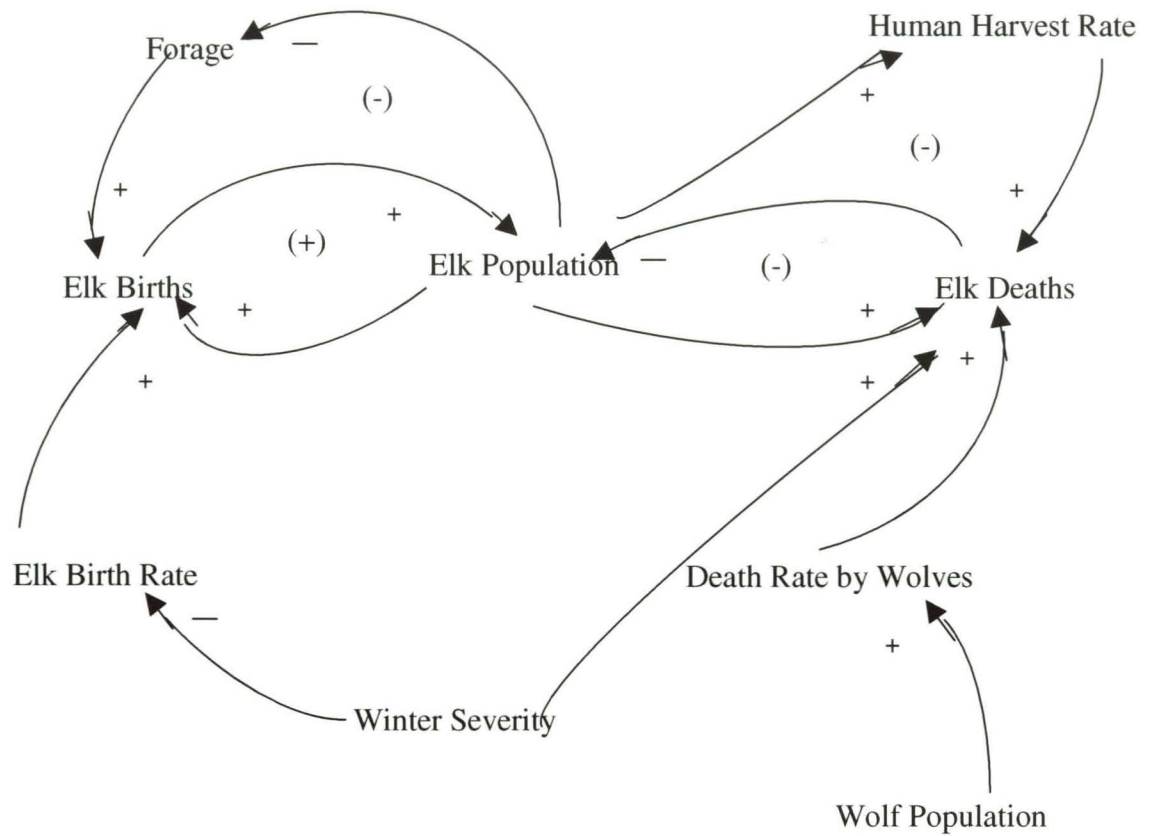


Figure 7. Basic Causal Loop Diagram

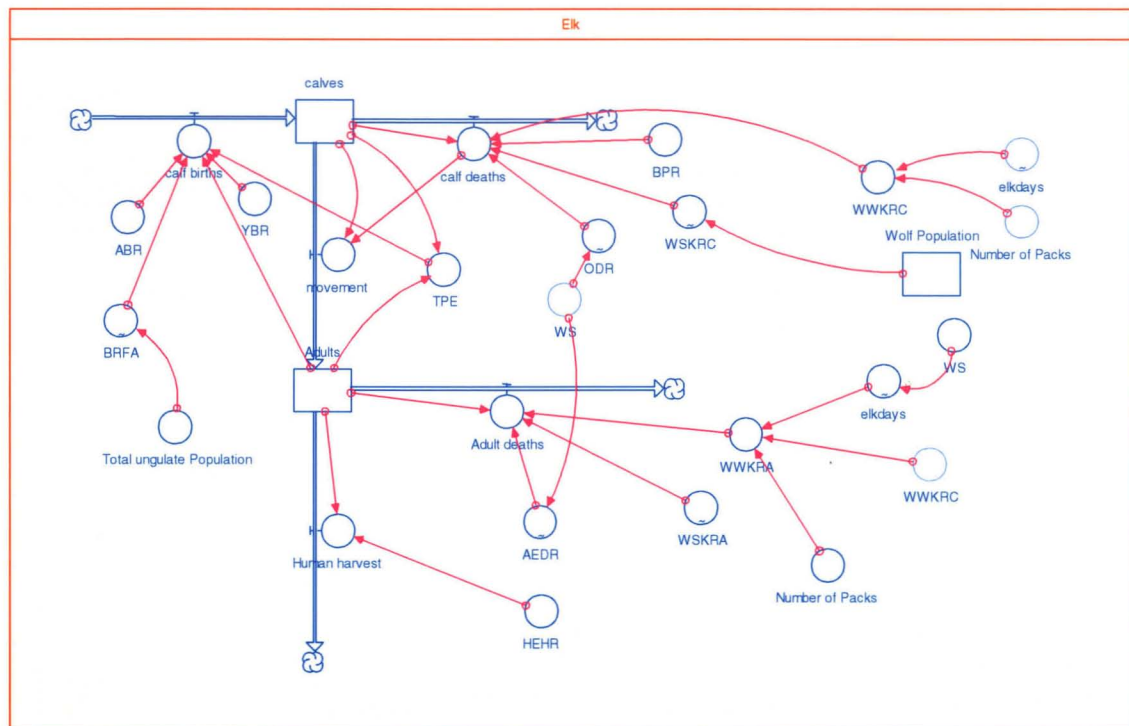


Figure 8. Feedback Loop Diagram

4.4 SECTORS OF THE MODEL

The sectors included the feedback loops. Within the model there were 5 sectors: the elk sector, the moose sector, the wolf sector, the winter severity sector and the total ungulate population sector. The data were utilized in the formulae and provided initial values of many of the variables in the model. The following section of the chapter highlights the 5 sectors and the use of the data in the sectors. The development of the model identified areas in which the data source for RMNP was lacking. This then required assumptions to be made for the model for some variables. The assumptions were based upon other research in which similar situations occurred. The initial values and terms for the model are in Table 1.

Table 1. Initial Values and Terms for Elk Model

Input variable	Model Code	Input Value	Source
Elk Calf Population	Calves	692	RMNP (2001a), RMNP (1988)
Adult Elk Population	Adults	2866	RMNP (2001a), RMNP (1988)
Elk Calf Births	Calf Births	Equation	
Elk Calf Deaths	Calf Deaths	Equation	
Adult Elk Deaths	Adult Deaths	Equation	
Movement of Elk Calves to Elk Adults	Movement	Equation	
Human Harvest of Elk	Human Harvest	Equation	
Other Death Rate (Calves)	ODR	Graph	
Wolf Winter Kill Rate for Calves	WWKRC	Equation	Carbyn (1980), Meleshko (1986)
Wolf Summer Kill Rate for Calves	WSKRC	Graph	Carbyn (1980), Meleshko (1986)
Bear Predation on Elk Calves	BPR	0.25	Singer <i>et al.</i> (1997)
One elk killed/number of days	Elk Days	Graph	Carbyn (1980), Paquet (1991)
Wolf Winter Kill Rate for Adults	WWKRA	Equation	Meleshko (1986), Carbyn(1980)
Wolf Summer Kill Rate for Adults	WSKRA	Graph	Meleshko (1986), Carbyn (1980)
Adult Elk Birth Rate	ABR	0.82	Carbyn (1980)
Yearling Elk Birth Rate	YBR	0.27	Carbyn (1980)
Available Forage Birth Rate Multiplier	AFBRM	Graph	
Total Elk Population	TEP	Equation	
Hunter Elk Harvest Rate	HEHR	0.10	MDC (1998), Rounds (1991)
Adult Elk Death Rate	AEDR	0.07	Assumed
Wolf Population	Wolf Population	50	RMNP (2001b)
Wolf Breeding Rate	WBR	Equation	
Wolf Death Rate	WDR	0.10	Assumed
Wolf Pup Numbers	Pup Numbers	5	Mech (1971), Fuller (1989), RMNP (1989)
Survival Rate of Wolf Pups	Survival Fraction of Pups	0.55	Fuller (1989)
Number of Packs	Number of Packs	Equation	RMNP (1997), Carbyn (1980,1983)
Wolves per Pack	Wolves per Pack	Graphed	RMNP (1997), Carbyn (1980,1983)
Hunter Harvest Rate of Wolves	HHRW	0.15	Carbyn(1980, 1983), RMNP (1997)
Breeding Pair Numbers of Wolves	Number of Breeding Pairs	Equation	Carbyn (1980), Paquet (1991)

Table 1 Continued...

Wolf Births	Wolf Births	Equation	
Wolf Deaths	Wolf Deaths	Equation	
Disease Rate of Wolves	Wolf Disease Rate	Random (0.02,0.40)	RMNP (1997)
Moose Population	Moose Population	1751	RMNP (2001a)
Moose Births	Moose Births	Equation	
Moose Deaths	Moose Deaths	Equation	
Moose Birth Rate	MBR	0.80	Assumed
Moose Death Rate	MDR	Graph	Assumed
Birth Rate Multiplier	Brfm	Graph	
Human Harvest of Moose	Human Harvest	Equation	
Human Harvest Rate of Moose	HHRM	0.08	MDC (1998), Rounds (1991)
Bear Predation on Moose Calves	BPRMC	0.25	Singer <i>et al.</i> (1997)
Harvest of moose by Wolves without Elk	HWNE	Graph	
Total Wolf Harvest of Moose	TWHR	Equation	
Harvest of Moose by Wolves with Elk	HWWE	Graph	
Winter Severity	WS	Stelfox Formula	Dolan and Tempany (1980)
Green Up Value	Green Up Value	Random (-15,25)	Trottier <i>et al.</i> (1983), Dolan and Tempany (1980)
Snow Depth	Snow Depth	Random (0,60)	Trottier <i>et al.</i> (1983), Dolan and Tempany (1980)
Snow Hardness	Snow Hardness	Random (0,20)	Trottier <i>et al.</i> (1983), Dolan and Tempany (1980)
Snow Density	Snow Density	Random (0,0.4)	Trottier <i>et al.</i> (1983), Dolan and Tempany (1980)
Winter Temperature	Winter Temperature	Random (5, -25)	Trottier <i>et al.</i> (1983), Dolan and Tempany (1980)
Total Ungulate Population in RMNP	Total Ungulate Population	Equation	

The basic source of data for the model came from RMNP. Aerial surveys, classified counts, and tracking surveys were obtained from the RMNP data source. The Manitoba Department of Conservation provided additional data relating to hunter harvests on elk and moose outside RMNP. The relationships between the various components of the model were developed and established from relationships observed in studies done by Carbyn, Trottier, Paquet, Meleshko and others on elk, moose and wolf populations both inside RMNP and in other areas.

4.5 ELK SECTOR

Elk Population

The population of elk was divided into two state variables. The first state variable was the calf population, which represented the summed calf population. The second state variable was the adult population, which represented summed yearling and adult populations.

Several steps were used to determine the initial values of the state variables. First, RMNP elk population estimates came from aerial surveys done from 1963-2001 by RMNP (Figure 4). Some of the techniques utilized in estimating the population during the 1950-1976 aerial surveys were different than those used for the other aerial surveys. This resulted in inconsistencies in the population estimates. The 1971-1974 results were not considered as accurate due to the techniques used to estimate the population (Rounds 1977). The most recent aerial surveys extended the survey region to include a small radius outside RMNP and have a confidence rate of 95% (RMNP 2001). Despite this high confidence rate, aerial surveys can have a wide margin of error as a result of: weather, techniques used, experience of observers, species behaviour and other factors.

Therefore, the population numbers obtained from the surveys are estimates of trends rather than absolutes (Rounds 1977).

The second step in determining the initial value of the state variables was through the use of classified counts. The classified counts, which were done throughout the years by RMNP, provided the early winter population structure of the elk population (calves:bulls:cows) (Figure 9). The classified counts were normally done in either November or December and the total population count was normally done in February. The classified counts for elk were provided by RMNP (1988), Carbyn (1980), and Meleshko (1986) and RMNP (2000). The classified count outlined in RMNP (1988) was done by an aerial survey over several blocks in the Park and the ratio of calves:cows:bulls was determined from the total number of each that were seen. The classified counts done by the other studies were done only in one block/herd in RMNP, rather than throughout the Park. The classified count carried out in December of 2000 was flown over three blocks of the Park that previously had a large number of elk (RMNP 2000). Classified counts suffer similar weaknesses as aerial surveys. Elk groups are usually comprised of cows, calves, yearlings and sometimes bulls, therefore during the classified counts some of the yearlings may be mistaken for cows, thereby increasing the cow number. As well, calves may not be in view during the survey and the bulls may not be apart of some of the groups counted, thereby leading to less accurate ratios.

The ratio provided by the classified counts were applied to the total elk population numbers to determine the number of cows, bulls and calves, which made up the population in a given year (Table 2). The cows and bulls were added together to establish the value of the adult state variable and the resulting calf number provided the

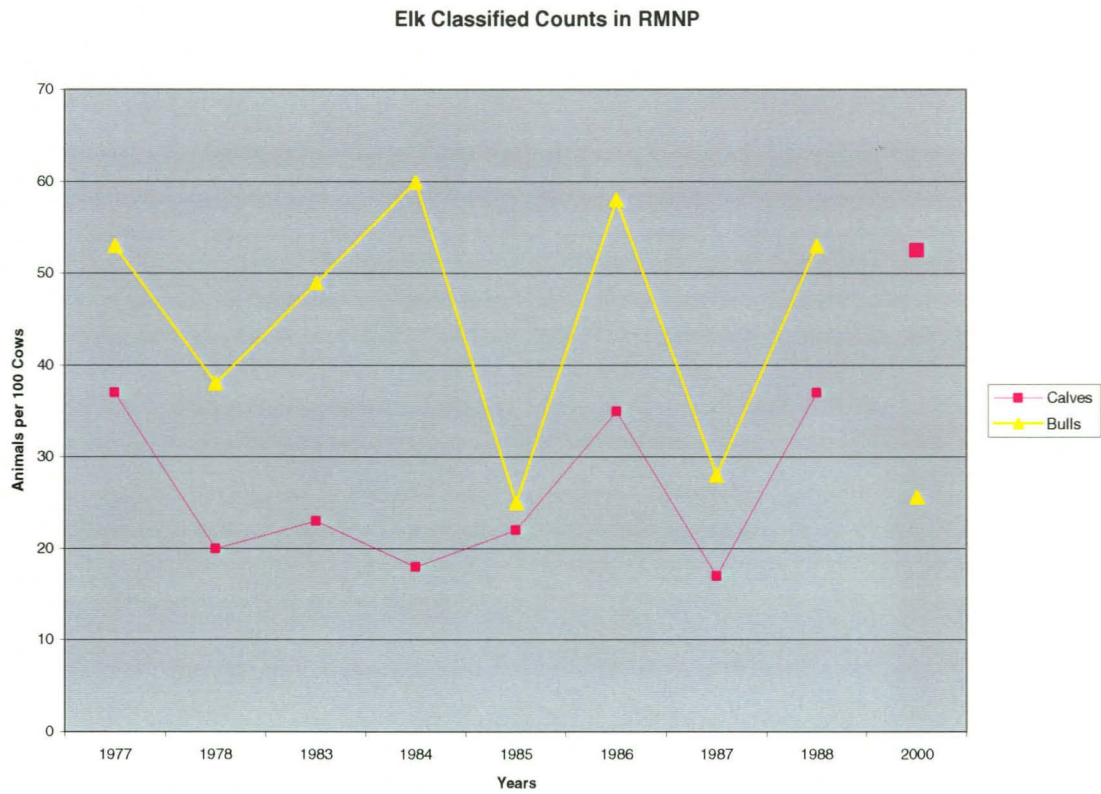


Figure 9. Classified Counts of Calves and Bulls/100 Cows in RMNP

Source: RMNP 1988, RMNP 2001a.

value for the calf state variable (Appendix 1). The population count and the classified count occurred over many years resulting in different estimates each year. For the model, the initial values for the calf and the adult state variables were determined from the 1989 aerial survey and the 1988 classified count. The initial values for the calf state variable was 962 calves and for the adult state variable was 2866 adults.

The adult and calves state variables were added together to indicate the total population of elk (TEP) in RMNP (Appendix 1). When either the adults or the calves fluctuated due to the flows that modified their population levels, the total population variable also fluctuated.

Table 2 - Estimated Numbers of Elk in Each Group, 1977-2000, Calculated from Classified Counts and Aerial Surveys of RMNP.

Group and Year				
Years	Calves	Bulls	Cows	Total
1977	1010	1447	2731	5188
1978	662	1258	3311	5231
1983	468	998	2036	3502
1984	303	1010	1683	2996
1985	550	625	2498	3673
1986	434	719	1239	2392
1987	414	681	2433	3528
1988	693	993	1873	3559
2000	723	353	1378	2454

Calf Births

The number of calves born each year was dependent upon the female portion of the adult population and the birth rate variables. Birth rate was split into yearling birth rate (YBR) and adult birth rate (ABR) variables. The birth rate variables determined the percentage of calves produced by the yearling and adult female populations each year. The yearling portion of the female population was the female elk that were the inexperienced breeders, calving for the first time at roughly two years of age and was approximately 10% of the total elk population (Carbyn 1980). The adult portion of the female population was the female elk that have had at least one calf. Carbyn (1979) determined pregnancy rates for yearling and adult elk in Jasper National Park and Elk Island National Park. The yearling pregnancy rate in Jasper was 40% under conditions of predation, whereas the yearling pregnancy rate in Elk Island was 14% with no predation. Carbyn (1980) used an average of the two pregnancy rates (27%) in his calculations of yearling pregnancy rate for the RMNP elk population. Yearling pregnancy rate can fluctuate from a low of 5% (Kittams 1953) to the 40% observed by Carbyn (1979) in Jasper National Park. Knight (1970) reported that calf production was higher for heavily harvested populations than those protected within preserves. As well, Carbyn (1979) found that the Elk Island population was subject to food stresses, possibly leading to a decline in the pregnancy rate. The adult pregnancy rate in Jasper was 91% and the pregnancy rate in Elk Island was 72% (Carbyn 1979). Again, Carbyn (1980) averaged the two pregnancy rates (82%) for his calculation of the adult pregnancy rate for the RMNP elk population. In Carbyn's (1979) study, it was assumed that the pregnancy rates were also the interval birth rates, ignoring the possibility of abortion and fetus

reabsorption. A similar assumption was made in the RMNP elk model for the birth rates of the adults and yearlings. Therefore, the initial value of the yearling birth rate in the model was 27% and the initial value of the adult birth rate in the model was 82%.

A multiplier was added to modify the birth rate of the elk. The multiplier was the available forage birth rate multiplier (AFBRM). The multiplier varied from a normal value of 1, to a low of 0. The total available forage that supported the total ungulate population in RMNP influenced the AFBM. During periods of normal conditions, the multiplier would not vary the birth rate. When the total ungulate population became too high, resulting in a decrease in available forage, the multiplier would have a value less than 1. Trotter *et al.* (1983) found that RMNP had the ability to support approximately 10,000 ungulates. Due to the extensive and increasing outside food source provided by the agricultural land surrounding RMNP as noted by Trant (1992), it was assumed that the Park would have the ability to support approximately 12,000 ungulates. As the total population of ungulates approaches 12,000, the birth rate multiplier begins to fall below one, which in turn decreases the birth rate because the available forage for all ungulates was beginning to decrease rapidly (Appendix 1). Banfield (1949) found that following the irruption of the elk population in 1946-47, lack of available food was one of the many factors that resulted in the dramatic decrease in the population.

Calf Deaths

In the model, three variables contributed to calf deaths. The first variable was predation by wolves; the second variable was predation by bears and the third variable was the "other" death rate. Total calf deaths were as a result of the three identified variables that contributed to calf deaths.

The “other” death rate (ODR) was defined as the deaths of calves as a result of any other means than predation. Deaths that would occur from starvation, deformities or disease were included in the other death rate. Because a value for ODR was not available, an assumption had to be made. One study on deer indicated that the death rate of deer in a situation of ample food and no predators was approximately 7%. Calves tend to have a higher death rate due a variety of factors such as decreased ability to survive on their own and increased susceptibility to the elements. Therefore, the initial value of the other death rate for calves was assumed to be around 10%. The ODR was then graphed against winter severity, which modified ODR. As the winter severity increased, the other death rate also increased.

The initial value for bear predation on calves was set at 25%. Predation by bears on calves can be as low as a few to upwards of 50% of the calf crop (Singer *et al.* 1997). In their study, Singer *et al.* (1997) found the bear predation on radiocollared elk calves to be around 23% of the total mortality of the marked calves. Larsen *et al.* (1989) indicated that the yearly predation on moose calves was random in number. Therefore, due to the nature of the predation, with no definitive causes for the variance in predation, 25% was value selected for the model.

Calf kill rate by wolves was determined separately for summer and winter. Winter kill rate on the entire elk population by wolf packs was determined using the number of days in the winter season, wolf pack numbers, the percentage of calves killed and elk days (Appendix 1). Elk days are the number of days in which a wolf pack takes to kill an elk. Carbyn (1980) determined the maximum kill rate for wolves on ungulates was 1 ungulate/pack/2.7 days in periods of severe winter weather. Meleshko (1986)

determined the ratio of biomass of each ungulate found within scat samples of wolves in a severe winter and determined the maximum rate of elk kills was approximately 1elk/pack/4 days (Appendix 1). Elk days were varied based on the winter severity component of the model. Elk days were graphed in relation to an increasing winter severity. Meleshko (1986) determined that the percentage of calves killed out of the total elk killed was approximately 27%. This number will fluctuate based upon the year, the winter conditions and the available calf population. Huggard (1993) found that during periods of minimal snow, calves and adults were killed at a similar rate, intermediate snow resulted in a higher predation rate on calves and during periods of deep snow, adults were the primary prey.

Summer kill rate on calves by wolves was not based upon elk days. Carbyn (1980) and Meleshko (1986) both found that the summer wolf diet varied greatly from the winter wolf diet due the availability of beaver as prey. Therefore, summer wolf kill was determined using the required food needs of the wolf population (Appendix 1). Once an initial kill number was determined based on a set population number, the summer kill rate was graphed against a changing wolf population (Appendix 1).

Adult Deaths

The adult population was made up of both yearlings and adults, therefore whatever was left over from the calf population after deaths and births moved directly into the adult population at one year of age.

As mentioned in the calf death section, there was no definitive other death rate for either calves or adults. In modeling the Kaibab deer herd, Ford (1999) assumed the death rate of the deer in the absence of predators to be approximately 7%, based on work done

by Armstrong (1987). The Kaibab deer herd inhabits an ecosystem very similar to that found in RMNP and face similar challenges for survival. Therefore, the adult death rate of the elk was assumed to be similar to the deer death rate and was set at 7%. The adult death rate was graphed against winter severity, which was used to modify the adult death rate. Increased winter severity resulted in an increase in the percentage of adult deaths.

The wolf winter kill rate on adults was determined by using the equation that was used to determine the calf kill rate, excluding the percentage that determined the calf killed numbers. The equation determined the total elk kills; therefore in order to acquire the adult kills, the equation was subtracted from the winter wolf calf kills (Appendix 1).

The summer kill rate on adults was determined in the same manner as the summer kill rate on calves. The kill rate was graphed in the same manners as the summer calf kill rate, against the changing wolf population (Appendix 2).

Human Harvest of Elk

The elk hunter success rate data was compiled from the Manitoba Department of Conservation for the years 1993-1999. The numbers compiled by the Provincial government do not include the number of poaching incidents. Rounds' (1991) study provided numbers on the elk and moose hunter kills around the Park for the years 1951 to 1989 (Table 3). Throughout the years, the harvest level varied, from an average of approximately 5% of the population to 53% in a year of very heavy harvest. Rounds (1991) found that in the last 20 years, the harvest rate of elk was usually less than 10%, but there were times when it was higher than 10%. Therefore, in the model, a harvest rate of 10% was initially set for the adult population. Carbyn (1980) found the majority

of hunter kills to be on elk, one year and older, therefore the hunters are applied to the adult population rather than to both adults and calves.

4.6 UNGULATE SECTOR

This sector represents the total ungulate population found within RMNP. Total ungulate population was calculated by adding the moose and elk population state variables together to indicate the total ungulate population within RMNP. White-tailed deer and mule deer were not included as a part of the ungulate population. Mule deer were not included because the population is extremely small and therefore it was assumed that the population would have no effect on the elk. The white-tailed deer population was not included because the population estimates are highly variable due to the difficulty in estimating deer numbers during the aerial surveys. Fluctuations in any of these two state variables altered the total ungulate population variable.

4.7 MOOSE SECTOR

RMNP and the Manitoba Department of Conservation provided moose data. The population data was collected in the same manner as the elk population, through aerial surveys. The Manitoba Department of Conservation (1998) and Rounds (1991) provided the hunting rate on moose for the same time frame as for the elk.

The initial value for the moose population state variable was 1751 moose. The value for the moose population was taken from the same survey year as the initial elk population values for the elk state variables.

Year	Elk			Moose			Combine		
	Kill	Pop	%Pop ¹	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 ²	16/14	1306	25,941 ²	5/4	12,195	115,447	11/10

¹ Harvests were not added back in to populations, so these percentages are higher than actual numbers.

² Calculated using only populations in years with hunting seasons.

Table 3 - Moose and Elk Hunter Kills.

Source: Rounds (1991)

In determining moose births, it was assumed that roughly 55% of the moose population was female and that the birth rate for the female population was approximately 80%. The births were modified by the birth rate forage multiplier (brfm).

Similar assumptions that were made for the elk adult death rates were made for the moose death rate. The death rate of moose was set at 7%. The death rate of moose was graphed against winter severity, which influenced the death rate of the moose. As the winter became more severe the death rate of the moose increased.

The harvest rate of moose by wolves was split into two harvest rates. The first harvest rate was determined with the presence of elk in RMNP. Carbyn (1980) and Meleshko (1986) have both indicated that the harvest of moose by wolves was lower than the harvest of the elk; therefore the first harvest rate by wolf packs was graphed at a very low percentage and only increasing slightly when wolf pack numbers increased. The second harvest rate was the harvest rate on moose when elk were at extremely low numbers or no longer present in RMNP.

The harvest rate of moose by humans was lower than the harvest on elk by humans; therefore the initial harvest rate was set at 8%.

4.8 WOLF SECTOR

Wolf Population

The wolf population estimates were taken from ground and tracking surveys done from 1975-2000 in RMNP (Figure 5). The initial value for the wolf population state variable was 50 wolves. The initial value was taken from the same year as the elk and moose population state variables in order to provide consistency within the model.

Wolf Births

Wolf births in RMNP were determined through an equation utilizing the number of wolves per pack, number of breeding pairs, number of packs, survival fraction of the pups and number of pups (Appendix 1). The average number of pups was obtained from Mech (1971) and Fuller (1989), who both indicated that number of pups in a litter was between 4 and 7. Carbyn (1980) also observed that the wolves in RMNP most likely did not produce litters of seven or more. Therefore, the number of pups produced was set at

5 pups per breeding pair. The number of wolves per pack was graphed against the wolf population variable. The trend in the wolf numbers per pack was determined from the data of RMNP (1997), Carbyn (1980, 1983). The number of wolves per pack varied with the population level. The number of packs was determined by dividing the wolf population by the number of wolves per pack. The number of breeding pairs was assumed to be equal to the number of packs unless there was less than one pack (i.e. less than three wolves in the population), then the number of breeding pairs was the wolf population divided by two (Appendix 1). This assumption was based upon literature by Carbyn (1980), Paquet (1991) and Meleshko (1986) who stated that the breeding pairs of the wolf population were normally the alpha male and alpha female of each pack, therefore limiting breeding to one pair per pack. In some instances breeding can occur in more than one pair or more than one litter per year may be born, but Carbyn (1980) found in RMNP that more than one litter or more than one breeding pair per pack rarely occurred. Fuller (1989) observed that the survival rate of wolf pups in north-central Minnesota was approximately 50%. Because of the abundance of food, the survival rate of the wolf pups for this model was set at 55%.

Wolf Deaths

Similar to the elk calf deaths, the wolf deaths were influenced by three variables. The first variable was human caused deaths; the second variable was death as a result of disease and the third variables was the wolf death rate. The addition of the three variables resulted in the total wolf deaths.

The wolf death rate was defined as death by any other means than human induced or disease. A value for the wolf death rate in RMNP was not directly available. In an

experiment to determine disease rate in RMNP, Carbyn (1981) found that roughly 14% of the radiocollared wolves died from reasons unknown. Fuller (1989) found that roughly 10% of the wolves died in a population in Minnesota, died by means other than humans and disease. Therefore the death rate of wolves was assumed to be around 10% of the population.

Canine distemper, bovine tuberculosis and mange are three diseases that have been found in the RMNP wolf population (Wolf Magazine 1997, Carbyn 1981, RMNP 1997). RMNP (1997) indicated that there had been an outbreak of mange in the RMNP wolf population and that almost all of the packs in the park had been observed with the disease. Carbyn (1981) found that at least 14% of the radiocollared wolves in RMNP died from disease-related causes and that disease was the second most recorded cause of wolf mortality. As well, Carbyn (1981) assumed that for every diseased animal discovered, several others went undetected. Therefore, because there were no definitive numbers as to how many of the wolves within RMNP have some form of disease, the disease rate for the wolf population was put on a random scale running between 2-40% of the population and added to the existing other death rate of wolves in Park.

Unlike the hunter harvest of elk, the number of wolves taken yearly in the hunting areas around RMNP were not reported. As well, an accurate number of wolves taken in poaching incidences and farmer kills on wolves are extremely difficult to determine. RMNP (1997) was able to confirm eight deaths out of 35 deaths indicated by the Province due to humans during two survey periods. Of those eight killed, two were poached and two were trapped and discarded due to mange (RMNP 1997). Recently, Gloria Goulet indicated that at least one third of RMNP's wolf population was being

harvested annually (Wolf Magazine 1997). Due the lack of definitive numbers of wolves killed by humans, the human harvest rate on wolves was set at 25%.

4.9 WINTER SEVERITY SECTOR

Winter severity was calculated from 1977 to 1980 in RMNP and winter severity for that time frame was calculated by using the equation developed by Stelfox (1976). Winter severity included the winter parameters of snow depth, snow density, mean temperature, snow hardness and green-up days. Snow depth and temperature were gathered from RMNP based on values from Dauphin, as well as from study conducted by Trottier *et al.* (1983). Some snow density values were obtained from Trottier *et al.* (1983). Snow hardness was run on a scale value from 0 to 20. Green-up values were the difference between date of green-up and the normal green-up date for the Park. The green-up values were obtained from Dolan and Tempany (1980). The monthly severity index was originally calculated and multiplied by 6 and added to the green-up values to determine the yearly winter severity.

Winter severity was determined by using all components and a slightly modified form of Stelfox's (1976) equation. The equation calculated the mean winter severity for each month and then each month was added together and added to the spring green-up value to determine the total winter severity. Because data were not available for all the components on a monthly basis, snow depth, snow density, snow hardness and temperature were set to run on random values and multiplied by the number of months of winter (6) and then added to the green-up values, which was also run on a random set of values (Appendix 1).

Winter Severity Index as calculated by Stelfox (1976):

Severity Index = $SD1 + SD2 + MT$ (if $<0^{\circ}\text{C}$) or $-MT$ (if $>0^{\circ}\text{C}$) where:

$SD1$ = mean snow thickness (cm). This is the reading at the end of the calculation period;

$SD2$ = mean snow density x 100;

SH = snow hardness;

MT = mean temperature (0°C)

Monthly indices (MS) were calculated as follows:

$(MS = SD1 + SD2 + SH + MT)$

For total winter severity, the MS for November to April were combined and added to the spring green-up value (GU).

The range in temperature, snow depth, snow density and green-up values were obtained from Carbyn (1980), Trottier *et al.* (1983) and information from RMNP. Snow hardness was determined through ocular estimates using the following criteria (Stelfox 1976).

Crust

0= none

5= light

10= moderate

15= hard

20= very hard

Supports

hares, lynx, mice

squirrel, mink, porcupine

wolves, coyotes, caribou

deer, sometimes elk, moose

All the sectors and the various components of the sectors highlighted in this chapter comprised the model. All the sectors highlighted in this chapter played an important part in the results of the model. Two components of the ecosystem that were not included as sectors in the model were forage and fire, due to lack of available data. The next step in the modeling process was to highlight the prospective runs of the model.

CHAPTER 5

MODEL RUNS

5.0 INTRODUCTION

Once the data were utilized to create the formulae and placed in the model, the model was run. Trial runs were performed on the model to test the sensitivity of the model to changes in various components of the model. This chapter outlines the values used in the trial runs and the additional runs tested on the model.

5.1 MODEL RUN

Once all the sectors were created utilizing the available data, the model was run to validate it. The original run consisted of data from the 1989 time series and was run for a time period of 30 years, with a time step interval of 0.5 year. The model was initially run on a 50 year time scale, but was reduced to 30 years for the subsequent runs because from a management standpoint a 50 year time period was too long. The model was also run initially on a one year time step, but was reduced to 0.5 year because it was more sensitive to changes in the population.

The model results from the initial data were compared to the range of the aerial surveys of the elk population collected by RMNP to provide validation to the model. Rather than using the exact number of the aerial surveys, the validation process used the range of the aerial surveys because as mentioned in Chapter 4, the aerial surveys themselves have a margin of error. RMNP (2000) and RMNP (2001) both recorded the elk population estimates plus or minus roughly 20%, therefore in the validation step the elk estimates from the aerial surveys were built with a 20% plus or minus on the

population number and the results of the elk model were plotted in the same graph to see if they fit within the range.

Once the model was validated, the results from the run with the initial data were recorded and various components of the model were compared.

5.2 SENSITIVITY ANALYSIS

Sensitivity analysis is the determination of the relative effect on a system's performance due to changes in various model parameters, usually with the idea of refining critical parameters and identifying parameters that have little effect (Miller 1974). A model's sensitivity to changes in inputs is a measurement of how the output of a model is controlled by the input parameters and initial conditions (Snowling and Kramer 2001). A model that shows large changes in output as a result of small changes in input parameters is considered to be sensitive (Snowling and Kramer 2001).

Therefore, once the initial run of the model was done, sensitivity analyses were performed by varying the data of the critical components of the model. Human harvest rate on elk, adult birth rate, yearling birth rate, wolf and bear predation were all run in sensitivity analyses to determine the model's sensitivity to each component. Winter severity was determined using variables that were set on random functions, which constantly varied the value of winter severity through the run; therefore winter severity was not included in the sensitivity analysis runs.

Sensitivity Runs

Five sensitivity runs were performed on the model. Each run varied a different component of the model to determine the sensitivity of the model to a change in a

particular component. The number of runs, and the start and end numbers of the runs were entered into STELLA, which randomly selected the other two numbers for the sensitivity analysis. During the runs all the sectors remained on and all sectors, except the one with a component being manipulated, ran with their initial values.

The first run varied the human harvest rate of the elk population. Human harvest was chosen because during the 20th century, elk harvest by humans played an important part in influencing the elk population in RMNP. The initial value of the human harvest rate was 10%. Rounds (1991) found that between 1951 and 1991, the harvest rate on elk varied from a high of 53% of the elk population to a low of 3% of the population, but a majority of the time the harvest rate was below 25%. Therefore, during the run, the upper limit of the harvest rate was set between the 53% and 25% harvest rates, and 0% was selected as the low value to determine how the population would react to no harvesting (Table 4).

Table 4 Human Harvest Rate of Elk

Run #	Human Harvest Rate of Elk (%)
1	0
2	11.7
3	23.3
4	35

The second and third runs varied the birth rates of the adults and yearlings. These two components of the system were chosen for the sensitivity runs because variance in

the birth rate contributes and replaces elk in the population, thereby possibly influencing the viability of the elk. Therefore it is important to test how sensitive the model was to any changes in either birth rates. Carbyn (1979) found in Jasper a 40% pregnancy rate for yearlings, but Kittams (1953) found a pregnancy rate as low as 5% for yearlings in Yellowstone National Park. In years of severe winter weather, the birth rate for elk can be 0. Therefore, in the 4 runs the yearling birth rate was varied from 0 to 40%. Carbyn (1979) found in Jasper and Elk Island, the pregnancy rate varied from 91% to 72%. Some of the age classes in the adult group had a pregnancy rate of 100% (Carbyn 1979). Therefore during the 4 runs the adult birth rate was varied from 45 to 95% (Table 5). The variations in the birth rates were then run simultaneously.

Table 5 Variations in Adult and Yearling Birth Rates

Run #	Yearling Birth Rate (%)	Adult Birth Rate (%)
1	0	45
2	13.3	61.7
3	26.7	78.3
4	40	95

The fourth run varied the bear predation rate on elk calves. Bear predation could possibly have quite an impact on the calf population, therefore it was important to test how sensitive the model was to changes in the bear predation rate. The initial value of bear predation was 25%. Singer *et al.* (1997) found that the predation of bears on calves can be virtually nothing, to at least half of the calf crop. Therefore, during the 4 runs the bear predation rate was varied from 0% to 50% (Table 6).

Table 6 Variation in Bear Predation Rate of Calves

Run #	Bear Predation (%)
1	0
2	16.7
3	33.3
4	50

The fifth run varied the wolf population numbers. A sensitivity analysis was done using the wolf population because elk are the primary prey for wolves in RMNP, therefore it is assumed that changes in the wolf population could possibly impact the elk population. The initial value of the wolf population was 50 wolves. As mentioned in Chapter 3, the wolf population in RMNP has varied greatly during the 20th century from no wolves in the Park during the 1920's and 1930's to a recorded high of 120 wolves in the 1970's. Therefore, during the 4 runs the wolf population number was varied from 150 wolves to 5 wolves (Table 7).

Table 7 Variation in the Wolf Population

Run #	Wolf Population
1	5
2	53.3
3	102
4	150

5.3 ADDITIONAL RUNS

Additional runs were carried out to determine the reaction of the elk population to different situations. The model was run with only the wolf, winter severity and elk population sectors turned on. The moose and ungulates sectors were turned off. This was done to determine the effects of only winter severity and the wolf population on the elk population. Once that run was complete, the ungulate sector was turned back on and the model was run again to see how the elk population would react to a steady state moose population. The winter severity and wolf population sectors remained on during this run.

The initial populations of the elk calves and adults were also varied, with the initial values of the other sectors remaining the same (Table 8). The second run utilized different initial values of the calf and adult elk population from the 1978 aerial survey and 1977 classified count.

Table 8 Variation in the Initial Run Values of Elk

Run #	Calf Population	Adult Population
1	1010	4178

Once the model was validated, the results of the run with the initial values were recorded and discussed in Chapter 6. As well, the results of the sensitivity runs and additional runs were also recorded and discussed in Chapter 6.

CHAPTER 6

RESULTS

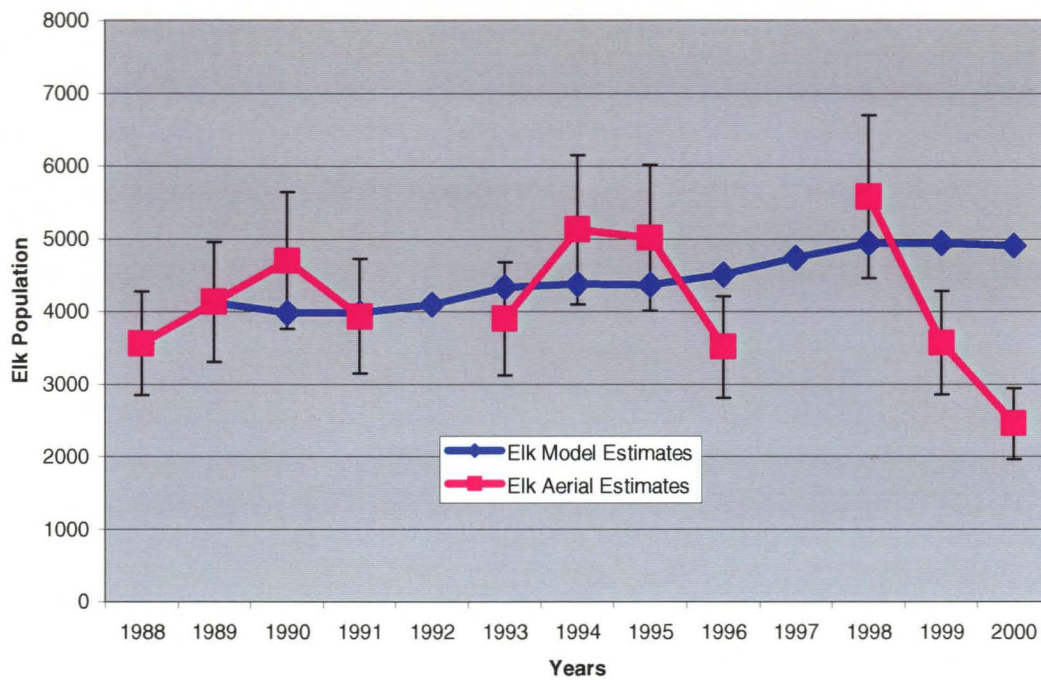
6.0 INTRODUCTION

This chapter highlights the results of the initial run, the sensitivity runs and the additional runs of the model.

6.1 RESULTS

Elk Population

The model was graphed against the already existing range of the aerial surveys to determine the validity of the model (Graph 1 and Table 9). For a majority of the run, the results of the model fell within the aerial surveys' range. Towards the end of the run, the model results fell outside of the range of the aerial surveys. The reason for this could be that there was components of the ecosystem not included in the model, therefore allowing the population in the model to continue fluctuating at higher population numbers than was seen with the aerial ranges. As well, many of the components utilized in the model were based on trends seen in other places, not exact values from RMNP. Errors do occur within the modeling process both within the development of formulas and the model structure. As previously mentioned, aerial surveys themselves are not absolutes and therefore there is always a margin of error with them, leading to differences between the aerial surveys and the model results



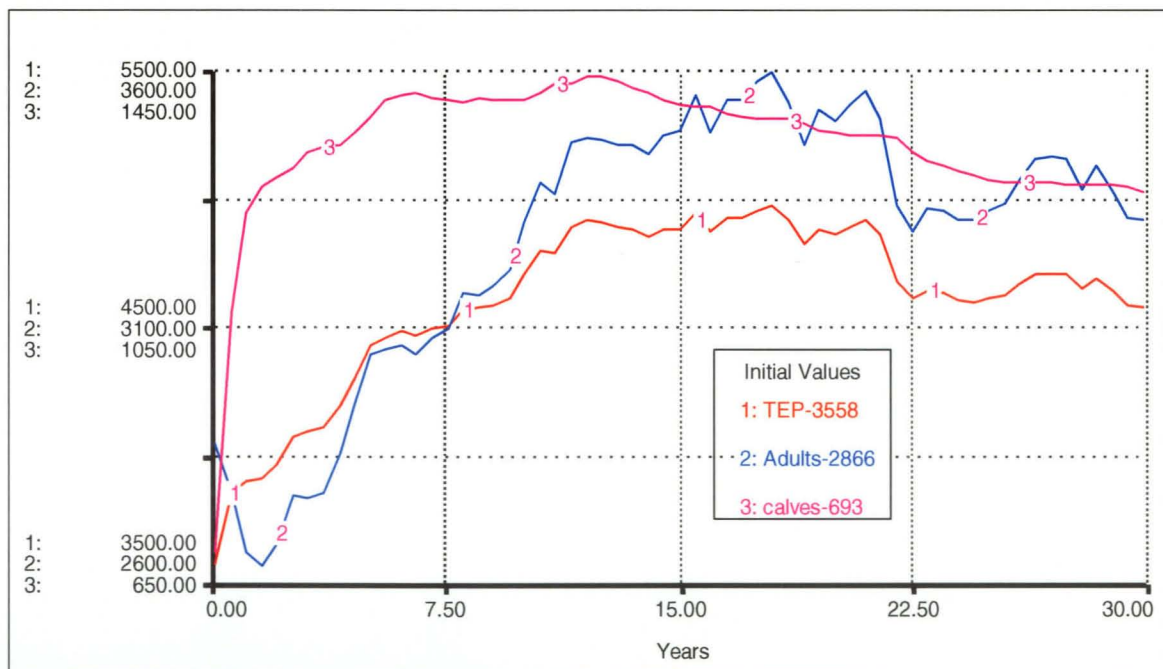
Graph 1. Comparison of Elk Model Estimates and Elk Aerial Estimates

Table 9. Comparison of Elk Survey Estimates and Elk Model Estimates

Elk Survey Estimates from 1989 onwards	Elk Model Estimates
3558	3558
4128	4119
4699	3978
3933	3980
	4096
3900	4332
5126	4377
5015	4370
3513	4515
	4736
5577	4940
3569	4944
2455	4909

After the validation step, the model was run using the initial conditions described in Chapter 4 and data values of the variables and the stocks in Table 1. The results of the

fluctuations of the elk population in the initial run are illustrated in Graph 2. Table 10 (Appendix 3) provided the numerical values for Graph 2. The results of the run indicate that by the thirty year time period, the elk population was starting to decline. This trend in the population agrees with the general trend seen in the aerial survey results. When the graph was extended to 50 years, the declining trend in the elk population continued. One of the possible reasons for the declining trend in the population could be that the human harvest rate on elk and the bear predation rate on elk calves were held consistent throughout the entire model run, with no fluctuation from year to year, thereby constantly reducing the elk population. In the natural setting the calf predation by bears and the human harvest rate on elk do fluctuate from year to year. In some years, the bear predation rate on calves and the human harvest rate are quite low, thereby allowing the population a chance to restock.



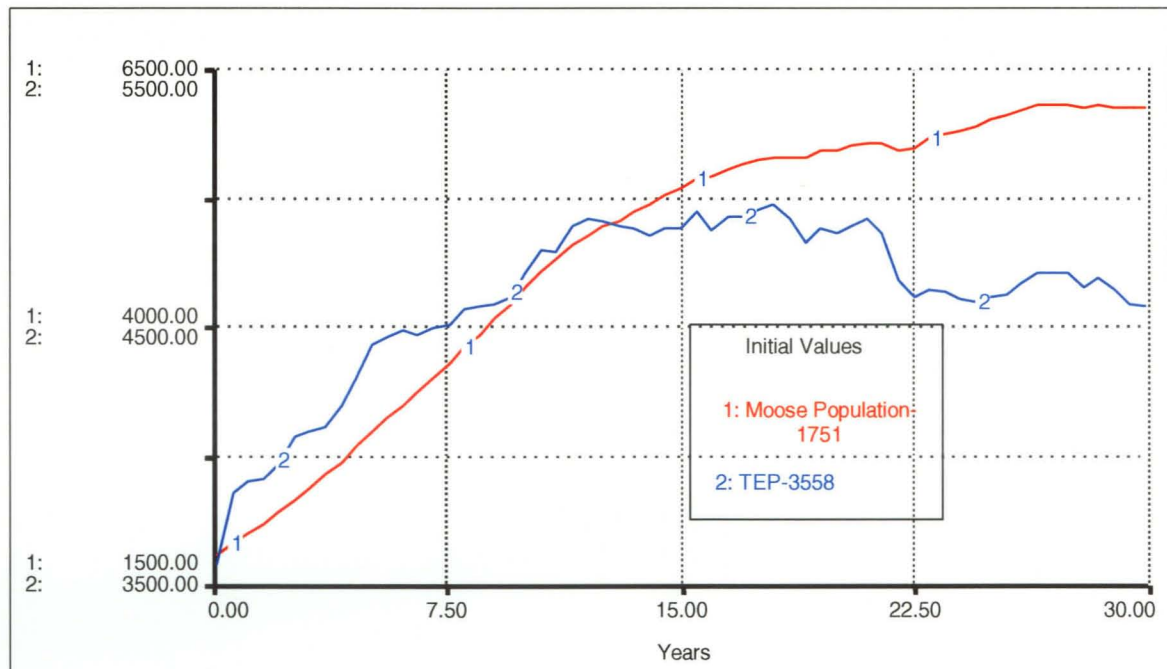
Graph 2 - Calf, Adult and Total Elk Results of Initial Run

Throughout the run of the model, the elk population showed an initial increase, but the general trend was a fluctuating but decreasing population. Table 11 (Appendix 3) indicated that in years of increased winter severity, the deaths of adults and calves increased. This was as a result of increased kill rate by wolves on both the adults and the calves and as well, an increase in the other death rate of calves and the adult death rate. The result was only marginal decreases in the elk population. In terms of the overall affect winter severity can have on a population, the decrease in the population number after a severe winter seem relatively lower than was expected. This could be because of the steady birth rates of both the adults and the yearlings. Another possible explanation was that due to lack of complete information, an adequate forage section was not included in the model. This could be having an affect on the overall results of the model.

Moose and Elk

The elk population was graphed against the moose population (Graph 3). In comparison to the elk population, the moose population showed an increasing trend in the population numbers. This was similar to the behaviour shown in the graphed aerial data from the Park. The moose and elk populations increased for the first 12 years with the elk population being larger than the moose, but around year 13, the moose and elk populations crossed over, with the moose continuing to increase and the elk starting to decline. One of the major reasons for the difference in behaviour of the two populations was that the elk population was modeled in a more complex and more accurate manner than was the moose. As well, the initial values for the human harvest rate and wolf harvest of moose were set lower than for the elk based on findings of Rounds (1991), Carbyn (1980, 1983) and Melelshko (1986), who found that in the natural environment

these harvest rates were lower for moose. In the natural environment, winter severity tends to have less of an impact on the moose population than it does on the elk population because of the ability of moose to move through deeper snow because of increased chest height and longer legs. As well, moose have a lighter foot-on-load-track than do elk, therefore they will be supported on snow that elk would not be (Trottier and Hutchison 1982). Therefore, in the model, the affect of winter severity on moose deaths was less than it was on elk deaths. With all these factors in favor of moose, it supports the findings of the graph that the moose population was increasing while the elk population is decreasing. As well, in the model run, RMNP was limited to 12000 animals (as indicated in Chapter 4), and once the moose population started increasing, the elk population started to decrease. When the model run time was extended to 50 years, it was seen that the elk population dramatically declined and the moose population continued to grow, possibly replacing the declining elk population.



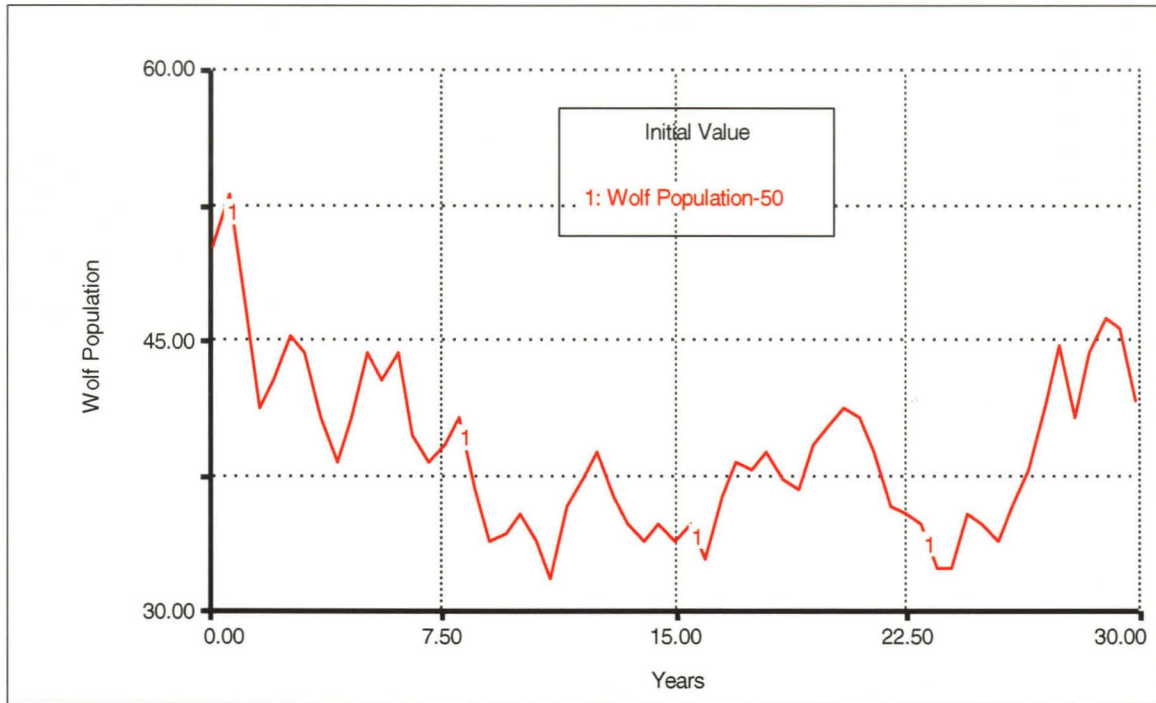
Graph 3 - Moose and Elk Population Trends from Initial Values

Wolf Population

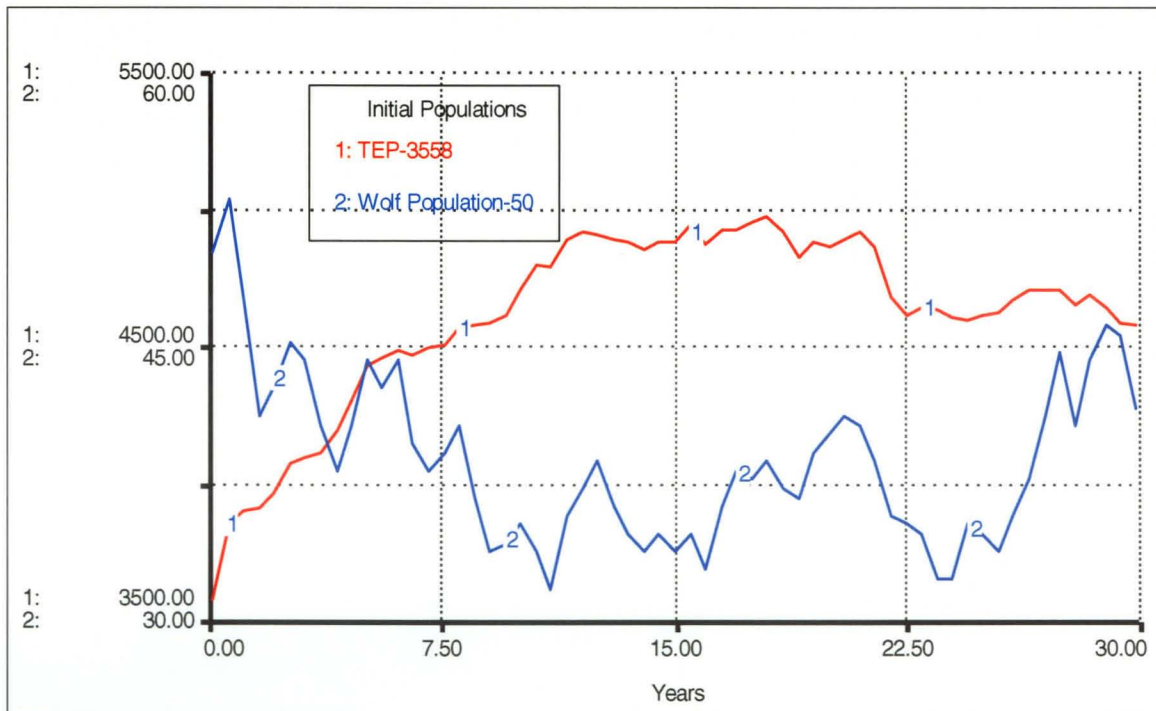
The wolf population fluctuated through the 30 year time run period (Graph 4). The trend for the wolf population was one of decline, but towards the end of the 30 years the wolf population began to increase. In comparison to the wolf survey numbers determined by RMNP, the wolf numbers from the model are slightly lower, but follow a very similar trend. One of the possible reasons for the general decline in the wolf population in the model was that the human harvest rate on the wolves in the model was held constant throughout the run, but at a relatively high harvest rate. In RMNP, the harvest of wolves by humans is considered to be as high as 1/3 of the wolf population on an annual basis (Wolf Magazine 1997). Therefore, the results in the model show a similar trend as seen in the natural population in RMNP. As well, the disease rate for the wolves was varied greatly during the run. Decline in the wolf numbers resulted in a decline in wolf predation numbers on all the populations, but especially the elk.

Wolf and Elk

When the wolf was graphed against the elk population, the fluctuations in the elk and wolf populations seemed to be inversely related to one another (Graph 5). When the wolf population began to decline, the elk population was increasing, which seemed to indicate that the wolf and elk population do influence one another and are not fluctuating independently as originally thought. The results of the model tend to disagree with the findings of Richards (1997), who indicated that in the natural setting the ungulate population and the wolf population are fluctuating independently of each other and that there was no negative or positive correlation between elk and wolves.



Graph 4 –Wolf Population Trends from Initial Values



Graph 5 – Wolf and Elk Population Trends from Initial Values

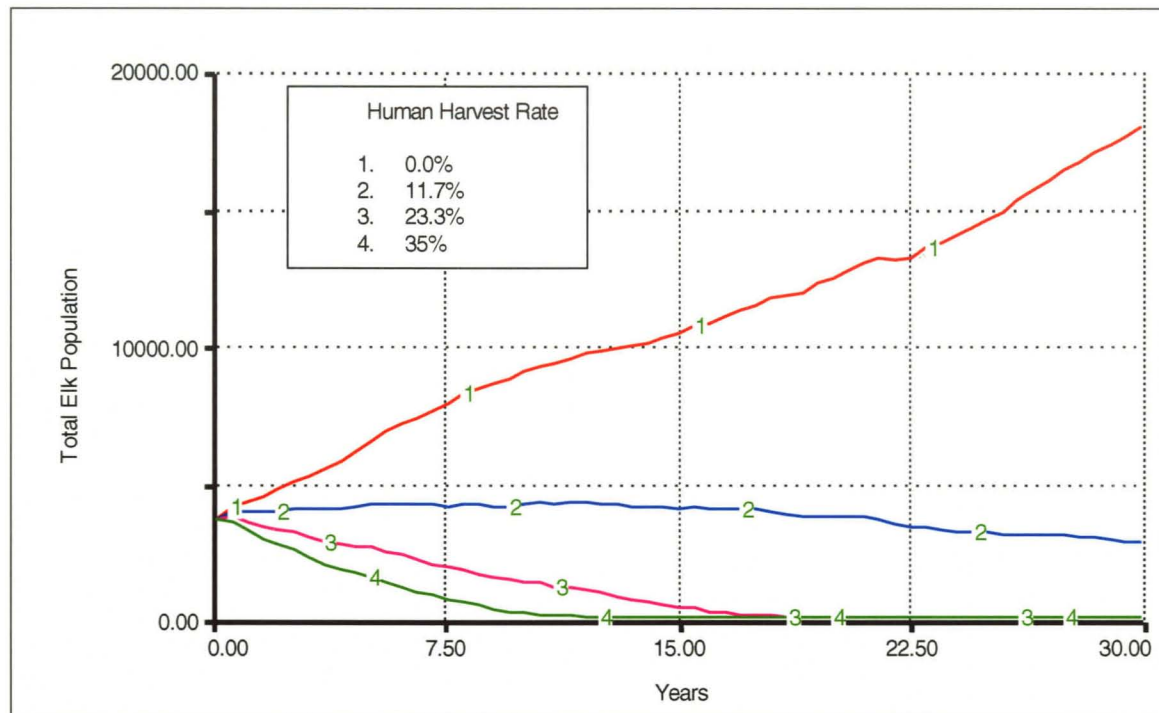
6.1 SENSITIVITY ANALYSES

In running the sensitivity analysis for the model, it was determined that a majority of the variables did not result in great changes in the elk population. The elk population was most sensitive to changes in adult birth rate, bear predation on calves and human harvest rate.

Human Harvest of Elk

The first runs involved fluctuating the human harvest rates on elk, which can provide some feedback to the Park on what type of affect the varying levels of harvest have on the elk population (Graph 6). When the harvest rate was set at zero, the elk population grew rapidly, resulting in a population of nearly 17,000 elk at the end of the run. A harvest rate of 35% resulted in a rapid decrease in the population. The population reached zero elk in approximately 13 years. In the initial run of the elk population the original harvest rate was set at 10% and only slight changes in the harvest to either 7.0% or 14% resulted in the population increasing to nearly 7,000 elk or declining to approximately 1000 elk in a 30 year time frame. The impact of changes in the harvest rate are similar to what was indicated by Rounds (1977) in RMNP in which high hunting rates resulted in significant declines in the elk population during the early 1950's and 1960's. High harvest rates did result in a decline in the total population, but due to the fact that the human harvest rate of the adult population was not separated into harvest rate of females and harvest rate of bulls, there was no way to determine if the decreasing elk population was attributed to not only a high harvest of elk, but a high harvest of the breeding females. Richards (1997) found that there was a negative correlation between hunter harvest and the elk population numbers. As well, Richards (1997) determined that

a high hunter harvest rate resulted in a two-year lag effect on the elk population. Because the human harvest rate variable was set at a consistent number for the initial value and for the varying values of the runs, it was difficult to verify the lag effect.

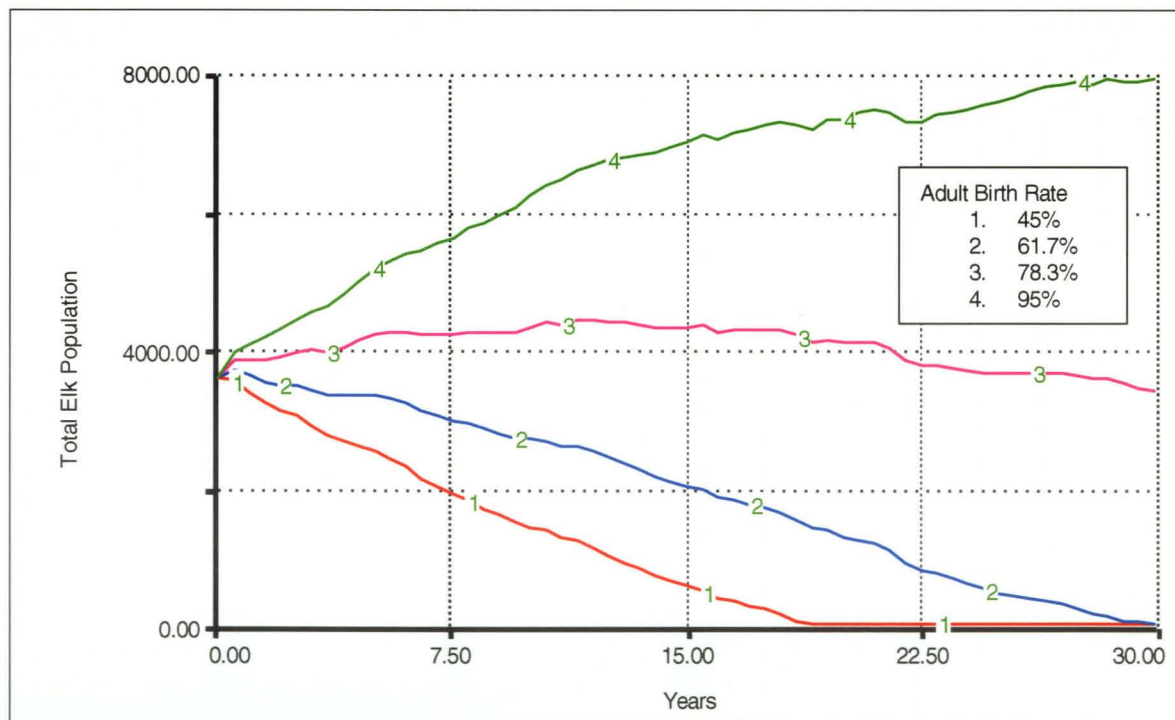


Graph 6 – Variation in Human Harvest of the Elk Population

Adult Birth Rate

Graph 7 indicated the results of varying the adult birth rate in 4 different runs. Similar trends seen with changes in the human harvest rate on elk were seen with changes in the adult birth rate of elk. Decreasing the birth rate below the initial value resulted in the elk population declining. When the adult birth rate was run at 45%, the population died off within approximately 18 years. When the adult birth rate was run at 95%, the elk population grew rapidly to approximately 8000 in 30 years. Even a 20% decline in the adult birth rate resulted in the elk population dying off within 30 years. The reaction of the elk population to changes in the adult birth rate indicated that the elk population was

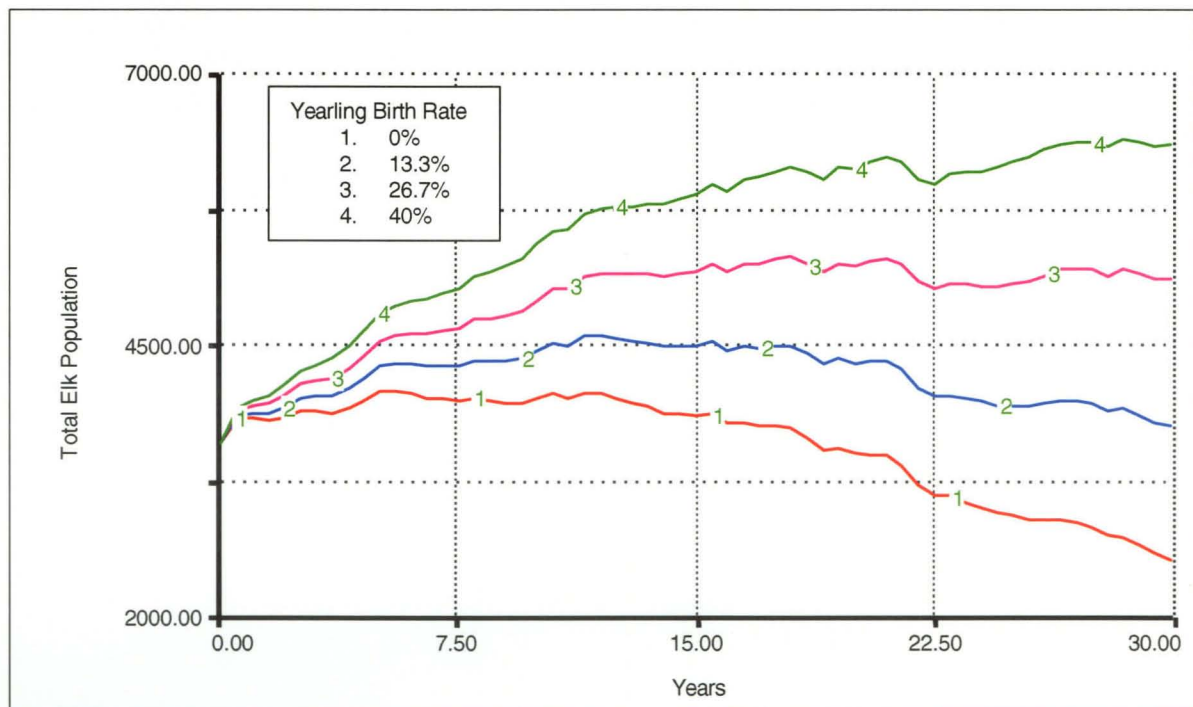
quite sensitive to changes in the adult birth rate. One possible reason for reaction of the elk population to changes in the adult birth rate was that the adult birth rate in the model was set at a higher value than the yearling birth rate, based on the findings of Carbyn (1979). Therefore, the adult birth rate was the variable that contributed more calves to the calf crop and in turn the population, than the yearling birth rate. As well, the yearling birth rate was low enough that it would not be able to compensate for a decrease in the adult female breeding rate. Therefore, a decline in the adult birth rate resulted in fewer calves, which resulted in a decline in the population, and an increase in the birth rate resulted in an increase in the population. Flook (1970) determined that in a natural situation, the elk that make up the adult breeding population were the experienced breeders, and the ones that would ensure population survival.



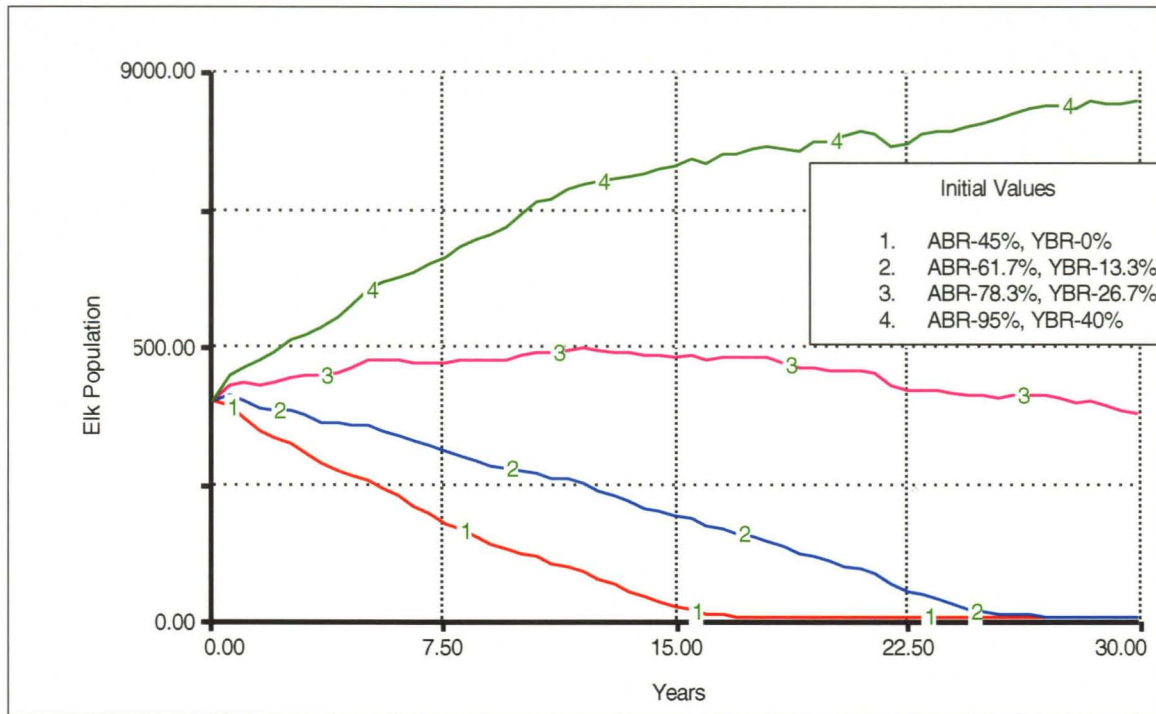
Graph 7 – Variation in the Adult Birth Rate on the Elk Population

Yearling Birth Rate

Variation in the yearling breeding rate resulted in the trends seen in Graph 8. The yearling female proportion of the population was significantly less than the breeding adult females. As well, the breeding rate of the yearlings in comparison to the adults was also significantly less. Unlike changes in the adult birth rate, varying the yearling birth rate to 0% did not result in the elk population dying off within 30 years. Carbyn (1979) indicated that the breeding rate of yearlings was always lower than the breeding rate of adult females, therefore contributing less to the population, so changes in that breeding rate had less of an impact than changes in the adult breeding rate as indicated by Graph 7.



Graph 8 – Variation in Yearling Birth Rate



Graph 9 – Variation in Yearling and Adult Birth Rate

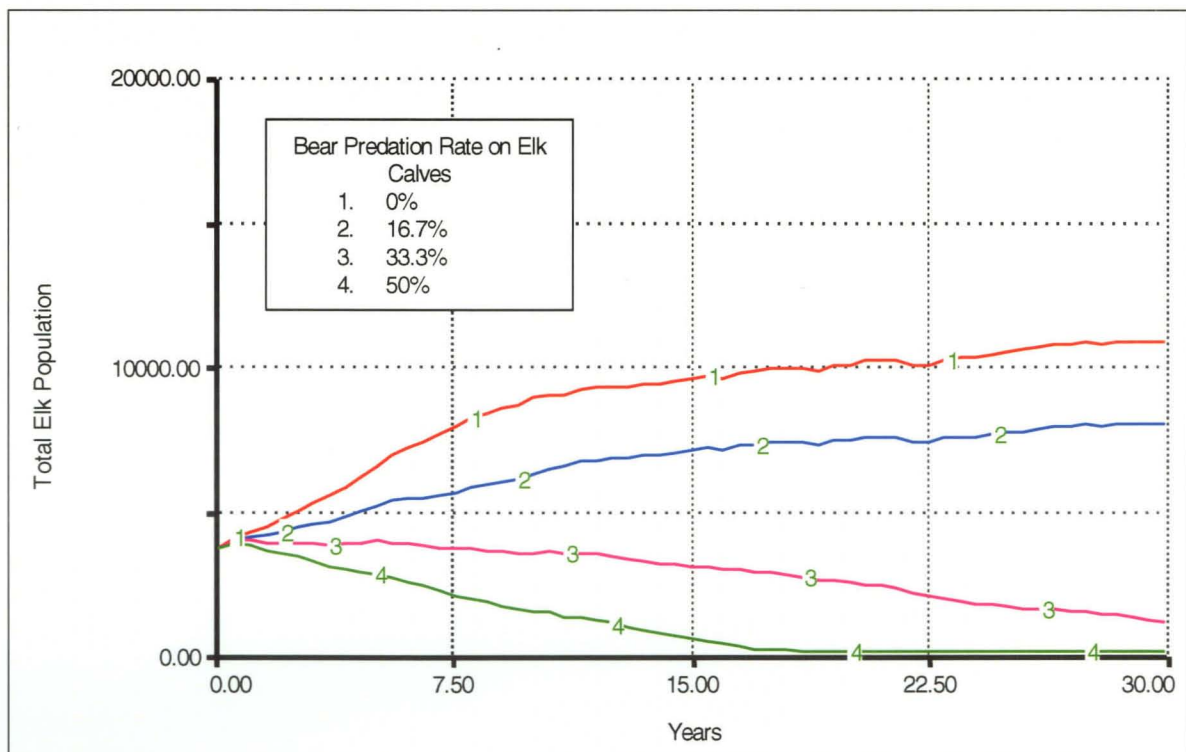
Adult and Yearling Birth Rates

The results of varying the adult birth rate and yearling birth simultaneously are shown in Graph 9. The results on Graph 9 are very similar to the results seen in Graph 7, when just the adult birth rate was varied. When the adult birth rate was run at 45% and the yearling birth rate was run at 0%, the elk population rapidly declined to zero animals in roughly 17 years. When the two birth rates were increased to their maximum level, 40% and 95% respectively, the elk population increased to approximately 8500 elk in 30 years. The trends in these runs seem to verify that the adult birth rate was contributing the most to the elk population and the yearling birth rate contributed very little.

Bear Predation Rate

The results of varying the bear predation rate on calves in four runs are indicated in Graph 10. When the bear predation rate was run at 0%, the elk population increased

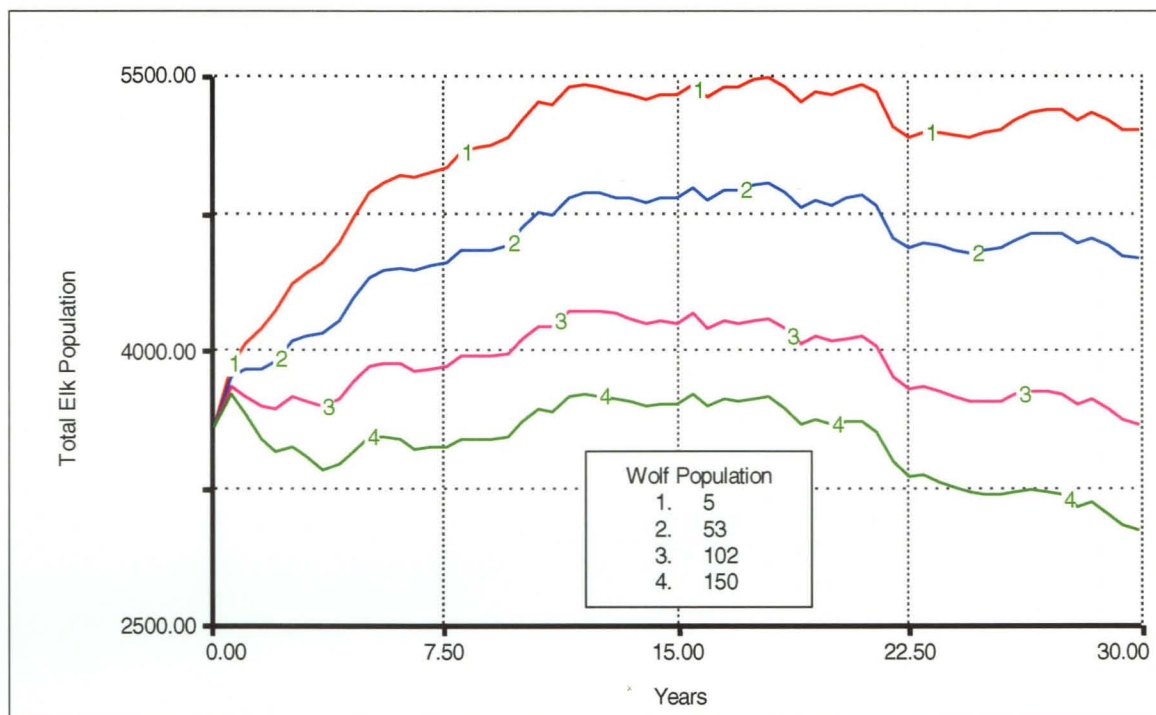
steadily to just over 10,000 elk in 30 years. When the bear predation rate was run at 50%, the elk population rapidly died off within 18 years. These trends are very similar to those with changes in the human harvest rate, indicating that the elk population is sensitive to changes in both the human harvest rate and the bear predation rate. An increase of the bear predation rate of less than 10% from the initial value of 25% resulted in the elk population declining to virtually no elk at the end of the 30 year run. One reason for the rapid decline in the population at a predation rate of 50% of one calf crop was that there would be fewer replacement animals once they move out of the calf stage, as well as fewer animals to replace and participate in future breeding. This result agrees with the finding of Hayes *et al.* (1991) that bear predation primarily affects the first age class.



Graph 10 – Variation of Bear Predation on Elk Calves of the Elk Population

Wolf Population

The wolf was one of two natural predators included in the model; therefore runs were carried out to determine the effects of an increasing and decreasing wolf population. The results of a fluctuating wolf population on the elk population demonstrated similar trends as those seen with the varying yearling birth rate (Graph 11). When the wolf population was five wolves, the fluctuations of the elk population were similar to those seen in Graph 2, but at a slightly higher population level. When the wolf population was run at 150, the elk population began to decline only after approximately 20 years of being exposed to this wolf population, and the decline was not substantial. Carbyn (1980) concluded that the wolf population in RMNP was an important natural mortality factor in RMNP yet “compensatory” to the degree that it contributes to the “dampening” of peak populations. The trends indicated by the runs changing the wolf population tend to agree with Carbyn (1980).

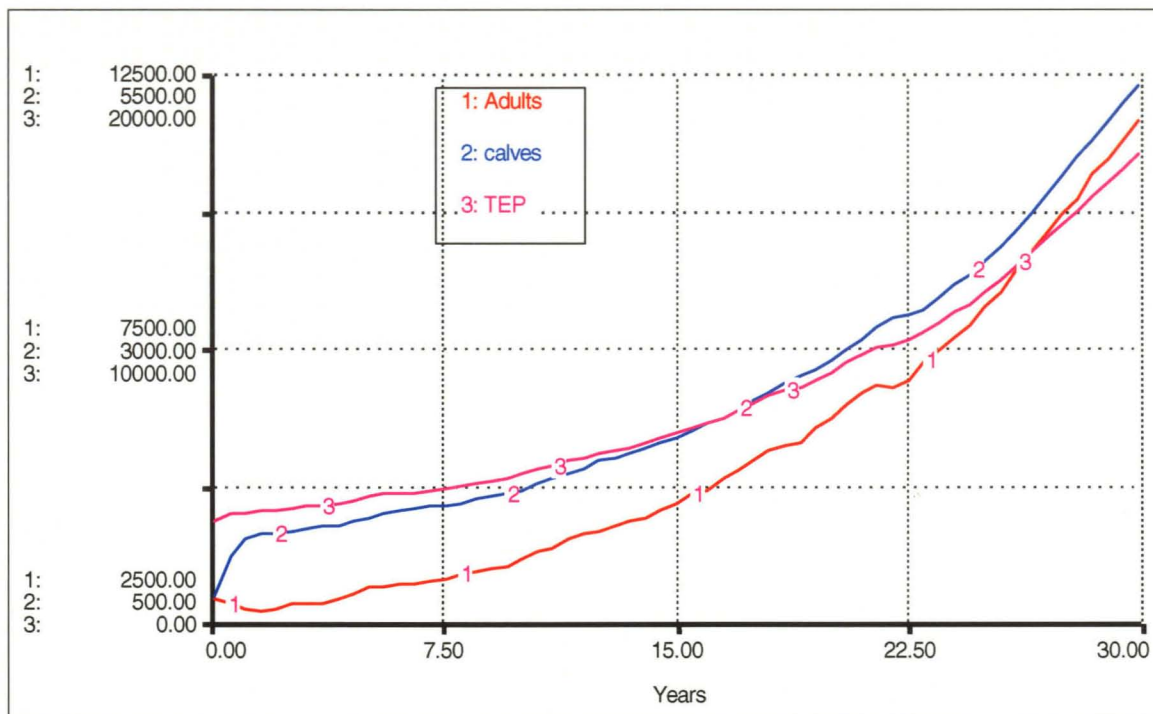


Graph 11 – Variation in the Wolf Population on the Elk Population

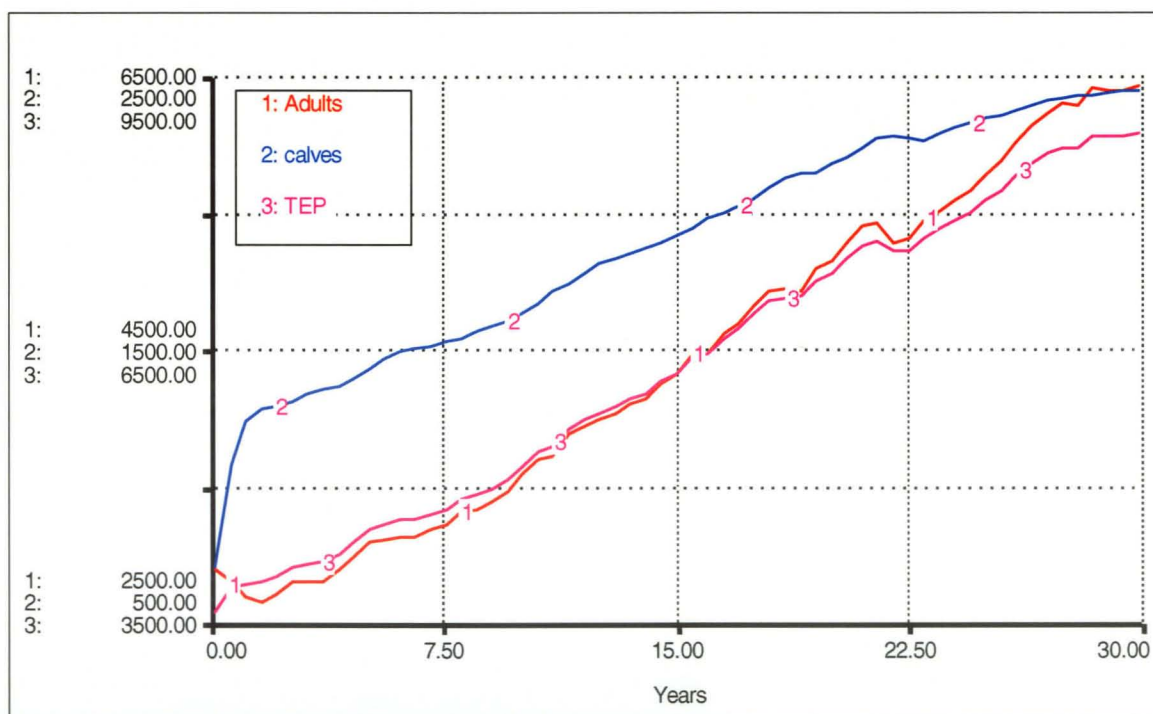
6.2 ADDITIONAL RUNS

The results of running the model with only the wolf sector and the winter severity sector resulted in an explosion of the elk population (Graph 12). One possible reason for the explosion of the elk population in the model was because the ungulate sector was turned off; therefore there was no limit on the number of ungulates in the Park. As well, with the ungulate sector being turned off, the BFRA variable no longer influenced the calf birth rates, resulting in no limitations on elk births. The results of this run also highlighted the possibility that the winter severity component of the model was not influencing the population to the extent that was expected. As well, wolf predation on calves and adults was having very little effect on limiting the elk population.

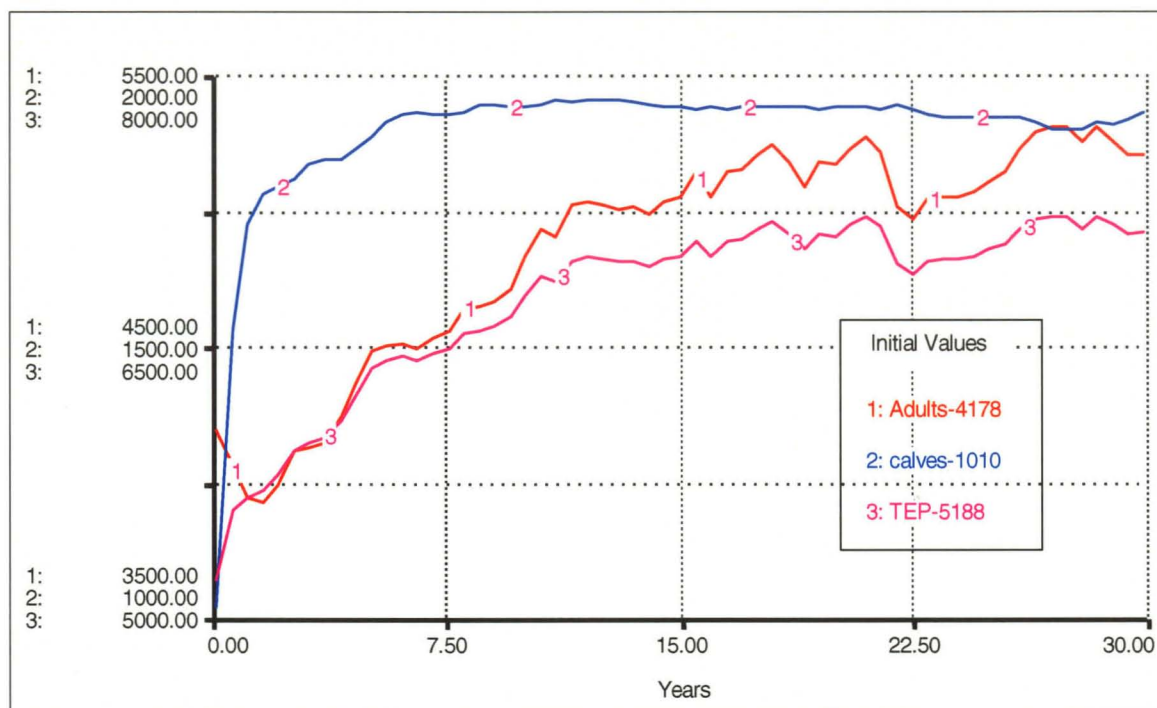
Once the ungulate sector was turned back on, the elk population climbed to around 9500 elk and continued to fluctuate at that point (Graph 13). The moose sector remained turned off, but provided a single population number to the additive total ungulate population. The original value for the moose population was held steady during this run, but contributed 1751 moose to the total ungulate population. Therefore, the elk population increased until it came close to its upper limit, which was around 10,000 elk, and then continued to fluctuate around that point.



Graph 12 – Wolf, Winter Severity and Elk Sectors Running



Graph 13 – Ungulate, Wolf, Winter Severity and Elk Sectors Only



Graph 14 – 1977/78 Initial Values for Elk Population

The result of running the model with 1978 aerial values and the 1977 classified count values for the elk population are in Graph 14. The graph showed very similar trends as seen in graph 2, but rather than beginning a declining trend, the elk population seems to be relatively steady, even slightly increasing. The reason for this could be that the initial values for adults and calves was larger in this run as compared to the first run, and therefore able to maintain the population at a higher level longer, while still being influenced by the components that may eventually cause a decline in the elk population.

The run of the model with the initial values showed an elk population that is beginning to decline. The results of the elk and wolf comparison indicated that the two populations seem to not be fluctuating independently as originally thought. The elk population model was most sensitive to changes in the bear predation rate, the human harvest rate, and the adult birth rate. As well, the additional runs indicated that the elk

population could increase greatly if moose were no a factor influencing the elk population.

CHAPTER 7

CONCLUSIONS AND RECOMMENDATIONS

7.0 CONCLUSIONS

The two objectives of this study were first to develop a model of the RMNP elk population to use in helping to assess the state of the ecological integrity of RMNP. The second objective was to identify areas in which the RMNP data was lacking. The first objective was achieved by utilizing the information and trends collected in the various studies and by RMNP, to create a dynamic, working example of the elk population. Wolves, moose, human harvest and winter severity were some of the main components included in the model. Through the development of the model, the second objective was addressed.

The results of the validity test on elk population model indicated that the results from the model's run fell within the range of the aerial surveys. The elk model results will not be completely identical to the results of the aerial surveys because the model was lacking key components such as forage and fire. As well, the runs of the model do not include the entire ecosystem. Rather the test was done to see how well the model results fit within the existing range of the aerial surveys. Based on this test, the model fit relatively well. The model will never be perfectly valid because there is no such thing. The best thing to do was continue to adjust parameters within the model to arrive at a closest fit to the existing data. One of the biggest misconceptions in the modeling process is to assume that a model cannot be used in any way or form until it has been validated or been proven accurate. Starfield (1997) found that if a model was being used as an experiment or a problem-solving tool, then the question of validity is irrelevant.

Rather, the modeler should focus on the justification of assumptions, to make sure that the model is internally consistent and to look for evidence that the results are being used in a sensible manner (Starfield 1997). With the elk population model, a point was made to develop the sectors in a consistent manner and each assumption was justified.

The results of the initial run indicated that the elk population was starting to decline. When the model was run on a 50 year time frame the elk population continued to decline. As well, the initial run indicated that the wolf population seemed to be inversely related to the elk population, indicating that the populations could be dependent on one another.

The declining trend in the elk population as produced by the model, could be an indication of a decline in the viability of the population and therefore possibly indicate a decline in the ecological integrity of RMNP. This would agree with Parks Canada (1998a) who found that the ecological integrity in all of Canada's southern National Parks (including RMNP) had declined over the last several years. The trend of the elk population of the model is as a result of all the different components within the model influencing the elk population. It could be concluded that after a long enough time frame (30 years) the elk population is unable to sustain itself under the influence of all the different components within the model, and thereby is beginning to decline. Because the state of ecological integrity can be defined by the viability of a vital species, the decline in the elk population could be indicating a decline in the ecological integrity of RMNP.

The results of the sensitivity model runs indicated that the model was most sensitive to changes in the human harvest rate, bear predation rate and adult birth rate. The model was sensitive to changes in the bear predation rate, but relatively insensitive to

changes in the wolf population. In the development process of the model, the bear and the wolf impact on elk were development in different manners, which may have resulted in the very different responses the elk population to changes in either of these components. As well, the wolf harvest of elk was influenced by winter severity, whereas the bear predation rate was not. The differences in the development and implementation of these two components could be the reason for the differences in the results. The elk population was more sensitive to changes in the bear predation level and less sensitive to changes in the wolf population than would have originally thought. The reason for this thinking is that bear predation only focuses on the calf population, whereas the wolf population and predation impacts both the adults and the calves. As well, the bear predation was not influenced by population size, rather it was a random occurrence, independent of the bear population, but the wolf predation was dependent upon the wolf population size. One solution to this problem would be to develop bear predation and wolf predation in the same manner and then compare the sensitivity of the model to changes in both the predation rates.

One of the major conclusions of the model results, based on the available data and assumptions made to create the model, was that human impacts, such as regulated human harvest on elk, play an important role in affecting the viability of the elk population and thereby influence the integrity of RMNP. Because RMNP managers work directly with Manitoba's provincial Department of Conservation in setting the regulated human harvest of elk and moose each year, the RMNP managers can have a direct affect upon and can focus on minimizing impact of this human induced activity on the RMNP elk population and the integrity of RMNP.

The model development process addressed the second objective of the thesis. Components such as forage and fire do interact with elk and can have an impact on the population. Both components were not included within the model due lack of data. Forage and fire are two important components of the elk ecosystem and their inclusions within the model could have only enhanced the model results, bringing them more closely to the results of the aerial surveys. The forage and fire components relate strongly to the effects of winter severity. Therefore the inclusion of these two components may result in increased effects of winter severity on the elk population.

Another component, which was not included because of data constraints, was white-tailed deer. The deer population is growing and competing with elk for forage and habitat and could have an influence on the viability of the elk population.

A next step for RMNP would be to extend the model to include other human disturbances and impacts, while still maintaining the existing natural influences, to determine their role in effecting the viability of the RMNP elk population and the ecological integrity of the Park. Poaching, farmer kills, and road kills of elk could be included in an extended model.

The model was a useful tool for this experiment. Although the modeling process was not and is not perfect, for the most part, the use of the model enabled one to better conceptualize how the system behaved. As well, the development process of the model aided in enhancing the basic understanding of the RMNP ecosystem, elk and its relationships with the RMNP ecosystem. The development process required extensive research of the various components and relationships that influenced the RMNP elk population, thereby enhancing the understanding the RMNP ecosystem. Another benefit

to the model was that it identified components that had the greatest affect on the elk, thereby giving RMNP managers an idea of what might be the cause of the changes to the elk population. As well, the model provided a useful tool to test the sensitivity of the model (elk population) to changes in components such as human harvest. The model indicated the viability of the elk population through several runs without the need to test these trials on the actual population. As well, the model provided the managers in RMNP a good starting point for further development and improvement in the modeling of ecological integrity for purposes of management in RMNP.

7.1 RECOMMENDATIONS

1. In light of recent outbreaks of bovine tuberculosis in the RMNP elk population and subsequent spread to cattle herds surrounding RMNP, the Manitoba Department of Conservation has increase the tag numbers of elk from 600 to 1000. Based on their estimates of roughly 4000 elk in the RMNP area, the legal harvest rate is roughly 25% of the total population. As indicated by the model, high human harvest will impact the population and in turn the ecological integrity of RMNP. Therefore the model could be used to focus on the effects of the prolonged hunt and possibly determine a sustainable level, which would benefit the cattle producers, while not devastating the RMNP elk herd. As well, another model could be developed to focus on the impacts of tuberculosis on the elk population.

2. The results of the model runs indicated that the elk population was sensitive to changes in the human harvest rate. Because this is a human induced change on the elk population, one recommendation would be to expand the model to look at the total effects humans have on the viability of the elk population. Factors such as poaching, farmer kills and road kills should be included.
3. Forage and fire are two important factors for the elk population in the ecosystem, therefore the model should be expanded to include these two factors to help increase the accuracy of the model and the results, once the corresponding data is collected to support these factors.
4. The literature review highlighted a link between winter severity and the birth rate of ungulates. Within this version of the model, neither the adult birth nor the yearling birth rate was directly influenced by winter severity. To improve the model, it is recommended that a link be established between winter severity and birth rate.
5. Richards' (1997) study indicated that the effects components such as winter severity and hunter harvest on elk population resulted in lag effects. The STELLA program has a DELAY function, which could be incorporated into the model for those components, which have been previously identified to cause a lag effect on the population.

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APPENDIX 1 - FORMULAE

Cow:Calf:Bull Ratio Formula

Total Elk Population Determined in February 2001 = 2455

Calf:Cow Ratio Determined in December 2000 = 52.5 calves/100 cows

Bull:Cow Ratio Determined in December 2000 = 25.6 bulls/100 cows

Cows = x

Calves = .525x

Bulls = .256x

Equation:

$$.525x + .256x + x = 2455$$

$$1.781x = 2455$$

$$x = 1378 \text{ Cows}$$

$$\text{Calves} = .525 * 1378$$

$$= 723 \text{ Calves}$$

$$\text{Bulls} = .256 * 1378$$

$$= 353 \text{ Bulls}$$

The equation was used to determine the calf, cow and bull populations from the total population of elk. The equation utilized the numbers from the classified counts and the total population estimates of the elk in RMNP.

Elk Days for Winter

This formula was based on estimates, findings and assumptions of Meleshko (1986) and Carbyn (1983).

Wolf pack numbers = 12

Assumed kill rate = 1 ungulate/pack/2.7 days

Days of Winter = 212

$$\text{Estimated ungulate killed} = (212/2.7) * 12$$

$$= 942 \text{ ungulates}$$

Ratio of biomass of deer per biomass of one elk in wolf diet = .30

Ratio of biomass of moose per biomass of one elk in wolf = .17

Elk = x

Deer = .30x

$$\text{Moose} = .17x$$

Estimated of elk, moose, deer in total ungulate population killed by wolves:

$$.30x + .17x + x = 942$$

$$1.47x = 942$$

$$x = 641 \text{ elk killed by wolves}$$

$$\text{Deer} = .30 * 641$$

$$= 192$$

$$\text{Moose} = .17 * 641$$

$$= 108$$

Based on the above determination of the number of elk killed, the maximum elk days based in a time of harsh winter severity is:

$$(641/12 \text{ packs}) = 53 \text{ elk killed per pack}$$

$$212 \text{ winter days} / 53 = 1 \text{ ungulate killed/pack/4 days}$$

Wolf Kills in the Summer

This formula was based on estimates, findings and assumptions of Meleshko (1986)

$$\text{Number adult wolves} = 59$$

$$\text{Number of pups} = 16$$

$$\text{Food Requirement of Adult Wolves} = 1.7 \text{ kg/day}$$

$$\text{Food Requirement of Pups} = 0.9 \text{ kg/day}$$

$$\text{Adult food consumption took place from May 1 to September 30} = 153 \text{ days}$$

$$\text{Pup food consumption took place from June 15 to September 30} = 107 \text{ days}$$

Adult food requirement:

$$59 * 1.7 * 153 = 15346 \text{ kgs of food}$$

Pup food requirement

$$16 * 0.9 * 107 = 1541 \text{ kgs of food}$$

Total wolf population food requirement:

$$15346 + 1541 = 16887 \text{ kgs.}$$

Dead weight conversion to live weight:

$$16887 / .75 = 22516 \text{ kgs of food}$$

$$\text{Percentage of calves in wolf diet} = 4.5\%$$

$$\text{Percentage of adults in wolf diet} = 79\%$$

$$\begin{aligned}\text{Adult elk in kg} &= .79 * 22516 \\ &= 17788 \text{ kg}\end{aligned}$$

$$\begin{aligned}\text{Calves in kg} &= .045 * 22516 \\ &= 1013 \text{ kg}\end{aligned}$$

$$\begin{aligned}\text{Assumed weight of adult elk} &= 247 \text{ kg} \\ \text{Assumed weight of calves} &= 30 \text{ kg}\end{aligned}$$

$$\begin{aligned}\text{Number of adults killed} &= 17788 / 247 \\ &= 72 \text{ adults}\end{aligned}$$

$$\begin{aligned}\text{Number of calves killed} &= 1013 / 30 \\ &= 34 \text{ calves}\end{aligned}$$

Formulae from the Model

Elk

$$\text{Adults}(t) = \text{Adults}(t - dt) + (\text{movement} - \text{Adult_deaths} - \text{Human_Harvest}) * dt$$

$$\text{INIT Adults} = 2866$$

INFLOWS:

$$\text{movement} = \text{calves} - \text{calf_deaths}$$

OUTFLOWS:

$$\text{Adult_deaths} = \text{INT}(\text{Adults} * (\text{AEDR} + \text{WSKRA}) + \text{WWKRA})$$

$$\text{Human_Harvest} = \text{INT}(\text{Adults} * \text{HEHR})$$

$$\text{calves}(t) = \text{calves}(t - dt) + (\text{calf_births} - \text{calf_deaths} - \text{movement}) * dt$$

$$\text{INIT calves} = 692$$

INFLOWS:

$$\text{calf_births} = \text{INT}((((\text{YBR} * (\text{TEP} * .10)) + ((\text{Adults} * .70 - (\text{TEP} * .10)) * \text{ABR}))) * \text{BRFA})$$

OUTFLOWS:

$$\text{calf_deaths} = \text{INT}(\text{calves} * (\text{BPR} + \text{ODR} + \text{WSKRC}) + \text{WWKRC})$$

$$\text{movement} = \text{calves} - \text{calf_deaths}$$

$$\text{ABR} = .82$$

BPR = .25

HEHR = .10

TEP = Adults+calves

WWKRA = INT(((212/(1/elkdays)*Number_of_Packs-WWKRC)))

WWKRC = INT(((212/(1/elkdays)*RANDOM(.15,.30,888)*Number_of_Packs)))

YBR = .27

AEDR = GRAPH(WS)

(0.00, 0.07), (60.0, 0.07), (120, 0.07), (180, 0.07), (240, 0.075), (300, 0.077), (360, 0.08),
(420, 0.085), (480, 0.09), (540, 0.105), (600, 0.145)

BRFA = GRAPH(Total_ungulate_Population)

(0.00, 1.00), (1200, 1.00), (2400, 1.00), (3600, 1.00), (4800, 1.00), (6000, 1.00), (7200,
0.96), (8400, 0.9), (9600, 0.85), (10800, 0.75), (12000, 0.5)

elkdays = GRAPH(WS)

(0.00, 0.03), (60.0, 0.04), (120, 0.05), (180, 0.055), (240, 0.065), (300, 0.085), (360, 0.1),
(420, 0.11), (480, 0.125), (540, 0.165), (600, 0.21)

ODR = GRAPH(WS)

(0.00, 0.105), (60.0, 0.105), (120, 0.105), (180, 0.105), (240, 0.115), (300, 0.115), (360,
0.125), (420, 0.13), (480, 0.145), (540, 0.17), (600, 0.2)

WSKRA = GRAPH(Wolf_Population)

(0.00, 0.00), (20.0, 0.016), (40.0, 0.02), (60.0, 0.03), (80.0, 0.035), (100, 0.05), (120,
0.06), (140, 0.063), (160, 0.07), (180, 0.085), (200, 0.09)

WSKRC = GRAPH(Wolf_Population)

(0.00, 0.00), (20.0, 0.015), (40.0, 0.03), (60.0, 0.035), (80.0, 0.04), (100, 0.06), (120,
0.065), (140, 0.065), (160, 0.075), (180, 0.075), (200, 0.1)

Moose

Moose_Population(t) = Moose_Population(t - dt) + (Moose_Births - Moose_Deaths -
Moose_hunter_harvest) * dt

INIT Moose_Population = 1751

INFLOWS:

Moose_Births = INT((Moose_Population*.55*Moose_Birth_Rate)*brfm)

OUTFLOWS:

Moose_Deaths =

INT(Moose_Population*(TWHR+Moose_Death_Rate)+(Moose_Births*BPRMC))

Moose_hunter_harvest = INT(Moose_Population*Hunter_Harvest)

BPRMC = .25

Hunter_Harvest = .08

Moose_Birth_Rate = .80

TWHR = IF(TEP<1500)THEN(HWNE)ELSE(HWWE)

brfm = GRAPH(Total_ungulate_Population)

(0.00, 1.00), (1200, 1.00), (2400, 1.00), (3600, 1.00), (4800, 1.00), (6000, 1.00), (7200, 0.95), (8400, 0.89), (9600, 0.78), (10800, 0.65), (12000, 0.5)

HWNE = GRAPH(TEP)

(0.00, 0.19), (1200, 0.12), (2400, 0.085), (3600, 0.075), (4800, 0.065), (6000, 0.05), (7200, 0.05), (8400, 0.04), (9600, 0.03), (10800, 0.015), (12000, 0.01)

HWWE = GRAPH(Number_of_Packs)

(0.00, 0.01), (2.00, 0.015), (4.00, 0.03), (6.00, 0.045), (8.00, 0.06), (10.0, 0.07), (12.0, 0.075), (14.0, 0.095), (16.0, 0.13), (18.0, 0.15), (20.0, 0.19)

Moose_Death_Rate = GRAPH(WS)

(0.00, 0.07), (60.0, 0.07), (120, 0.07), (180, 0.07), (240, 0.073), (300, 0.076), (360, 0.08), (420, 0.084), (480, 0.088), (540, 0.1), (600, 0.12)

Ungulates

Total_ungulate_Population = (Moose_Population+TEP)

Winter Severity

green_up_value = RANDOM(-15,25,333)

snow_density = RANDOM(0,0.4,888)

snow_depth = RANDOM(0,60,333)

snow_hardness = RANDOM(0,20,333)

winter_temperature = RANDOM(5,-25,333)

WS =

((snow_depth+(snow_density*100)+snow_hardness+winter_temperature)*6)+green_up_value

Wolf Population

Wolf_Population(t) = Wolf_Population(t - dt) + (Wolf_Births - Wolf_Deaths) * dt

INIT Wolf_Population = 50

INFLOWS:

Wolf_Births = INT(WBR*survival_fraction_of_pups)

OUTFLOWS:

Wolf_Deaths = INT(((Wolf_Disease_Rate+WDR+HHRW)*Wolf_Population))

HHRW = .25

Number_of_breeding_pairs =

INT(IF(Number_of_Packs<1)THEN(Wolf_Population/2)ELSE(Number_of_Packs))

Number_of_Packs = INT(Wolf_Population/Wolves_Per_Pack)

Pup_numbers = 5

survival_fraction_of_pups = .55

WBR = (Number_of_breeding_pairs)*Pup_numbers

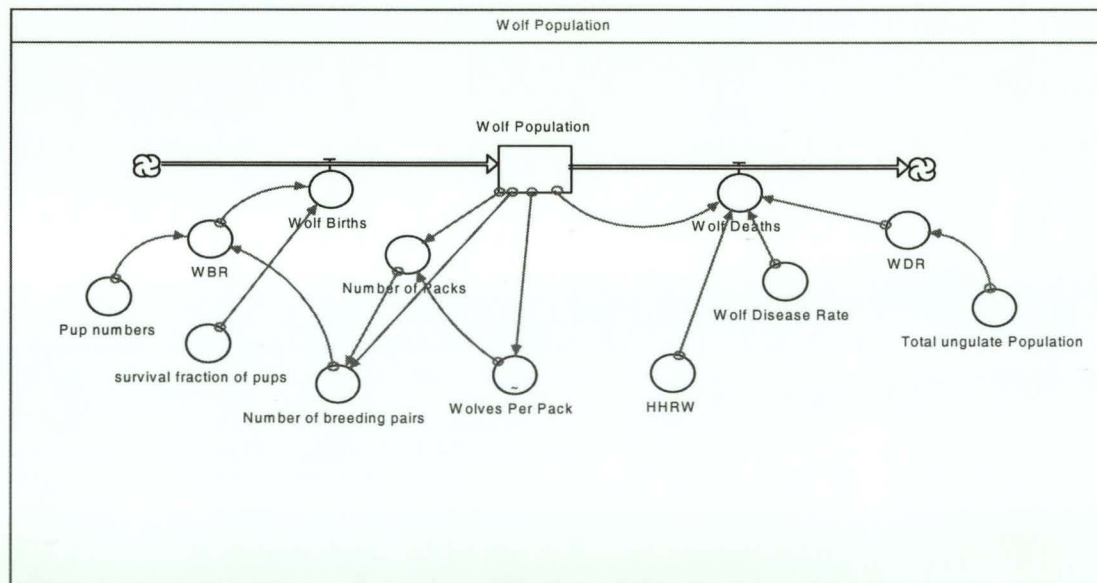
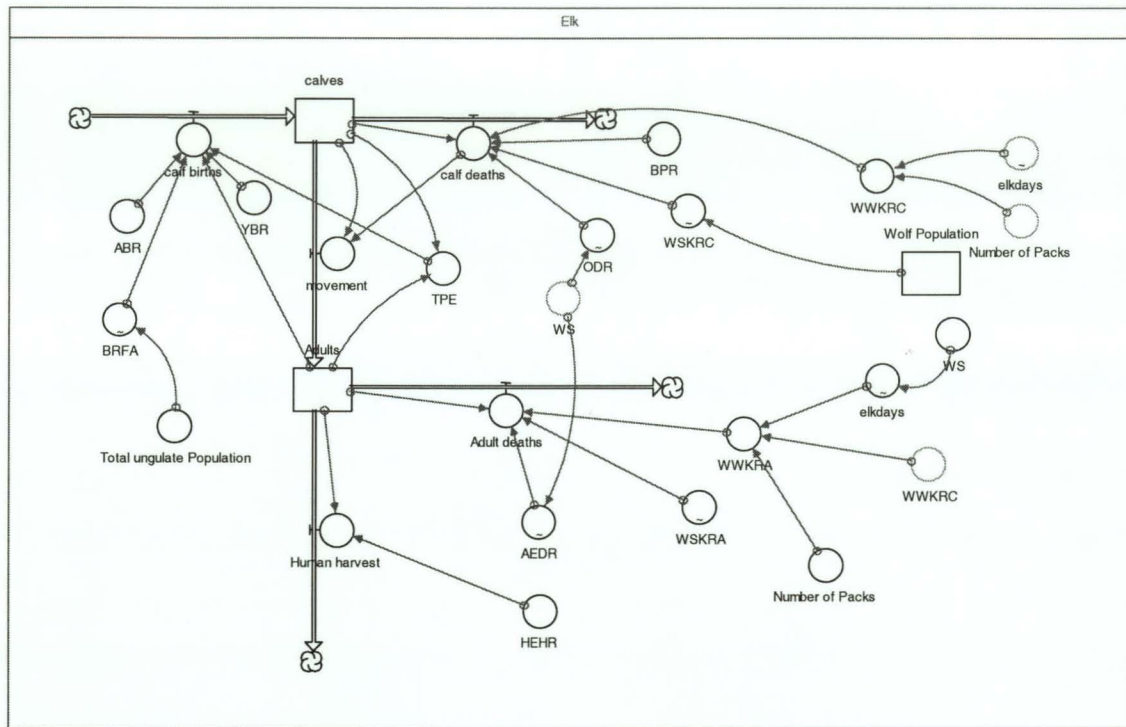
WDR = IF(Total_ungulate_Population<1000)THEN(.50)ELSE(.10)

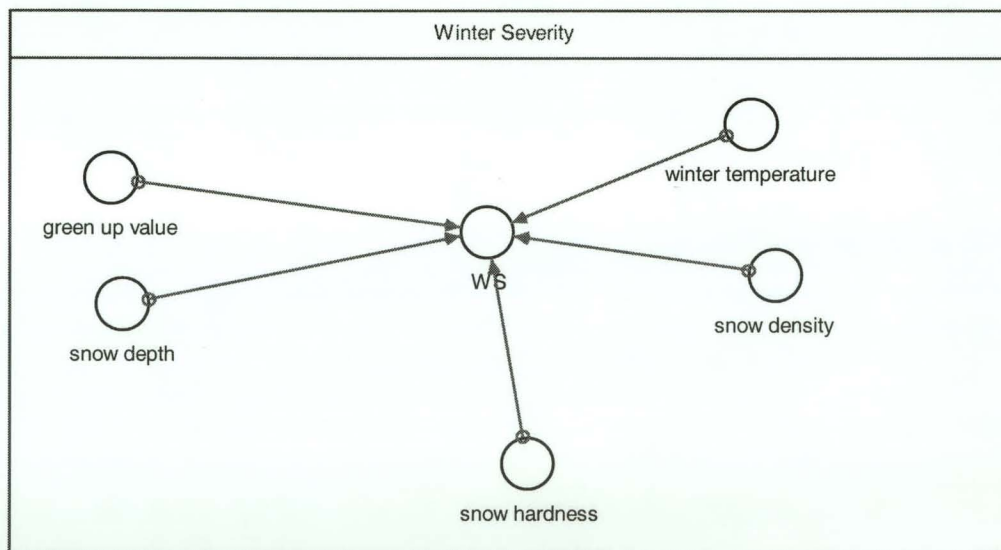
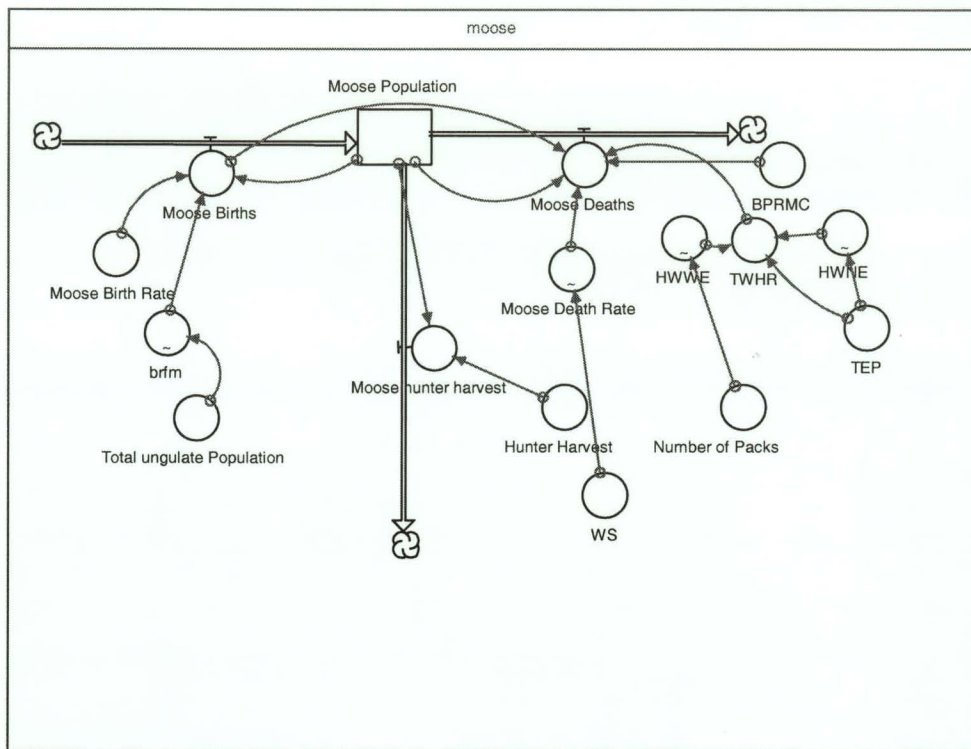
Wolf_Disease_Rate = RANDOM(0.02,0.40,888)

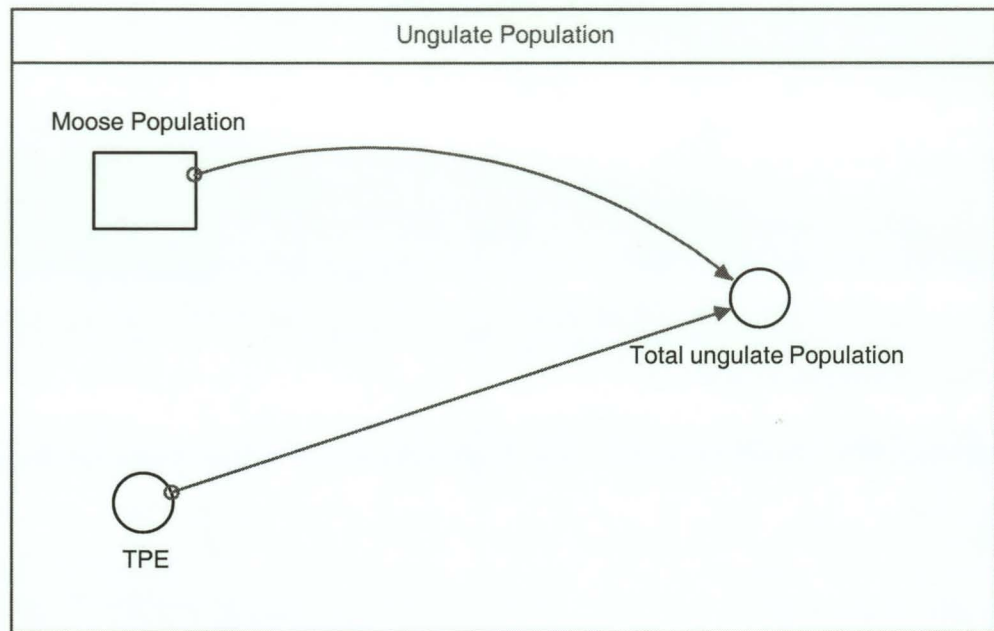
Wolves_Per_Pack = GRAPH(Wolf_Population)

(0.00, 0.00), (20.0, 3.00), (40.0, 4.90), (60.0, 6.00), (80.0, 7.00), (100, 8.00), (120, 8.90),
(140, 9.40), (160, 10.1), (180, 11.2), (200, 12.2)

APPENDIX 2 –MODEL SECTORS







APPENDIX 3 –TABLES FROM INITIAL RUNS

Table 10. Results from Initial Run

Years	Adults	Calves	Adult Deaths	Calf Births	Calf Deaths	TEP
.0	2,866.00	692.00	325.00	1,449.00	277.00	3,558.00
.5	2,768.00	1,070.50	498.00	1,377.00	522.00	3,838.50
1.0	2,655.25	1,223.75	440.00	1,310.00	576.00	3,879.00
1.5	2,626.63	1,266.88	387.00	1,293.00	537.00	3,893.50
2.0	2,667.06	1,279.94	321.00	1,309.00	502.00	3,947.00
2.5	2,762.53	1,294.47	448.00	1,347.00	576.00	4,057.00
3.0	2,759.77	1,320.73	436.00	1,337.00	595.00	4,080.50
3.5	2,767.13	1,328.87	342.00	1,335.00	552.00	4,096.00
4.0	2,846.57	1,331.93	327.00	1,365.00	523.00	4,178.50
4.5	2,945.53	1,348.47	332.00	1,401.00	531.00	4,294.00
5.0	3,041.27	1,374.73	453.00	1,430.00	602.00	4,416.00
5.5	3,049.13	1,402.37	467.00	1,420.00	606.00	4,451.50
6.0	3,061.82	1,411.18	489.00	1,414.00	657.00	4,473.00
6.5	3,041.41	1,412.59	429.00	1,396.00	612.00	4,454.00
7.0	3,075.20	1,404.30	457.00	1,400.00	611.00	4,479.50
7.5	3,089.85	1,402.15	379.00	1,396.00	573.00	4,492.00
8.0	3,160.93	1,399.07	462.00	1,412.00	628.00	4,560.00
8.5	3,157.46	1,405.54	441.00	1,401.00	615.00	4,563.00
9.0	3,174.73	1,403.27	428.00	1,398.00	593.00	4,578.00
9.5	3,207.37	1,400.63	353.00	1,401.00	545.00	4,608.00
10.0	3,298.68	1,400.82	361.00	1,426.00	555.00	4,699.50
10.5	3,376.59	1,413.41	487.00	1,443.00	634.00	4,790.00
11.0	3,354.30	1,428.20	346.00	1,426.00	549.00	4,782.50
11.5	3,453.40	1,427.10	461.00	1,450.00	597.00	4,880.50
12.0	3,465.45	1,438.55	485.00	1,436.00	616.00	4,904.00
12.5	3,461.22	1,437.28	481.00	1,424.00	635.00	4,898.50
13.0	3,448.86	1,430.64	466.00	1,413.00	616.00	4,879.50
13.5	3,451.18	1,421.82	488.00	1,403.00	624.00	4,873.00
14.0	3,433.59	1,412.41	424.00	1,390.00	576.00	4,846.00
14.5	3,468.30	1,401.20	445.00	1,389.00	592.00	4,869.50
15.0	3,477.40	1,395.10	370.00	1,382.00	541.00	4,872.50
15.5	3,545.95	1,388.55	538.00	1,389.00	643.00	4,934.50
16.0	3,472.72	1,388.78	374.00	1,366.00	533.00	4,861.50
16.5	3,540.11	1,377.39	456.00	1,374.00	568.00	4,917.50
17.0	3,539.81	1,375.69	402.00	1,367.00	554.00	4,915.50
17.5	3,573.15	1,371.35	418.00	1,371.00	559.00	4,944.50
18.0	3,591.83	1,371.17	518.00	1,371.00	615.00	4,963.00
18.5	3,531.41	1,371.09	548.00	1,357.00	634.00	4,902.50
19.0	3,449.46	1,364.04	351.00	1,339.00	529.00	4,813.50

19.5	3,519.48	1,351.52	473.00	1,349.00	575.00	4,871.00
20.0	3,495.74	1,350.26	396.00	1,341.00	536.00	4,846.00
20.5	3,530.37	1,345.63	402.00	1,345.00	540.00	4,876.00
21.0	3,555.68	1,345.32	506.00	1,348.00	597.00	4,901.00
21.5	3,499.34	1,346.66	649.00	1,335.00	692.00	4,846.00
22.0	3,327.67	1,340.83	500.00	1,299.00	604.00	4,668.50
22.5	3,280.09	1,319.91	371.00	1,286.00	528.00	4,600.00
23.0	3,326.54	1,302.96	427.00	1,291.00	558.00	4,629.50
23.5	3,319.52	1,296.98	443.00	1,284.00	554.00	4,616.50
24.0	3,304.01	1,290.49	433.00	1,275.00	532.00	4,594.50
24.5	3,301.76	1,282.74	391.00	1,270.00	524.00	4,584.50
25.0	3,320.63	1,276.37	390.00	1,269.00	523.00	4,597.00
25.5	3,336.31	1,272.69	351.00	1,267.00	495.00	4,609.00
26.0	3,383.16	1,269.84	360.00	1,272.00	496.00	4,653.00
26.5	3,421.08	1,270.92	408.00	1,269.00	512.00	4,692.00
27.0	3,425.54	1,269.96	419.00	1,269.00	517.00	4,695.50
27.5	3,421.52	1,269.48	478.00	1,268.00	564.00	4,691.00
28.0	3,364.26	1,268.74	352.00	1,264.00	496.00	4,633.00
28.5	3,406.63	1,266.37	485.00	1,270.00	541.00	4,673.00
29.0	3,356.81	1,268.19	483.00	1,262.00	551.00	4,625.00
29.5	3,306.41	1,265.09	414.00	1,251.00	533.00	4,571.50
Final	3,300.45	1,258.05				4,558.50

Table 11 Results of Elk Run

Years	Calves	Calf Deaths	Calf Births	Adults	TEP	Adult Deaths	WS	WWKRA	WWKRC
.0	692.00	277.00	1,449.00	2,866.00	3,558.00	325.00	17.55	53.00	9.00
.5	1,070.50	522.00	1,377.00	2,768.00	3,838.50	498.00	481.04	175.00	64.00
1.0	1,224.00	576.00	1,310.00	2,655.00	3,879.00	440.00	459.24	143.00	60.00
1.5	1,267.00	537.00	1,293.00	2,626.50	3,893.50	387.00	330.88	127.00	30.00
2.0	1,280.00	502.00	1,309.00	2,667.00	3,947.00	321.00	178.26	78.00	15.00
2.5	1,294.50	576.00	1,347.00	2,762.50	4,057.00	448.00	430.14	149.00	41.00
3.0	1,321.00	595.00	1,337.00	2,759.50	4,080.50	436.00	427.54	139.00	50.00
3.5	1,329.00	552.00	1,335.00	2,767.00	4,096.00	342.00	235.71	80.00	29.00
4.0	1,332.00	523.00	1,365.00	2,846.50	4,178.50	327.00	136.59	72.00	15.00
4.5	1,348.50	531.00	1,401.00	2,945.50	4,294.00	332.00	102.68	67.00	12.00
5.0	1,375.00	602.00	1,430.00	3,041.00	4,416.00	453.00	387.07	136.00	41.00
5.5	1,402.50	606.00	1,420.00	3,049.00	4,451.50	467.00	401.34	148.00	33.00
6.0	1,411.50	657.00	1,414.00	3,061.50	4,473.00	489.00	472.23	149.00	59.00
6.5	1,413.00	613.00	1,396.00	3,041.00	4,454.00	429.00	357.26	126.00	42.00
7.0	1,404.50	611.00	1,400.00	3,074.50	4,479.00	457.00	401.67	141.00	40.00
7.5	1,402.50	574.00	1,396.00	3,089.00	4,491.50	379.00	237.36	87.00	22.00
8.0	1,399.50	628.00	1,412.00	3,159.50	4,559.00	461.00	417.89	130.00	55.00
8.5	1,406.00	615.00	1,400.00	3,157.00	4,563.00	441.00	407.23	116.00	44.00
9.0	1,403.00	593.00	1,398.00	3,174.50	4,577.50	428.00	358.86	115.00	32.00
9.5	1,400.50	545.00	1,401.00	3,207.00	4,607.50	352.00	188.30	66.00	17.00
10.0	1,401.00	555.00	1,426.00	3,298.50	4,699.50	361.00	197.37	63.00	22.00
10.5	1,413.50	634.00	1,443.00	3,376.50	4,790.00	487.00	456.41	127.00	49.00
11.0	1,428.50	549.00	1,426.00	3,354.00	4,782.50	346.00	61.64	50.00	9.00
11.5	1,427.50	597.00	1,449.00	3,453.00	4,880.50	461.00	353.65	120.00	26.00
12.0	1,438.50	616.00	1,436.00	3,465.00	4,903.50	485.00	373.10	137.00	36.00
12.5	1,437.50	635.00	1,424.00	3,460.50	4,898.00	481.00	392.94	127.00	51.00
13.0	1,431.00	616.00	1,412.00	3,448.00	4,879.00	466.00	386.82	117.00	38.00
13.5	1,421.50	624.00	1,403.00	3,450.50	4,872.00	488.00	434.91	126.00	42.00
14.0	1,412.50	576.00	1,390.00	3,432.50	4,845.00	424.00	292.23	97.00	25.00
14.5	1,401.50	592.00	1,389.00	3,467.00	4,868.50	445.00	341.54	106.00	35.00
15.0	1,395.50	542.00	1,382.00	3,476.00	4,871.50	370.00	149.10	62.00	15.00
15.5	1,389.00	643.00	1,388.00	3,544.00	4,933.00	538.00	490.71	143.00	53.00
16.0	1,388.50	533.00	1,366.00	3,471.00	4,859.50	374.00	163.91	67.00	12.00
16.5	1,377.50	568.00	1,374.00	3,538.00	4,915.50	456.00	324.57	112.00	23.00
17.0	1,376.00	554.00	1,367.00	3,538.00	4,914.00	402.00	207.96	77.00	24.00
17.5	1,371.50	559.00	1,370.00	3,571.50	4,943.00	418.00	230.96	84.00	23.00
18.0	1,371.00	615.00	1,370.00	3,590.00	4,961.00	517.00	430.27	139.00	51.00
18.5	1,370.50	634.00	1,356.00	3,530.00	4,900.50	547.00	482.00	160.00	54.00
19.0	1,363.50	529.00	1,338.00	3,448.00	4,811.50	350.00	30.14	43.00	8.00
19.5	1,351.00	575.00	1,348.00	3,518.00	4,869.00	473.00	339.62	126.00	34.00
20.0	1,349.50	536.00	1,341.00	3,494.00	4,843.50	396.00	193.67	78.00	19.00

20.5	1,345.50	540.00	1,345.00	3,528.00	4,873.50	402.00	200.46	77.00	22.00
21.0	1,345.50	597.00	1,347.00	3,553.50	4,899.00	506.00	408.00	136.00	47.00
21.5	1,346.50	692.00	1,334.00	3,497.00	4,843.50	649.00	545.14	201.00	85.00
22.0	1,340.50	604.00	1,298.00	3,325.00	4,665.50	500.00	471.57	140.00	42.00
22.5	1,319.50	528.00	1,285.00	3,277.00	4,596.50	371.00	215.31	70.00	20.00
23.0	1,302.50	558.00	1,290.00	3,323.50	4,626.00	426.00	342.67	101.00	40.00
23.5	1,296.50	554.00	1,283.00	3,316.50	4,613.00	443.00	370.32	114.00	36.00
24.0	1,290.00	532.00	1,274.00	3,300.50	4,590.50	433.00	331.17	113.00	24.00
24.5	1,282.00	524.00	1,269.00	3,298.00	4,580.00	391.00	253.50	80.00	23.00
25.0	1,275.50	523.00	1,267.00	3,317.00	4,592.50	389.00	252.91	77.00	25.00
25.5	1,271.50	495.00	1,266.00	3,333.00	4,604.50	351.00	97.98	56.00	12.00
26.0	1,269.00	496.00	1,270.00	3,379.00	4,648.00	360.00	110.31	59.00	12.00
26.5	1,269.50	512.00	1,268.00	3,417.00	4,686.50	408.00	228.10	89.00	17.00
27.0	1,269.00	516.00	1,267.00	3,421.00	4,690.00	419.00	237.53	93.00	16.00
27.5	1,268.00	564.00	1,267.00	3,417.00	4,685.00	478.00	372.96	125.00	48.00
28.0	1,267.50	496.00	1,262.00	3,359.50	4,627.00	352.00	25.08	49.00	8.00
28.5	1,265.00	540.00	1,269.00	3,401.50	4,666.50	485.00	356.15	139.00	28.00
29.0	1,267.00	550.00	1,260.00	3,351.50	4,618.50	482.00	365.97	136.00	35.00
29.5	1,263.50	532.00	1,249.00	3,301.50	4,565.00	413.00	259.56	89.00	32.00
Final	1,256.50			3,295.50	4,552.00		179.49	75.00	18.00