University of Alberta

CONSERVATION OF WOODLAND CARIBOU *(Rangifer tarandus caribou)* IN WEST-CENTRAL ALBERTA: A SIMULATION ANALYSIS OF MULTI-SPECIES PREDATOR-PREY SYSTEMS.

by

Robert Bruce Lessard

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

in

Wildlife Ecology and Management

Department of Renewable Resources

Edmonton, Alberta
Fall 2005

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

0-494-08673-4

Your file Votre référence
ISBN:
Our file Notre reterence
ISBN:

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

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

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

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

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Growing old is difficult, but it's the only way to live a long time.

– Benetto Biron (Possagno Italy, 2005)

To Ariadna Miknevičiute Peteraïtis (Oct 2, 1918 - Aug 19, 2004)

The complexities of ecosystem interactions were trivial to my grandmother. I was continually amazed at how easily she grasped what I considered to be complex ecological concepts. How pragmatically she accepted them! She survived far more complex and difficult times herself.

Abstract

In the wake of human impacts in forested landscapes, life histories of woodland caribou (*Rangifer tarandus caribou*) have changed such that they increasingly interact with moose (*Alces alces*). Empirically observed predation rates and demographic responses suggest that wolves (*Canis lupus*) are probably the principle shared predator between the two ungulate species. I show with theory, models, and empirical trends that caribou may not be capable of persisting when moose populations colonize caribou ranges.

I fit models to empirical trends, estimate parameters, and show ranges of uncertainty around parameter estimates and predicted trends. I then perform a sensitivity analysis on each model to examine the effect of varying parameters in response to environmental change. By examining various behavioural mechanisms, I show that a narrow range of qualitative outcomes results regardless of which model is used. I show that there are a limited number of conditions that allow caribou to persist. I explore these conditions and propose management recommendations to mitigate caribou population declines.

I also examine how habitat distribution and availability impact population stability and persistence. A spatially explicit behavioural model examines the spatial distributions of predators and prey species, in particular the effect of spatial heterogeneity on the functional response of predators to prey at different spatial scales. Results indicate that the distribution and spatial structure of resources affects habitat selection patterns. Three key patterns are shown: 1) the availability of prey resources limits predator avoidance, 2) the abundance of alternate prey limits prey selection potential, and 3) spatial distribution of resources limits the accessibility of prey to predators. Results show that if a sufficient quantity of prey resources is distributed at a spatial scale larger than the scale of predator searching, then the functional responses will demonstrate prey switching as a direct result of spatial behaviour.

Acknowledgements

This research was supported through the West-Central Alberta Caribou Standing Committee by donations from Canadian Forest Products, Weyerhaeuser and others. I would like to thank my co-supervisors for encouraging me to pursue this project. Fiona Schmiegelow consistently brought important resource management perspectives to bear. The scholarly and profane advice of Carl Walters inspired and fuelled much creativity and innovation. Committee members Mark Boyce and Stan Boutin both provided insights and comments that were very helpful.

This would not have been possible without coaching and support from fellow grad students, friends and family. Academic "bull-sessions" and talks of encouragement were deeply appreciated. The labs at U of A and UBC were valuable sources of new ideas, conflicting ideas, inspirations and breadth. Nathan Taylor, Rob Ahrens, Steve Martell, Mike Melnychuk, Mark Hebblewhite, Laura Prugh, Joanne Saher, Heiko Wittmer and Alastair Franke all brought important perspectives and thought provoking ideas to my attention. I cannot hold a candle to Robyn Forrest's or Brian Starzomski's perspicacity. They were punished for it by being asked to read and comment on my first draft. Friends and family outside the academic community endured the sound of the academic fiddle on more than one occasion and were invaluable reminders of life beyond science. My parents, grandparents, sister and nieces, Adie Deeks, Bob Deeks, Bill & Julie, *Knockando Manor*, Anita Boehm, Minnicog Island, Alex Tavuchis, Brian Carrow and Becky Halvorson enriched my life profoundly during this period of my life. Paulo Biron, Simone, Benetto, Mauro, Isabella, Manuele, Eddy, Claudio, Telli, the ghost of Casa Biron and Possagno Italy will never be forgotten. *Yamato damashi!*

Table of Contents

List of Tables

List of Figures

Chapter 1

General introduction

This thesis presents a study of the population dynamics of an ecotype of woodland caribou (*Rangifer tarandus caribou*) in the foothills of Alberta. Caribou ranges are increasingly overlapping with moose (*Alces alces*) due to human alteration of forested landscapes. Observed predation rates and demographic responses suggest that wolves (*Canis lupus*) are probably their most important shared predator. Theory, models and empirical trends all suggest that caribou and moose populations may not be able to coexist, yet little has been done to empirically test models. Understanding the trophic interactions between these three species under changing environmental conditions is essential to the development and implementation of caribou conservation policies.

This study reconciles patterns observed on local scales with patterns observed across larger spatial and temporal scales. I build predator-prey dynamics models to investigate population responses to increasingly complex spatial and demographic details. I fit models to empirical trends observed in one system then examine the effect of varying key parameters with environmental conditions to compare them to patterns observed on larger scales. The goal is to identify the most robust predictive model across spatial and temporal scales. By examining various behavioural mechanisms, I show how some well known species interactions can dominate a system such that predictions fall within a narrow range of outcomes regardless of model selection.

I statistically fit empirical models to data, estimate parameters and show ranges of certainty around parameter estimates. I then perform a sensitivity analysis on each model to examine the effect of varying parameters with environmental change. The nature of the data makes estimation of some parameters very difficult. In the absence of good parameter estimates, I show the qualitative differences arising from variation in those parameters.

This is a study of the coexistence of two prey species and a predator: a study of the way habitat availability and distribution impact species interactions. The balance between the demographic and behavioural rates that determine the trophic interactions is a difficult one in changing environments and leaves little room for error. There are a limited number of conditions under which both species can persist. I explore these conditions and evaluate management strategies to mitigate population declines of a threatened ungulate species.

1.1 Statement of problem

Many woodland caribou populations are considered *threatened* by provincial and national wildlife conservation agencies. Several caribou populations in British Columbia and Alberta have been declining for decades (Bergerud and Elliot 1986; Bergerud and Elliott 1998; Brown and Hobson 1998; Edmonds 1998; Dzus 2001) (see Chapter 2 for a more detailed discussion). The prevailing view is that colonisation by moose follows forest harvesting, which provides the young seral forests favoured by moose, and that caribou herds face increased predation pressure from wolf populations that increase along with moose populations. In Alberta, there is evidence that energy sector activities have effectively decreased supplies of late seral forest as well (Schneider et al. 2003). Though forest inventory data do not reflect this, an examination of seismic line densities and their relative widths reveals that energy sector activities are responsible for a significant amount of disturbance (Oberg et al. 2002).

What remains to be demonstrated is whether or not caribou populations can persist under *status quo* conditions (i.e., high moose and wolf densities). There are alternative views about predation mechanisms, and the assumptions therein dictate what is predicted. Assumptions about functional responses, additive and compensatory mortality and density dependence give rise to a plethora of potential dynamics. A broad scale empirical test of predation mechanisms has not been attempted to date for this system. In this thesis, I construct models of some of the more plausible and tractable mechanisms.

The literature is filled with empirical studies that are focussed on finding relationships between abundances of prey and predators (e.g., (Peterson 1977; Gasaway et al. 1983; Fuller and Keith 1980; Fuller 1989; Bergerud and Elliott 1998; Gasaway et al. 1992)), prey recruitment rates and predator abundances (Bergerud and Elliot 1986; Bergerud 1990), and even looking for emergent statistical summaries of complex ecological systems (Peterson et al. 1984). Less has been done to predict the behaviour of predator prey systems by fitting models to data. Advances have been made (Carpenter et al. 1994; Jost and Arditi 2001), but these have used laboratory systems and aquatic micro-organisms, and dealt mainly with identifying whether or not functional responses are *prey-dependent* or *predator-dependent.* Given the qualitative differences that the more popular model assumptions predict, it is surprising that so little has been done to estimate parameters under various model assumptions. Such estimates provide the basis for predicting future system behaviour and comparing qualitative behaviour among models. Perhaps this failing is due both to the nature of the empirical studies, which are typically designed to monitor general population abundance trends, or the tendency biologists have shown towards demonstrating small scale biological behaviour of potentially little significance to broad scale patterns. It may also be a distrust of models and a belief that nature cannot be captured this way. This is not without good reason, but neither is it a reason to stop trying.

1.2 Thesis overview

I adhere to the philosophy that complex relationships in ecology *do* have mathematical expressions and can be represented with models. Exploring relationships with models helps develop our understanding of the mechanisms that drive patterns. Sometimes we must resign ourselves to the fact that discarding some of the more enticing complexities can in fact lead to more stable models where parameter estimates across observable conditions remain within predictable boundaries. Searching for these *stationary* properties is key in the development of models. Predator-prey models are no exception, but bear the burden of being very difficult to fit to empirical data. This is true of any complex system of dynamic equations where there are interactions between state variables. It is particularly true of coupled trophic models. The caribou/moose/wolf system is no exception.

Models must also address the uncertain nature of nature itself. We must characterize how this uncertainty propagates and attempt to capture it. Ultimately our models aim to include uncertainty in predictions. We must also deal with the way model structures introduce biases to both quantitative and qualitative predictions.

In this thesis I build alternative models to do three things: 1) to reconstruct historical population trends, 2) to predict probabilities of future trends by accounting for parameter uncertainty and 3) to explore the emergent properties of fine-scale spatial behaviour. I compare the qualitative behaviour of alternative models and discuss these in terms of assumptions and known behaviour of other similar systems.

A review of empirical trends observed in natural and managed wolf-ungulate systems is presented in Chapter 2. Patterns are summarized and provide the basis for model structures that are developed in later chapters. In Chapter 3, I reconstruct the historical trends of one particular system with a number of models, all of which explain something different about how the system behaves. I fit each of these models to empirical trends by maximizing the value of an objective function. I also simulate future events using empirically derived estimates of the range of uncertainty inherent in each parameter. This provides estimates of times until extirpation of caribou. A probability distribution of the time until extirpation is provided. Chapter 3 fails to distinguish which of the models better explains historical trends, but concludes that since all models show the same short-term decline, caribou are at risk of declining to low densities or being extirpated if nothing is done to change the *status quo*.

In Chapter 4, I consider population responses to changes in environmental conditions that arise from natural disturbances and human activities. I force key parameters to vary with environmental fluctuations for each of the models developed in Chapter 3. Long term patterns are examined in the context of management options that give rise to different landscape patterns.

In Chapter 5, I propose a mechanism by which spatial behaviour can give rise to emergent patterns when fine scale dynamics are integrated over larger spatial and temporal scales. I construct a model that implicitly captures the behaviour of animals responding to spatial gradients on the landscape, providing a view of the effects of foraging in response to habitat conditions. The product is a model that predicts the spatial distribution of animals and the spatial distribution of kills. I then demonstrate that the spatial distributions can have a stabilizing effect on population dynamics, and that under certain conditions, the spatial distribution of animals leads to apparent prey switching.

Thesis goals

1. Reconstruct the population histories of caribou, moose and wolves using empirical data from the winter range of a caribou population.
2. Contrast alternative population dynamics models.
3. Predict caribou extirpation probabilities using alternative models.
4. Examine the effect of variation in environmental conditions on projected abundance trends.
5. Explore the broad-scale emergent properties of fine-scale spatially explicit foraging
6. Identify management alternatives to reverse the decline of caribou. behaviour.

Chapter 2

Empirical trends in predator-ungulate systems

Introduction

This chapter reviews the life history of woodland caribou and provides a background on predator-ungulate ecology in managed systems. I review findings from a variety of predation studies pertinent to modelling the population dynamics of woodland caribou. Empirical studies over the last forty or so years provide an indication of the more important interactions and provide the basis for much of the theoretical modelling that has followed. This review focusses on long-term studies that have demonstrated fluctuations in species abundances that provide insight into the dynamics of predator-prey systems that is useful to building models.

Many agencies are still reluctant to use models to direct empirical research and field studies. The majority of empirical testing has been limited to subcomponents of the models instead of testing how well models predict population dynamics trends (i.e., we are not exploiting the predictive power of models). Nonetheless, there is a strong push to compare structurally distinct models and to understand the repercussions to population viability under alternate hypotheses (Pascual et al. 1997). In many cases managers are forced to make assessments in the face of conflicting information and knowledge gaps.

Models designed to contrast the alternatives and contend with poor data can be extremely valuable tools to guide decision making and research. When data are inadequate to make good predictions about future trends in the face of environmental change, we should then seek to demonstrate the alternatives that arise under the various assumptions. At the very least, the models provide us with a baseline comparison of what we can expect to see under various conditions.

To add to the confusion of selecting from alternative models is the seemingly never-ending debate about what causes populations of predators and prey to fluctuate over time. Empiricists center discussions on conceptual ideas about whether or not populations are in *balance*. The debates concern whether or not negative effects of predators on prey subside when prey abundances are low or whether the effects remain strong enough to drive populations to extremely low levels. Theoreticians and modellers find the language of these discussions vague and have pushed for more direct tests of behavioural assumptions expressed in models. Empiricists and theoreticians share the common goal of wanting to predict population trends. What remains prevalent however, is that many studies are unable to find the resources or the long term commitment to collect data at the spatial and temporal scales required to test alternative models.

2.1 Background

Woodland caribou are a caribou subspecies that is divided into three ecotypes, each based on characteristic adaptations. One ecotype migrates seasonally between foothill forests and sub-alpine areas. Another lives year-round in boreal forests. A third ecotype is distributed over elevational gradients at different times of year to seek refuge and take advantage of snow conditions. There is some confusion among provincial and federal agencies about the naming of these populations. Alberta agencies refer to their migrating populations as *mountain* caribou and refer to the forest dwelling populations as *boreal* caribou. The Canadian Species at Risk Act act (SARA) defines migrating populations as *northern* caribou, boreal forest dwellers as *boreal* caribou and the ones that distribute along elevational gradients as *mountain* caribou. Northern ecotype herds are found throughout Alaska, the Yukon, northwest and north-central British Columbia (BC), and west-central Alberta (AB). Mountain populations are found mainly in mid-central to southeast BC, due mainly to the snow depths seen across that region. Boreal populations span most of Canada's boreal forest. Boreal and northern populations in Alberta are considered *threatened* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2000) while mountain populations in BC are *endangered.* All ecotypes are referred to as woodland caribou and patterns of population dynamics are very similar despite differences in spatial and temporal habitat use and the alternate prey composition of the systems that they are part of. Other subspecies of caribou include barren ground caribou (*Rangifer tarandus groenlandicus*), Peary caribou (*Rangifer tarandus pearyi*) and Grant's caribou (*Rangifer tarandus granti*). Each exists in an environment to which it has adapted unique characteristics.

Woodland caribou tend to inhabit areas that have low densities of moose (*Alces alces*), elk (*Cervus elaphus*) and deer (*Odocoileus* spp.). These prey attract wolves, to which caribou are very susceptible as prey (Bergerud et al. 1984; Bergerud and Elliot 1986; Seip 1990). Migrating herds of caribou go to higher elevations for calving and occupy winter habitat with minimal alternate prey and predators (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1990; Seip 1991; Seip 1992a; Brown and Hobson 1998). They are also typically found at quite low densities (less than 0.1/km^2), which also helps to keep predation at bay (Bergerud 1992).

Woodland caribou are associated with older forests because slow growing lichens, an important food source, are primarily found in mature forests (Servheen and Lyon 1989; Dzus 2001). For boreal caribou this means they will primarily be found in peatland complexes composed of black spruce (*Picea mariana*) and larch (*Larix laricina*) and will seldom be found in upland stands (Fuller and Keith 1981). Mountain caribou select habitat in relation to lichen availability as affected by snow cover. In general, caribou prefer older, denser stands and use snow pack to access arboreal lichens (Servheen and Lyon 1989; Szkorupa 2001). Their adaptation to harsh winter conditions distinguishes them from other ungulates and provides them with mechanisms to cope with the habitats they select. Large crescent shaped hooves, which bear their weight effectively on snow, are quite sharp and facilitate travel on ice.

The demographics of caribou are well documented. The breeding season occurs in early to mid October and calves are born in mid May to early June. Adult cows begin breeding at 1.5 years of age, though a greater proportion first breed at 2.5 years. Pregnancy rates ($\simeq$94%) and adult survival rates ($84 - 93\%$) are relatively invariant compared to juvenile survival (Fuller and Keith 1981; Stuart-Smith et al. 1997; Rettie and Messier 1998; McLoughlin et al. 2003). Calves experience mortality rates from 30 to 70% in the first 15 days (Adams et al. 1995) and annual mortalities range from 70 to 100% (Bergerud and Elliot 1986). Density dependent recruitment has been attributed to calf loss by nutritionally stressed cows, suggesting a carrying capacity as high as $5/\mathrm{km}^2$ in domesticated herds in Scandinavia (Skogland 1985). Carrying capacities would be considerably lower for wild herds. Bergerud (1974) and Bergerud (1988) suggested that a caribou population would decline if recruitment dropped below the 10% necessary to balance adult mortality. Predation by wolves is considered the major cause of adult mortality (Bergerud 1988; Edmonds 1988; Seip 1992a; Thomas 1995; Edmonds 1998;

Rettie and Messier 1998). Calves are vulnerable to bear predation in the first few weeks following birth (Bergerud and Page 1987), but predation by bears is not considered as significant as by wolves.

Moose occur to the northern reaches of the boreal forest but are limited to the south by warm climate (Karns 1997). They primarily browse forbs and shrubs (Renecker and Schwartz 1997) and as such prefer early seral forests characteristic of post-fire regeneration (Peterson 1977). The have been found at their highest densities about 20 years post fire, declining in abundance thereafter (Schwartz and Franzmann 1989; Loranger et al. 1991). Populations in North America range from densities as low as 0.05-1.0/km^2, with regional populations potentially erupting to 2.5/km^2 for short periods of time (Schwartz 1997). Crete (1989) estimates the average carrying capacity of moose to be in excess of 2/km^2 but few populations are seen in that range, leading to arguments regarding natural processes regulating populations below that level (Crete et al. 1981; Gasaway et al. 1983; Messier and Crete 1984b; Boutin 1992; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994; Messier and Joly 2000).

History in British Columbia has shown that colonisation by moose into harvested forests leads to an increase in wolf populations and therefore wolf predation on caribou (Bergerud 1974; Bergerud and Elliot 1986; Seip 1992a). The colonisation roughly followed a south-westward path from British Columbia's northeast boreal forest region. The prevailing view is that forest activities along the colonisation route contribute to moose colonisation. Although it can't be denied that industrial activities have altered the age structure and spatial structure of forests, neither can it be truly said that these activities *caused* the colonisation of moose. Colonisation may have begun *before* large scale forest activities existed in central British Columbia (Bergerud and Elliott 1998). Regardless of the cause of the colonisation, the historical events following it are not in doubt. Moose and wolf densities increased (Bergerud 1974; Bergerud and Elliot 1986; Bergerud and Elliott 1998).

Industrial activities create conditions that favour moose productivity, which leads to higher moose and wolf densities in many current caribou ranges. This potentially alters the historically observed habitat use strategy of caribou and creates a new relationship with predators. The fear is that avoidance of oil exploration seismic lines (Dyer 1999; Dyer et al. 2001; Oberg et al. 2002) and residual forestry impacts, such as clearcuts (Smith et al. 2000) and roads (Dyer 1999), will increase encounters with predators.

Moose breed in the fall and give birth to calves in spring. Depending on body condition, most calves are born of animals greater than three years old, although animals as young as 16-17 months occasionally breed. Pregnancy rates are generally $> 80\%$ but can be much lower in an unhealthy or older population (Schwartz 1997). Twinning rates as high as 52% have been observed, though rates vary and depend on habitat and proximity to carrying capacity (Gasaway et al. 1992; Schwartz 1997). Adult mortality is lower in females than in males and increases with age. Peterson (1977) found that few male moose live beyond 15 years and few females live beyond 19 years. Average adult natural mortality rates are believed to range from 20% (Gasaway et al. 1992) to less than 10% (Bangs et al. 1989; Larsen et al. 1989).

Wolves prey on several ungulate species, including moose, mountain sheep (*Ovis* spp.), elk (*Cervus elaphus*), deer (*Odocoileus hemionus*) and caribou (Seip 1991; Mech et al. 1995). Their summer diet diet also includes smaller animals such as beaver (*Castor canadensis*) and hare (*Lepus spp.*) (Peterson 1977; Thurber and Peterson 1993). The total density of wolves has been used as a predation indicator (Fuller 1989) but social structure and prey density are also considered significant. The number of packs can determine how many hunting units use the same prey base (Walters et al. 1981) and territory size can determine the effectiveness of a pack within its territory (Haber 1977; Walters et al. 1981; Messier 1984). Peterson et al. (1984), Ballard et al. (1987) and Fuller (1989) found that larger packs had larger territories when prey densities were similar. Messier (1984) found area per wolf to be inversely proportional to moose density. The size of the pack in relation to its territory size will also affect the tendency of the pack to split, thereby creating more hunting units. Haber (1977) found that pack sizes were generally in the 7-9 range and packs tended to split if they reached more than 12 animals. Establishment of new pack territories is considered to be the most significant overall factor leading to increases in wolf densities (Peterson et al. 1984; Thurber and Peterson 1993; Bergerud and Elliott 1998; Hayes and Harestad 2000a; Hayes et al. 2000).

Mech et al. (1995) found that wolves consumed 47% moose, 42% caribou and 11% Dall sheep in Denali National Park, Alaska. In contrast, Ballard et al. (1987) found that moose comprised 71% of kills and caribou comprised 21%, and that moose calves were consumed disproportionately to their numbers during November-April, suggesting increased vulnerability of calves in winter. In northeastern Alberta, where beavers are abundant, wolves killed beavers in proportion to their abundance and beavers composed up to 50% of kills in summer (Fuller and Keith 1980). On the other hand, Hayes et al. (2000) found that wolves did not kill caribou in relation to availability but rather continued to kill moose even as caribou numbers increased.

Grizzly bears *(Ursus arctos)* are known to prey upon moose (Boertje et al. 1988; Ballard and Van Ballenberghe 1997) and caribou (Bergerud and Elliot 1986; Boertje et al. 1988; Adams et al. 1995). They are thought to be the primary cause of mortality for moose in the southwest of the Yukon (Larsen et al. 1989; Orians et al. 1997), being responsible for 60% of juvenile mortality before mid June and 25% thereafter. Gasaway et al. (1992) found that grizzly bears in interior Alaska posed only a minor predation impact on moose, but also noted that moose and grizzlies were spatially separated most of the year. In other parts of Alaska, grizzly bears were found to prey significantly on moose (Ballard et al. 1991; Miller and Ballard 1992).

2.2 Predator-prey dynamics

Any study of predator-ungulate dynamics will invariable involve a discussion the moose/wolf system. All the processes normally considered in predator prey dynamics have in one way or another been at the forefront of a moose or wolf study somewhere in North America. Wolf colonisation to the island of Isle Royale in Lake Superior Michigan, marked the beginning of a long-term study of moose/wolf dynamics (Peterson 1977). Wolf control was initiated in Alaska to recover moose populations (Gasaway et al. 1983; Haber 1987; Gasaway et al. 1992) from low densities. Wolf-moose systems were at the center of debates about the natural regulation of large mammal populations (Crete et al. 1981; Messier and Crete 1984b; Bergerud et al. 1983; Bergerud and Snider 1988; Thompson and Peterson 1988; Sinclair 1989; Van Ballenberghe and Ballard 1994; Messier and Joly 2000). Kill rate studies were used to provide empirical evidence of the functional response forms that describe the trophic interaction between the two species (Messier 1994; Hayes and Harestad 2000b; Hayes et al. 2000).

Moose population dynamics studies have mostly discussed predation using the terms *limitation* and *regulation*. In short, limiting factors are unrelated to the density of the species of concern and regulating factors are proportional in some way to the density. It has been suggested that wolves and/or bears are a limiting factor to moose populations (Fuller and Keith 1980; Bergerud et al. 1983; Gasaway et al. 1983; Messier and Crete 1984a; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994) that needs to be managed to protect moose from reaching low densities. Conversely, it is thought that wolves act as a natural regulation to moose (Gasaway et al. 1983; Messier and Crete 1984b; Messier 1994; Gasaway et al. 1992), and are not the cause of any of the drastic declines observed. This has been a contentious issue for decades. The alternative view is that predators are not a significant enough agent of mortality to cause serious declines of moose populations and that moose are ultimately regulated by competition for food resources (Peterson 1977; Thompson and Peterson 1988; Skogland 1985) or food and weather (Mech et al. 1987; McRoberts et al. 1995). Boutin (1992) contends there is insufficient evidence to conclude one way or the other. It is important to note that most studies draw conclusions on the dynamics of vastly different systems, usually involving different predator and alternate prey regimes as well as climatic conditions. Additionally, as Boutin (1992) points out, hypotheses have not been fully tested. Many studies rely on predator control and monitoring programs that have not been executed over large enough areas or for adequate lengths of time (Orians et al. 1997).

The following summarises the hypothesised dynamics that could arise from limiting and regulating predation as well as food factors (Boutin 1992):

1. The *predator limitation hypothesis* predicts that predation is a significant limiting factor but does not regulate prey, and that prey populations experience periodic fluctuations driven by a combination of predation, weather and hunting. Prey populations do not return to an equilibrium density after they are disturbed.
2. The *single-state predator regulation hypothesis* (Predation hypothesis) predicts that prey populations will be kept down by density-dependent predation, never to reach high enough densities for food competition to be important.

3. The *two-state predator-food regulation hypothesis* (Predator-pit hypothesis) predicts that predation is density dependent at low to medium densities but inversely density dependent at high densities. If prey densities escape being regulated by predators and rise into the inversely density dependent range, density increases to a level where it is regulated by food.

4. The *stable limit cycle hypothesis* predicts that prey populations will periodically increase or decrease due to weather and food availability but predation is not regulating.

Boutin (1992) points out how we can design experiments that test these hypotheses and what we can expect to see when we control certain aspects of the system. The problem is that this does not allow us to make quantitative statements about the density dependence of key rates nor does it predict long term trends in abundance.

Functional responses

The functional response (FR) describes the rate at which a consumer will deplete its resources as densities of those resources vary (Holling 1959; Turchin 2002). The two most commonly used forms in ungulate ecology are the Type 2 and 3 functional responses. A Type 2 functional response is hyperbolic. It is given by $FR_2 = a'N/(1+a'hN)$. a' is the rate at which resources are found and consumed, which is called the *effective rate of search*. h is the *handling time* interval between feeding events, and N is the density of resources per unit area. A Type 3 functional response is sigmoidal and is given by $FR_3 = b'N^2/(1 + ahN^2)$, where b is interpreted as the slope of the relationship $a(N) = b'N$, meaning that FR_2 is a special case of FR_3 where $a(N) = a'$. The functional response can describe vegetation consumption by herbivores or prey consumption by predators. Kills per predator per unit time is the common empirical measure (Messier 1994; Hayes and Harestad 2000a; Hayes and Harestad 2000b; Hayes et al. 2000).

Throughout discussions of the limitation and regulation of populations, the functional response is consistently discussed as an important, if not *the* important process determining whether or not predator and ungulate populations will remain stable, increase, or decrease from a given density. It is widely discussed for moose/wolf systems (Gasaway et al. 1983; Messier and Crete 1984b; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994; Eberhardt 2000; Messier and Joly 2000). If the predation rate declines as prey densities decreases there is the possibility that predators will not drive their prey to extinction, which is regulatory. Alternatively, predators will drive prey down if the predation rate does not decline as prey densities decrease. Messier (1994) examined 27 published studies of wolves preying on moose and concluded that the best fit to the data was a Type 2 functional response with a maximum killing rate of 3.36 moose/wolf/100 days during the winter. The study concluded that the predation rate was strongly density dependent up to ~ 0.65 moose/km^2 and inversely density dependent thereafter. At low densities, the influence of increasing predator populations was the principle factor contributing to the predation rate. This has profound effects in multiple prey systems where one prey species is at low density. If predators respond numerically to alternate prey, a significant amount of predation could be linked directly to the abundance of alternate prey. Messier (1995) found that when alternate prey were modelled into the dynamics, density dependence in the predation rate dissapeared. Simulations indicated that a Type 2 functional response always yields density dependent predation at low densities but that with the addition of the alternate prey, very efficient killing at low prey densities could cause predation to be depensatory with no density dependent phase. This dynamic would predict the extinction of the more vulnerable prey species as in Seip

(1992a). Marshal and Boutin (1999) point out that because such a high number of samples of kill rates are required to differentiate between Type 2 and 3 functional responses, it can often be more meaningful to estimate total predation losses rather that distinguishing between functional forms. For purposes of estimating short-term responses within narrow ranges of prey and predator densities this is true, but the form of the functional response still determines the qualitative behaviour across broad density ranges.

I have performed an analysis of functional response data that is pertinent to the rest of this thesis. I have re-analysed the data found in Messier (1994) and estimated a and h for both Type 2 and Type 3 functional responses. According to each model, it takes over 30 days for a pack to handle one moose. This seems rather high but the kill rate data only account for moose kills, whereas wolves may well have been feeding on other prey. Excluding the other prey from the calculation forces the model to raise the value of h to compensate for this. The Type 3 model estimated a high handling The sum of squares is lower when fitting the Type 2 model to the data, indicating that it is a better fit. The models predict different maximum killing rates ($1/h$) because when the estimation procedure forces a fit through the data, it is doing so with fundamentally different functional forms. The best fit may come from a higher or lower value of a or h, depending on the model.

Table 2.1: Maximum likelihood estimates of moose functional response parameters. Effective rate of search is in units of km^2 (100 days)$^{-1}$. Handling time is the proportion of 100 days.

	Type 2	Type 3
Sum of squares	5.41125	5.80917
a	8.57342	46.0464
h	0.302739	0.388225

The parameter estimates represent the joint maximum likelihood estimates, but there is still unexplained variation in parameters. I performed Markov

Chain Monte Carlo (MCMC) simulations to explore the range of variation inferred in each parameter. The Metropolis-Hastings algorithm (Chib and Greenberg 1995) was used to simulate the probability distributions of the parameters. The posterior distributions are shown in Figure 2.1. The confidence range inferred from random draws from the posterior estimates of a and h is shown in Figure 2.2, which shows the functional response evaluated at 100 random draws from the joint posterior distribution of effective rate of search and handling time. There is a great deal of uncertainty in the functional response at lower moose densities. The functional response tends to overestimate. It is difficult to judge the cause of this since Messier (1994)'s tabulated data comes from a mixture of studies that involve different packs from different geographic locations. In some cases the data is averaged over several packs.

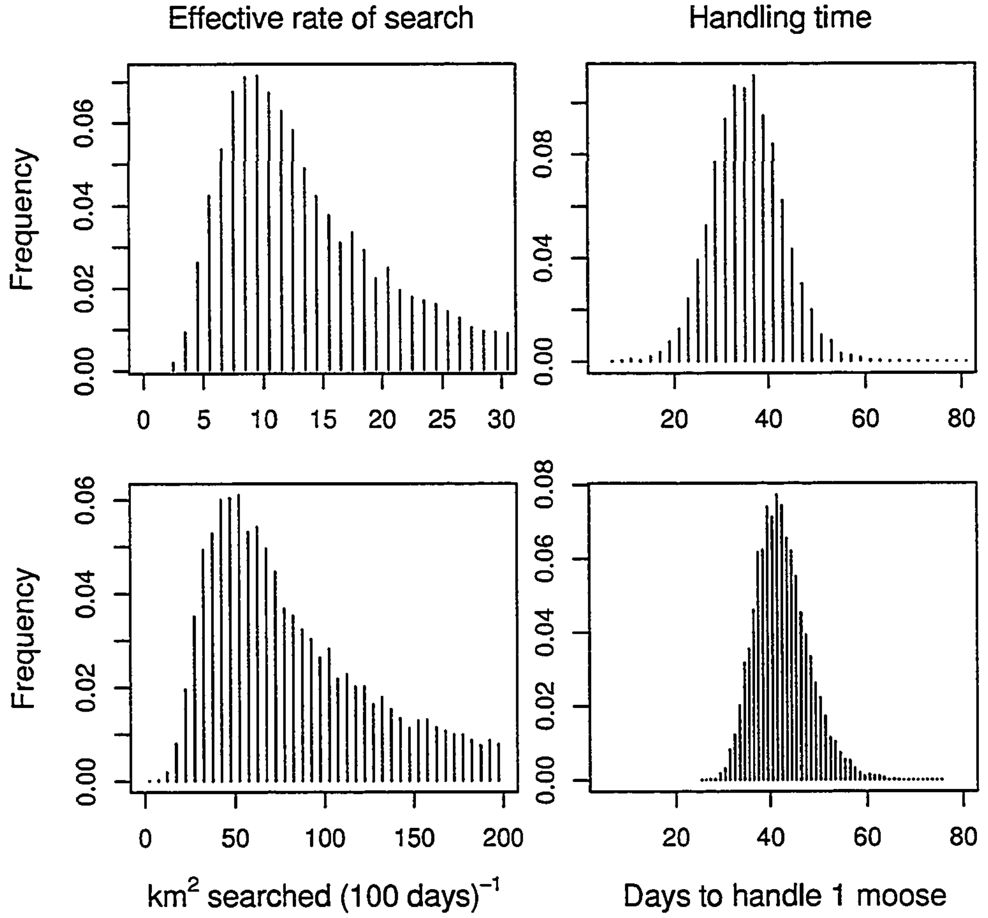


Figure 2.1: The top row shows the posterior estimates of effective rate of search and handling time for a Type 2 functional response. The bottom row shows the same for a Type 3 functional response.

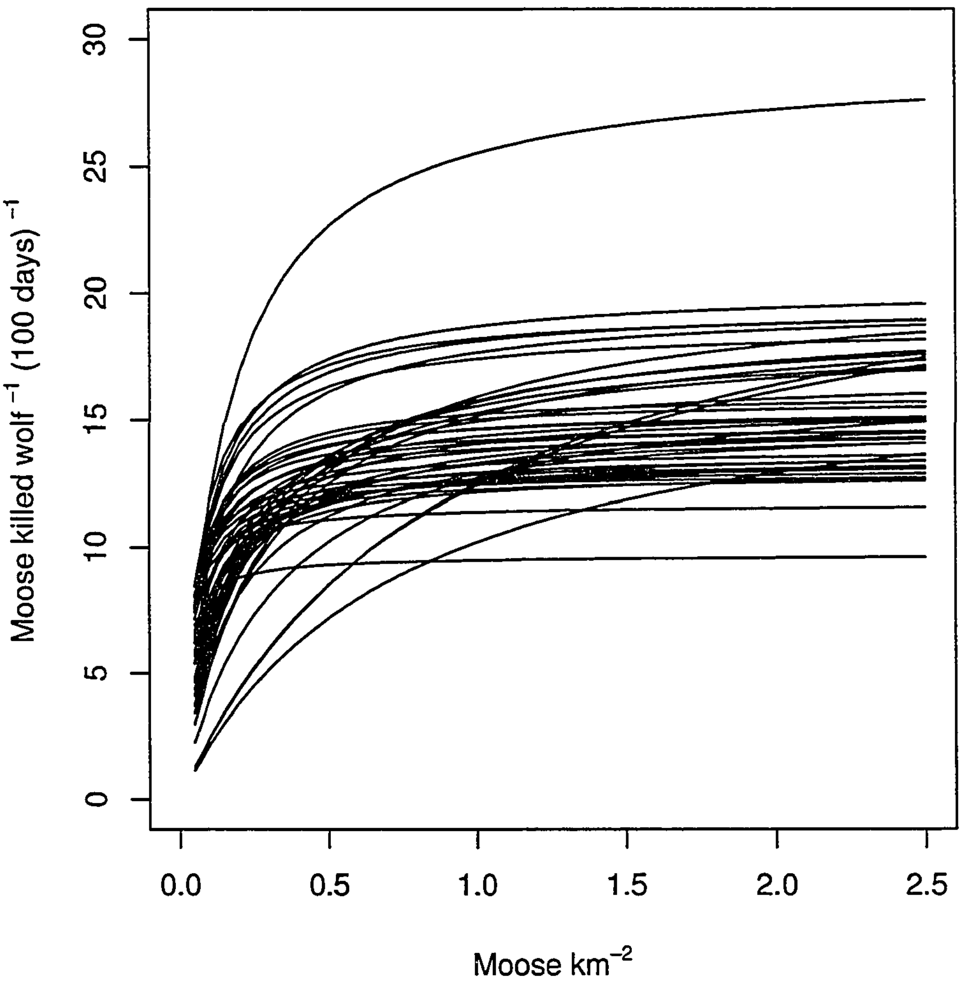


Figure 2.2: Functional response evaluated at 100 random draws from joint posterior estimate of effective rate of search and handling time

Dale et al. (1994) also found a Type 2 functional response for wolves preying on barren ground caribou, but found a much steeper functional response curve, indicating that kill rates are higher on caribou than on moose. The study proposed that a caribou/wolf system had a Type 2 functional response and a type 1 numerical response based on Fuller (1989)'s predator:prey ratios. Predicted predation rates in Dale et al. (1994) are consistent with observations but Messier (1995) warns that because of the potential for caribou to be the more desirable prey at low moose densities, the inversely density dependent predation rate would be exacerbated if alternate prey also became scarce. This case seems to indicate that there is the potential for caribou populations to be driven to extinction if densities are allowed to drop too low, a conclusion supported by Seip (1992a) in a system of similar predator and prey composition. Messier (1995) contends that a caribou/moose/wolf system would likely result in caribou as the primary prey because their vulnerability (i.e. high probability of being successfully killed) make them the optimal choice. However, Hayes et al. (2000) found it not to be the case in a system in the Yukon where caribou and moose were both abundant. Moose were available year-round and were the preferred prey. This suggests that availability, selectivity and vulnerability all play a role in diet selection. It could occur in large caribou herds (Dale et al. 1994) where caribou outnumber moose but woodland caribou exist at low densities to avoid predation (Bergerud 1992) or separate themselves spatially (Bergerud and Page 1987; Seip 1991). Despite being less vulnerable, moose are still considered to be the primary prey because of their relative abundance (Bergerud and Elliot 1986; Seip 1992a; Bergerud and Elliott 1998; Edmonds 1998). Bergerud and Elliot (1986) show how rising moose populations expanded into caribou ranges and caused increases in predation on caribou and Seip (1992a) points out that decreases in moose populations following succession of forests into older seral stages would cause wolves to switch to caribou. The danger to woodland caribou lies in the fact that wolves can continue to respond numerically to moose at low caribou densities so that caribou experience inversely density dependent predation and risk extinction (Seip 1992a; Messier 1995).

2.2.1 Case Studies

Predator control studies during the last 40-odd years have mainly focussed on the moose/wolf system, which in some cases also involves substantial caribou and bear dynamics. Table 2.2 summarises the studies in terms of species composition, densities, rates of predation and predator control. Each entry is classified under the predator-prey hypothesis that it would support, if not specifically by the author(s) then by my own conclusion.

East-central Alaska: Game Management Unit 20E

Wolves were removed for 3 years in the early 1980's to assess the role of wolves in limiting moose populations. Gasaway et al. (1992) concluded that predation mortality had an additive [1] effect at low densities. The study also concluded that the removal was insufficient to judge if wolves were the primary cause of limiting moose at low densities when grizzly bears were abundant because increases in grizzly bear predation were compensating for reduced wolf predation. Boertje et al. (1988) found that grizzly bears accounted for 52% of moose calf mortalities. Additionally, 89% of adult moose mortality caused by wolf and grizzly predation was found to be additive (Gasaway et al. 1992). Results, however, were confounded by an increase in caribou numbers that could have alleviated some of the predation on moose anyway. The final conclusion was that the combination of wolf and bear predation kept moose populations well below carrying capacity (Gasaway et al. 1992).

East-central Alaska: Game Management Unit 20A

From 1972 until 1982, public wolf kills and Alaska Department of Fish and Game (ADF&G) sponsored reductions collectively removed between 16% and 60% of the wolf population in GMU 20A. From the beginning of the control program in 1976 until the end in 1982 the wolf population was reduced from 14 to 8 wolves per 1000 km^2. During the period of control, moose populations saw increases of approximately 15% annually (Gasaway et al. 1983). Moose

---

[1] Additive mortality occurs in addition to other sources of mortality. In contrast, a compensatory mortality source merely replaces what would have occurred due to another source of mortality (Caughley and Sinclair 1994)

Table 2.2: Summary of wolf-ungulate studies in North America

Hypothesis[a]	Area	Authors	Period	Species[b]	Density[c]	Predation Rates[d]	Reduction[e]
PLH	Nelchina, AK	Van Ballenberghe 1985; Ballard et al. 1987; Bergerud and Ballard 1988; Bergerud and Ballard 1989; Van Ballenberghe 1989	1960-87	M,C,W,B	~0.3(M), ~1(C), 0.8-2.3(W), (G)	Mpkc = 44%(G), 3%(W)	W,G
	Kenai, AK	Peterson et al. 1984; Schwartz and Franzmann 1989	1976-81	M,W,B,G	11-20(W), 0.10-0.37(M)		W,B
	GMU 20A, AK	Gasaway et al. 1983	1976-82	M^p,C,W,B,G	0.2-1.5(M),0.17-1.4(C), 1.6(G)	13-34%W	61%(W)
	Northeastern AB	Fuller and Keith 1980	1975-78	M^p,C,W,G,B	0.18(M),6(W)	Mprc=73%(W)	
	Isle Royale	Van Ballenberghe 1987; Van Ballenberghe and Ballard 1994	1959-86	M,W			
	Pukaskwa, ON	Bergerud et al. 1983	1976-79	M^p,C,W,B	0.2-0.4(M),0.1(C),7-15(W)		
	Wells Gray, BC	Seip 1992b	1984-88	M,C,W,B			W
	Gates of the Arctic	Dale et al. 1994; Dale et al. 1995	1989-90	M,C,W,B	0.06-2.34(C)		
PRH	GMU 20E, AK	Boertje et al. 1988; Gasaway et al. 1992	1981-86	M^p,C,W,G	~0.15(M),1.2-1.6(G)	Mprc=52%(G), 12-15%(W), Mpra=89%(G+W)	28-58%(W),8%(G)
	Denali, AK	Mech et al. 1995; Van Ballenberghe 1987	1974-82	M,C^p,W,G	~4(G)		W,B
	Finlayson, YK	Hayes and Harestad 2000b	1990-96	M,C^p,W,G	0.26-0.44(M)	10-15%(W,M)	49-85%(W)
	Northern BC	Bergerud and Elliot 1986	1980-87	M^p,C,W,B	0.1-1.0(M), 1-10(W)		(80%)W,B
	Isle Royale	Peterson and Page 1988	1950-88	M,W	1-2.5(M), 20-92(W)		
PPH	Denali, AK	Haber 1977; Walters et al. 1981	1950-75	M,C,W,G	0.1-0.26(M), 0.1-0.4(C)		W
	Isle Royale	Messier 1991	1950-88	M,W	~1(M), 20(W)		
	Quèbec	Messier and Crete 1984b; Messier 1991	1980-84	M,W,B	0.17-0.4(M),3.6-13.8(W)	Mprc=6.1-19.3%(W)	W
SLC	Isle Royale, MG	Peterson et al. 1984; Mech et al. 1987; Messier 1991	1950-88	W,M	~1-3(M),20-90(W)		
	Puskaskwa, ON	Thompson and Peterson 1988	1976-79	M,C,W,B	~0.33(M),13(W)		

[a] PLH = Predator Limitation Hypothesis, PRH = Predator Regulation Hypothesis, PPH = Predator-Pit Hypothesis, SLC = Stable Limit Cycle hypothesis

[b] W = wolves, C = caribou, M = moose, B = black bears, G = grizzly bears

[c] density(spp.), density(spp.),... Prey in animals/km^2, wolves in animals per 1000 km^2, bears in animals per 100 km^2

[d] Mpkc(W) = moose proportion killed of calves by wolves Cpka(G) = adult caribou killed by grizzlies

[e] W = wolf reduction, B = black bear reduction, G = grizzly reduction

[p] primary prey

population growth continued for 12 years after the termination of the wolf control program but slowed to an average of 5%. Caribou populations increased by 16% annually during reduction and by 6% afterwards (Orians et al. 1997).

Within 3 years of terminating the wolf control program, and despite a continued 25% public harvest, wolf populations returned to near pre-control levels. Several winters of heavy snowfall (89-90, 90-91 and 92-93) may have hastened the decrease of caribou populations, which declined at an average annual rate of 22%. Subsequent ground-based wolf reductions of 62% and 56% in 1993 and 1994 failed to recover caribou beyond a brief increase in 1993-94 (Orians et al. 1997).

Gasaway et al. (1983) found that moose and caribou populations were limited by predation and experienced periodic fluctuations from the combined effects of predation, harvesting and over-browsing, which were considered additive. The study concluded that ungulate populations can have difficulty escaping low densities when human harvest is excessive. Gasaway et al. (1983) was criticized by Haber (1987), who points out that moose population estimates between 1953 and 1978 are derived entirely from the 1978 estimate by assuming a 7% increase from 1977 and extrapolation back to the early 1960's with an index of abundance. He claims that more likely the moose population fluctuated around the 6000-8000 in the 1960s and declined to 2000-4000 by 1975 following heavy harvest in the early 1970s. He also adds that bear predation should be considered compensatory because delayed bear predation following wolf reduction would only occur once bears learn of reduced risk of harassment from wolves. This being the case, the benefits of wolf control would be lost after the time lag of bear responding to lack of wolf harassment. If calf mortality is a major driver of declines, this compensation may not be evident due to the fact that bear predation occurs during calving when wolves are likely tied to den sites, in which case only calves near dens would be at risk.

There appears to be ample evidence that wolves limit moose recruitment and survival but Gasaway et al. (1983) do not conclusively demonstrate that harvest was not a more significant factor. If Haber (1987) is correct in assuming a far lower population in the 60's, the proportion harvested would be quite high at an average of 5% in the 60's vs. 1-3% in the Gasaway et al. (1983) estimate. In actual fact, greater than 17000 moose represents densities in excess of $1/\text{km}^2$, a density rarely exceeded by moose populations with natural predators. Additionally, Haber (1987) cites late 1960's and early 1970's ADF&G reports that put numbers in the 6-8000 range. It seems more likely that the 1960's and early 1970's populations were lower than (Gasaway et al. 1983) estimated and that harvest played a more important role in the decline of moose populations.

Nelchina, Alaska: Game Management Unit 13

Government sponsored wolf reductions from 1948-1953 reduced wolves to a total of 12 animals. Caribou then started an increase which lasted quite a few years after wolf reductions ended but wolves were still considered by some to be instrumental in the decline (Bergerud and Ballard 1988). Van Ballenberghe (1985) proposed that the herd was increasing before the wolf reduction took place in the 50's and that reduction was unnecessary. Bergerud and Ballard (1988) proposed that wolf control in the 1950's triggered the eruption of the caribou population. The study attributes the collapse of the herd in the mid 1960's to three consecutive deep snow years compounded with recruitment loss to wolf predation. With 350-450 wolves at that time, the contention was that wolf control in the early 1960's could have prevented the decline.

The two studies fail to agree on the effect of alternate prey. Van Ballenberghe (1985) contends that the presence of moose reduces predation of wolves on caribou whereas Bergerud and Ballard (1988) support the notion that alternate prey facilitate predation on caribou by supporting wolf populations at low caribou densities. The two studies agree that overharvest seriously impacted caribou, particularly since it occurred during and following the bad winters of 1964, 1965 and 1966. By the early 1970's, caribou populations had declined due to overharvesting, and possibly predation. The central questions are: 1) Did wolves cause the decline in the early 1960s? and 2) Why did predation not limit recovery in the 1970s? Both questions are confounded by bad estimates of predator, primary prey and alternate prey populations. It is suggested that wolves can only cause a decline in caribou if they are numerous enough and that in the early 70's there is no indication of an inverse relationship between wolf numbers and recruitment (Van Ballenberghe 1985). However, Bergerud and Ballard (1989) counter with the argument that Van Ballenberghe (1985) reduced wolf numbers in his analysis for those years. Van Ballenberghe (1989) also uses the same reduced wolf numbers in the argument that the ungulate biomass index per wolf was high enough that wolves would not have experienced a decline.

I believe that overharvest of caribou in the 60's and early 70's brought about the decline of the herd because harvest was density invariant while caribou were declining and thus had an increasing impact on the population. I also think that bear predation needs to be considered in the analysis of the Nelchina herd. Predation on moose calves by bears, for instance, was found to account for 44% of mortality (Miller and Ballard 1992). Poisoning in the late 40's likely reduced bears whereas later aerial reductions targeted only wolves. The rapid increase in the 50's was likely due to the fact that both wolves and bears were at very low densities. Caribou population increase in the early 70's was not as rapid, owing possibly to the fact that only wolves were reduced at this time.

As Van Ballenberghe and Ballard (1994) point out, the combination of having multiple predators and human influence on prey and predator populations can cause a system to mimic multiple stable states, cycles or recurrent fluctuations (the PPH, SLCH and PLH hypotheses from 2.2). Since predation rates are the result of both functional and numerical responses (Messier 1994; Messier 1995), alternate prey can support predators at low primary prey density and primary predator reductions can be compensated by secondary predation. In the context of predicted outcomes at various prey and predator densities (see Boutin (1992)), we would need to observe numerical responses of alternate prey and secondary predators in response to experimental removals as well.

Gates of the Arctic, Northern Alaska

Killing rates were monitored during three 30-day periods in 1989-90. The study was aimed at detecting regions of wolf-induced stability on a caribou population in a multi-species predator-prey system. Killing rates were measured across caribou densities of 0.06 to 2.34/km^2 (Dale et al. 1994; Dale et al. 1995). Predation rates on these densities rapidly decreased with increasing prey density. The study used relationships from Fuller (1989) to get an assumed numerical response of predators to ungulate prey biomass and modelled the total response and predation rates on that basis. The hypothesis of a Type 3 sigmoidal functional response was rejected because it did not fit empirical observations as well as the Type 2. The study concluded that any switching to alternate prey was not evident in the functional response of caribou. The conclusion was that the presence of alternate prey could cause the per capita predation rate to increase at low densities because the numerical response of predators would not be solely dependent on the primary prey. This is compounded with the presumption that bears, at low densities exhibit either a density independent predation rate (Boertje et al. 1988) or an inversely density dependent predation rate (Ballard et al. 1987). The only process that has the potential to compensate for this increased predation at low densities is that wolf packs become less likely to split into high-efficiency pairs at low wolf densities (Fuller 1989).

I agree with the conclusions of Dale et al. (1994) and Dale et al. (1995) that data indicate anti-regulatory predation by wolves. However, I do not believe the numerical response of wolves need be linear as assumed from Fuller (1989). Messier (1995) shows many types of predator numerical responses that could act with a Type 2 functional response to exhibit the predation rates observed.

Northern British Columbia

In an effort to recover caribou populations thought to be declining, wolves were culled in several treatment areas in Muskwa and Kechika areas of Horseranch, British Columbia and caribou recruitment was compared to that seen in untreated areas (Spatsizi and Level-Kawdy), which had 9-10 wolves per 1000 km^2. Between 1979 and 1982, untreated areas declined by 13% and 12% respectively. In contrast, Muskwa and Kechika caribou populations saw increases of 6% per year at reduced wolf densities of around 1-4 per 1000 km^2 (Bergerud and Elliot 1986). During the 10 years of wolf removals, all prey species in treatment areas saw increases in abundance via increased juvenile survival.

This case provides little evidence to support any biological hypotheses of regulation, merely that wolves are a source of mortality. It does, however, provide evidence to link recruitment rates to wolf density. Results suggest that above 6 wolves per 1000 km^2, caribou recruitment is insufficient to balance natural death rates. Conversely, moose populations are capable of sustaining their numbers at greater than 8 wolves per 1000 km^2 (Messier 1985). Muskwa and Kechika had relatively high moose densities at 1.0 and 0.7/km^2 (Bergerud 1990). This alone is capable of sustaining wolf densities seen prior to control. As such, it is not surprising that wolves recovered quickly after reduction.

Had this study been more carefully planned, results may have been more meaningful. During removal years, untreated areas adjacent to treated areas saw increases in calf:cow ratios. This was explained by immigration into wolf control areas from wolves in untreated areas. This would have reduced wolf predation in untreated areas, making it difficult to measure the true effect of wolf reductions. This study would have benefited from measurement of kill rates of wolves on each prey species.

Isle Royale, Michigan

The moose/wolf system on the island of Isle Royale in Lake Superior, Michigan is of particular interest because it is a closed, single predator system. Moose population dynamics were first studied in the late 60's and early 70's (Peterson 1977). At that time the contention was that vegetation ultimately regulated moose populations. Detailed wolf-pack dynamics were reported and many moose kills (~100) were observed. Nutritional stress was thought to be the primary cause of reduced adult survival, though possibly also a catalyst to increased vulnerability to predation.

Peterson (1977), Mech et al. (1987) and Peterson and Page (1988) all considered the moose population to be regulated by a combination of moose density, forage and weather, with wolf predation being a secondary influence. Peterson and Page (1988), however, believed the effects of food, weather and density caused moose populations to be cyclic in relation to wolves. After observing the recovery of moose and the decline of wolves it was proposed that moose/wolf systems systems can cycle with a period of ~40-years (Peterson et al. 1984). Mech et al. (1987) and McRoberts et al. (1995) maintained that snow depths were significant enough to have cumulative effects on the physical condition of moose, predisposing them to predation. This opinion was countered by Bergerud et al. (1983), who found no correlation between snow and adult survival, but instead concluded that wolf predation significantly limited moose calf survival. Messier (1991) concluded that food competition and wolf predation explained 80% of the variation in moose abundance and that competition for food was a regulatory process. This was countered by McRoberts et al. (1995), who felt that Messier (1991)'s analysis removed variation in moose population data by smoothing Mech et al. (1987)'s data, and that a three-year cumulative snow effect was evident in offspring.

Isle Royale represents one of the few systems where high densities of moose have been observed ($\sim 1.5/\text{km}^2$). It is also one of the longest studied predator-prey system and so it is the only area with data spanning a long enough time period to discuss the possibility of periodic behaviour. Peterson and Page (1988) studied the dynamics of territoriality and pack splitting in wolves. They demonstrated that the availability of food per pack is correlated to moose mortality in winter (r^2=0.65). Territoriality appears to have emergent properties with respect to predation rates. Territory formation could occur fast enough that expansion and contraction of territories in response to wolf densities could lead to time-lagged reductions in moose densities. The cyclic behaviour seen in Peterson et al. (1984) could be generated by such a mechanism. They suggest that increased kill rates can trigger a decline of moose and a dwindling food supply for wolves that can be modelled with delay-differential equations of 7 to 10 years. This is explained by the fact that decreased prey base at high wolf densities motivate packs to split so as to increase per pack rate of food intake. They still maintain that predation plays a secondary role to moose/forage interactions and that ultimately, historical moose declines resulted from reduced browse in maturing post-fire stands.

Wells Grey, Southeastern BC

During the period 1984-1989, approximately 20 adult female caribou were collared and monitored in Quesnel Lake and Wells Gray Park. During that time, moose were also collared in each area and wolves were reduced in Quesnel Lake. Calf:cow ratios and adult survival were analysed in relation to wolf abundance throughout the wolf reduction period. The study also analysed habitat relationships of moose and caribou in summer and winter.

In Quesnel Lake, caribou recruitment was 7% when wolves were present versus 14.7% when wolves were absent (Seip 1992a). The combined recruitment was 9.9%. Calf:cow ratios dropped significantly between August and October in wolf controlled areas and that this was attributed to movement of new wolves after reductions. In Wells Gray, recruitment was 17.7% and survival rates were higher as well.

Radiotelemetry of caribou and moose indicated that caribou in Wells Gray used high elevations and were separated from wolves and moose, particularly in summer. This contrasted with observations in Quesnel Lake, where moose and wolves occupied similar elevations more often. The same pattern was evident across habitat types. Caribou, once again, could be seen to overlap less with wolves in Wells Gray than in Quesnel Lake. In all cases, the ability of caribou to separate from wolves appears to be more pronounced in winter. Seip (1992a) speculates that wolves could be sustained by moose as caribou numbers decline, possibly leading to extirpation of caribou. Seip (1990) recommends keeping wolf numbers low by maintaining low numbers of moose, thereby preventing predation on caribou.

Finlayson, Yukon

From 1982 to 1990, 2000-2500 wolves were removed from the 23000 km^2 area in southwestern Yukon. During reduction years, caribou recruitment approximately doubled that of pre-treatment census and adjacent untreated areas also experienced improved recruitment. Moose densities roughly doubled over the course of the reductions as well. Subsequent monitoring of wolf recovery and predation rates provide good information on possible density dependent effects of wolf recovery and predation (Orians et al. 1997).

In a detailed monitoring study of wolf recovery, Hayes and Harestad (2000a) found that the rate of recovery of wolves was negatively correlated to pack size, mean number of packs and wolf density, but that it was also strongly related to dispersal rate. This makes sense since the dispersal rate should be related to pack size and lead to more packs. At least for the short term, and similar to what was observed on Isle Royale (Peterson and Page 1988), wolf density should increase in response to an abundance of moose.

Hayes and Harestad (2000a) conclude that social behaviour of wolves determines the numerical response to increased prey resources via dispersal. Killing rates of moose were analysed to assess the potential for regulation at low equilibrium (Hayes and Harestad 2000b). Results indicate that the functional response is stronger at lower densities than previously accepted. Data were added to the comprehensive analysis of Messier (1994), resulting in a predicted low equilibrium between 0.07 and 0.12 moose/km^2. The Type 2 functional response fit the data best. Hayes et al. (2000) concluded that the functional response was independent of moose density but only considered this over a narrow range (0.26-0.44). Additionally, the study concluded that killing rates were related to number of packs and that there was no evidence for switching to caribou when caribou became more abundant.

Hayes et al. (2000), Hayes and Harestad (2000a) and Hayes and Harestad (2000b) ignore an important consideration. In the fashion that Messier (1994) analysed predation rate by combining the effects of the numerical response with the functional response, Hayes et al. (2000) should have considered dynamically the results of the number of packs on the functional response to get the total response and subsequently the predation rate. Demonstrating this in relation to moose density would provide a stronger argument about the regulatory nature of wolf predation.

2.3 Discussion

A large body of research exists on wolf-ungulate systems. The major conclusions seem to be as follows:

1. Wolf predation can be density dependent across some ranges of prey densities.
2. One prey can support predator populations when another prey is at low densities. This can lead to local extinction of the low density prey unless encounter rates are extremely low.
3. Wolf control can bring about a reversal in the decline of ungulates but wolves will recover quickly unless wolves are reduced drastically and across a large area.
4. Human harvest and extreme weather can cause serious declines in ungulate populations.
5. Ungulate recruitment can be improved three fold with a sufficient wolf removal barring new wolf colonization and providing that bears don't prey in lieu of wolves.
6. Wolf social structure may be responsible for periodic trends in a single prey system.
7. When moose densities are high, large number of wolves can cause caribou recruitment to drop below replacement levels.

The conventional views are that ungulates and their predators will either exhibit stable populations, periodic fluctuations due to random disturbances, or cyclic behaviour. The conditions for each of these situations involve specific assumptions about predation, food limitation and both environmental and demographic stochasticity. Most case studies report trends that suggest one dynamic or another, but in general are confounded by human induced impacts that render system dynamics undistinguishable. In many cases, studies were not conducted over sufficient areas or for long enough periods of time. Additionally, when predator were removed, the removal of a single predator may have lead to compensatory predation by another predator species.

A philosophy that persists mainly due to its convenient agreement with management paradigms, is that populations are ultimately in balance with nature. Populations fluctuations are expected but no increase or decrease is expected to persist without encountering a regulatory mechanism. Even if these mechanisms are intrinsic in nature, some populations may no longer live in environments where the behaviour that leads to these mechanisms is favoured. A persistent divide between theoreticians and empiricists is that models predict behaviour that is not observed in nature. We do not see as many extinctions as models predict nor do we see as many examples of cyclic patterns.

Many models predict cyclic behaviour in ungulate and wolf populations, a phenomenon that appears feasible given theoretical (May 1972; Kendall et al. 1999) and historical evidence (Peterson et al. 1984). Even models that predict stable populations can become unstable with slight changes to key parameters. The classic Rosenzweig-MacArthur model (Rosenzweig 1971) can be forced from a stable system to an unstable one by increasing the prey carrying capacity or the effective rate of search of predator (Gilpin 1972; Abrams and Walters 1996). If populations cycle, management questions should then consider the time scale of cycles and reflect whether or not conditions causing cycles are human induced or not. Interesting management implications arise from such considerations, since human impacts have the potential to alter aspects of the system that may affect these parameters.

The Hudson's Bay Company records show an apparent cycle of 25-40 years in the combined number of elk and deer pelts and the combined number of wolf and coyote pelts sold to the company by trappers. Figure 2.3 shows these cycles. Unfortunately, the dataset confounds more than one type of animal into a single index of abundance. To view the dynamics of such a system in modern-day exploited environments suggests that we should at least employ mechanistic models that are capable of reproducing these patterns, and to look at the ramifications of environmental changes on the fundamental behaviour of the system.

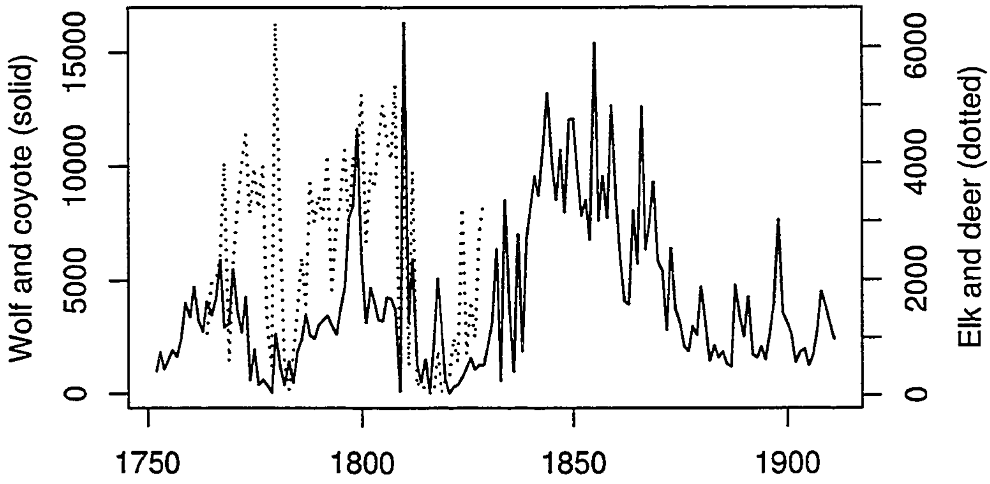


Figure 2.3: Periodic trends in fur bearing mammals of North America. Figure shows the number of wolf, coyote, deer and elk pelts received by the Hudson's Bay Company for 150 years. (Turchin 2002)

There are a limited number of mechanisms that facilitate the persistence of caribou in the presence of a wolf populations sustained by moose. Because caribou are more susceptible to attack than moose, encounter rates with predators must be low, owing to some mechanism that limits access to caribou or reduces predator interest in searching for caribou. Given the assumptions that caribou are less likely to survive a wolf attack than moose, that they do not reproduce as fast as moose, and that predation is defined by a type II functional response (Messier 1994; Dale et al. 1994), caribou populations should decline or even go extinct (Seip 1992b; Dale et al. 1994; Bergerud and Elliott 1998). The logic is simple. Wolves sustain themselves on an abundant and rapidly replenishing moose population. The caribou, which are comparatively easy to kill, but less frequently encountered, experience increasing predation mortality as the number of wolves increases. Even if wolf populations stabilize, there is the potential that incidental predation on caribou is sufficient to cause a sustained decline leading to extinction. Similar cases have been recorded where the consumer has been supported by a primary resource and caused a decline or extirpation of a secondary resource. Blue whale and fin whale populations in Antarctica could have avoided reaching near extinction levels had not fishing fleets continued to sweep the oceans in search of other baleen whales (Walters and Martell 2004). Similarly, bluefin tuna reached catastrophically low densities when fleets continued to catch bluefin while targeting yellowfin tuna (Walters and Martell 2004). Finally, introduced European foxes that depend upon European rabbits have driven many marsupials to extinction in Australia (Sinclair 2003).

Another factor that contributes to the decline of caribou populations is the fact that natural disturbances and industrial activities create precisely the type of habitat alteration that favours moose production, reduces caribou food supply, and increases interactions with wolves (Bergerud and Elliott 1998; Dyer 1999; Smith et al. 2000). Forest activity creates large openings that supply young seral forests for moose to browse once deciduous seedlings and shrubs establish. The increased food supply for moose leads to colonisation and improves overwinter moose survival. Moose populations increase and wolf populations increase with them. This results in an increase in predation pressure on caribou because of a higher encounter rate.

The life history of caribou suggests that an effective strategy is to avoid predators as much as possible during calving (Bergerud et al. 1984; Bergerud and Page 1987), and to exist at low densities so as not to be sufficiently abundant to support a large enough wolf population to cause their decline strategy does not work when moose colonize caribou ranges, causing wolf populations to increase independently of caribou densities. Caribou are hypothesized to spatially separate themselves from predators to avoid predation (the *Spatial separation hypothesis*). This often appears to be a direct avoidance of alternate prey (the *Alternate prey hypothesis*). Either way, caribou use spatial refuges to distance themselves from predation risks. For instance James et al. (2004) showed that caribou predation rates by wolves were higher in cells that were also occupied by moose.

Given that caribou populations have been declining in the presence of elevated moose and wolf population throughout British Columbia and Alberta (Bergerud and Elliot 1986; Bergerud and Elliott 1998), this thesis is aimed at detailing the underlying spatial and temporal causes for mechanisms of the caribou/moose/wolf system and the cause of the decline. I will do this by fitting models to empirical data and performing a model selection. I will also propose management options that potentially reverse declines.

The analysis in this thesis will focus on one caribou herd for which a 10-year time series of relative abundances is available for caribou, moose and wolves. The brevity of the time series is a cause of concern but there is little option if we are to gain any insight into the future of this herd, and indeed into any caribou system involving elevated moose and wolf populations. I will construct models that explain the dynamics in different ways and compare how they each fit empirical trends. I will also look at the predicted long term dynamics of the models and compare these to broad scale patterns that have been observed in other systems. In an effort to capture the dynamics of the RPC herd, I have had to consider some trade-offs between building models that describe broad scale trends and models that are sensitive to local ecology and empirical data. On the one hand, we must try to understand what is going on with caribou herds in west-central Alberta, subject to local environmental changes that undermine the dynamics, but on the other hand, we are also interested in broad scale patterns of which the RPC system is a subset.

Chapter 3

Population trends of the Redrock Prairie-Creek caribou herd in west-central Alberta

Introduction

This chapter is a reconstruction of the population trends of the key species inhabiting the winter range of a woodland caribou (*Rangifer tarandus caribou*) herd. I characterize the population dynamics as a foundation for exploring management implication in later chapters. The Redrock Prairie-Creek (RPC) herd in west-central Alberta was studied to infer local dynamics that are significant to larger scale patterns. I build a series of non-spatial models, each capable of describing the trends observed, but each capturing a different mechanism of interest to ecology, management or both. I assume that parameters implicitly capture average demographic and behavioural rates that predominated during the period of time for which the data exist. I also assume that fine-scale spatial behaviour and environmental processes are encapsulated in these parameters. The models describe several ways that caribou, moose (*Alces alces*) and wolves (*Canis lupus*) interact. The models were selected to reflect competing hypotheses about how predation and habitat factors influence population dynamics.

Although it is difficult to evaluate which model better describes system dynamics, it is possible to examine the behaviour of each model and discuss the management implications given its assumptions. I fit models to empirical trends in the RPC and assume statistical *stationarity* in parameters. Each model targets a particular process that may explain something of the observed trend and/or say something distinctly different about the qualitative behaviour of a system with two prey types (caribou and moose) and one predator (wolves). I explicitly model only what I consider to be the most essential components of the system: wolves because they are known to be significant predators in winter, moose because their numbers are considered to be so closely associated with wolves, and caribou, the species of interest. Predation by bears is assumed to occur in the summer range and be reflected primarily in the net birth rates of caribou and moose.

A broad scale analysis of the dynamics of the RPC system has not been attempted to date. Trends in abundances, recruitment, migration and survival have been documented (Edmonds 1988; Edmonds 1998; Brown and Hobson 1998; Dzus 2001), and the general view is that caribou populations in the RPC range declined in the early 80's and have been relatively stable since then. Surveys indicate that moose and wolf populations have been on the rise since 1989 (see trends and empirical model fitting in section 3.4).

I use the results of previous monitoring to build a quantitative and qualitative view of the population dynamics of the RPC caribou system. I examine the possibility that the dynamics of the RPC range have undergone (or may be presently undergoing) a shift in equilibrium densities *or* a transformation from a system with equilibrium population densities to a system that cycles with some period. Such a transition has a theoretical foundation that is pertinent to the RPC caribou system.

In recent years, logging and energy sector activities have altered the landscape in precisely the way that gives rise to limit cycles in predator and prey systems (e.g, increased carrying capacity of prey (Rosenzweig 1971; Gilpin 1972; Abrams and Walters 1996)). Dynamics in the wake of these activities may be quite different than before they came into effect. Even if we assume that caribou evolved to co-exist with predators and historical habitat conditions, we must recognize that both of these elements have changed: there are more predators and alternate prey and there has been an unprecedented amount of habitat alteration in recent years due to resource extraction activities. With apparent increases in moose populations, and a conversion of forest habitat from old to young, we must question the possibility that a transformation has occurred in population dynamics as it pertains to caribou.

3.1 Study area

The 2158 km^2 Redrock/Prairie Creek caribou winter range is in west-central Alberta (54°E, 119°W), on the eastern slopes of the Rocky Mountains north of Jasper National Park and south of Grande Prairie (see Figure 3.1). It is an upper foothills landscape with areas affected by timber harvest, oil and gas exploration and coal mining (Szkorupa 2001). Surveys from the area indicate large abundances of moose and small localised populations of elk (*Cervus americanus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos americanus*). Predator species include wolves (*Canis lupus*), black bears (*Ursos americanus*), grizzly bears (*Ursus arctos*), coyotes (*Canis latrans*) and cougars (*Felis concolor*). The RPC herd was estimated at approximately 300 animals (Brown and Hobson 1998). Wolf densities were most recently estimated at 0.011 wolves/km^2 (Kuzyk 2002), which is above the 0.0065 wolves/km^2 thought to be the threshold below which caribou populations are capable of persisting (Bergerud and Elliot 1986).

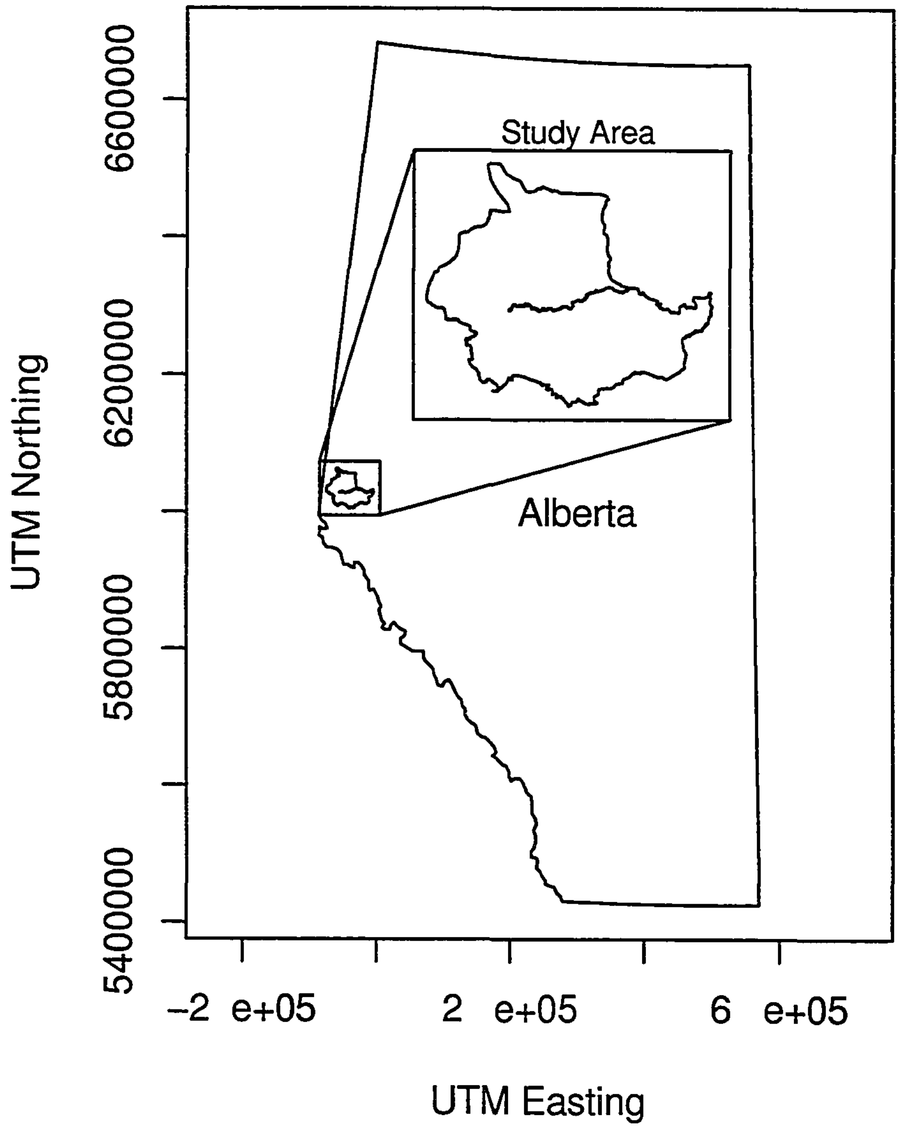


Figure 3.1: Map of Redrock Prairie Creek caribou winter range in west-central Alberta.

3.2 Data

A variety of data sources are used, each having different spatial and temporal resolution. Indices of abundance come from aerial snow track surveys flown from 1989 to 1998 (Rohner et al. 2000). The surveys were intended to capture the relative abundances of major predator and prey species in the RPC caribou winter range. The first survey of each year occurred in December and the second occurred between mid January and mid February. The flight paths were generally consistent between surveys. Slight differences do not present a problem since the index of abundance used is tracks per 10 km of transect flown. Tracks were identified to species from the air and later ground truthed. Species identification is considered to be 95% accurate. Tracks were spatially referenced to 2×2 km grids.

A second aerial survey of the RPC range is available from 1983 to 1996, but the amount of time spent surveying and the observability were not recorded, making it impossible to use animal counts to estimate abundance. Nonetheless, I use the information to provide upper and lower bounds to animal densities. I transform the number of calves-at-heel into a total population rate of recruitment for a specific reference point in modelled dynamics (i.e., just prior to the winter predation period).

I include density estimates of caribou and wolves for the year 1998. The caribou estimate was 300 animals (Brown and Hobson 1998), which I convert to a density of 0.14/km^2. Kuzyk (2002) estimated 0.011 wolves/km^2 in winter of 1998. Using 1999-2001 caribou GPS collar data (Szkorupa 2001), I calculate the number of daily caribou observations inside and outside of the winter range and concluded that caribou spend 31.8% of the year in the winter range. I assume that temporal use of summer and winter ranges would be well represented across a selection of animals regardless of which year it was recorded.

Moose surveys were conducted by Alberta Fish & Wildlife division in areas within and surrounding the RPC winter range. The wildlife management units (WMUs) directly in the RPC range include WMUs 442, 445, 446, 355 and 356. The majority of the RPC winter range is covered by WMU 355, but the bulk of the survey data available are from unit 356, which covers a northern strip of the range. Given the absence of density estimates available for the other units, I assume the densities for unit 356 are representative of the RPC winter range. These density estimates were 0.46 moose/km^2 in 1993 and 0.57/km^2 in 1996. Recruitment was obtained from the same surveys (0.34 and 0.29 per adult respectively). An analysis of these data included estimates of annual survival rates for each WMU and and a pooled survival rate (Anonymous 1998). With information on dates of death of collared animals, Alberta Fish & Wildlife scientists calculated a daily mortality rate and subsequently an annual mortality rate. A similar procedure is repeated in this analysis for caribou (see Section 3.3.2). The pooled moose natural mortality rate is calculated to be 0.14/year, which I accept for the purpose of this analysis.

3.3 Methods

This section describes how models were constructed and how the empirical data were used to test the models. Some parameters are estimated from time series data and others were inferred from collar data and then assumed fixed for the purpose of estimating the other parameters. The RPC data consist of a short time series of abundance trends and a sparse recruitment trend for one species. At the onset of this thesis, it was assumed that it would be difficult to estimate wolf behavioural parameters without wolf recruitment data or kill rate information. Similarly, since there are no abundance estimates or harvest data for moose, we must expect a lot of uncertainty in the estimates. Nonetheless, it is possible to use empirical information and published values to bound some parameters and reduce the number of estimated parameters.

3.3.1 Alternative models

The following are brief descriptions of the models used to infer the dynamics of the RPC system. Models reflect issues of ecological or management interest as well as data availability.

Model 1 Wolves prey on ungulate calves and adults with distinct effective rates of search for each prey species and age class. I choose to add age structure because there is sufficient information available about the relative vulnerability to predation at different age classes (Haber 1977). Wolves encounter prey in proportion to spatial and temporal distribution but there is no prey switching (i.e., Type 2 functional response). I choose to put density dependence directly on recruitment because there is strong evidence for it at high densities (Skogland 1985).

Model 2 Same as Model 1 but search rate on caribou declines with decreasing densities of caribou (i.e., a Type 3 functional response on caribou).

Model 3 Same as Model 1 but search rate on caribou declines when moose densities are higher. The hypothesis is that wolves will search for caribou more often when there are less moose available. This is of management interest because there is concern that reductions of moose may lead to an increase in predation rates on caribou. The structure of this model lends itself to evaluation with controlled experiments and monitoring.

Model 4 A portion of the prey population is invulnerable to predators at any given time (Abrams and Walters 1996). Instantaneous rate parameters represent movements into and out of vulnerable and invulnerable states.

This implicitly captures spatial foraging behaviour without explicit spatial modelling. The use of vulnerable and invulnerable states can allow caribou to persist in the presence of elevated wolf populations if movement rates effectively reduce predation exposure. Density dependence is modelled through the instantaneous rate of increase. No age structure is modelled.

The generic formulas for Models 1, 2 and 3 are given below. A description of symbols can be found in Table 3.1.

$$\frac{dN_i}{dt} = J_i - F_i - m_i N_i - \delta_i N_i \tag{3.1}$$

$$\frac{dW}{dt} = \varepsilon W \left(F_1 + F_2\right) - m_w W \tag{3.2}$$

$$\tag{3.3}$$

where

$$J_i = r_i N_i \left(1 - \frac{N_i}{K_i}\right) \tag{3.4}$$

$$F_i = \frac{a_{ij} J_i^f \omega_{ij} + a_{ia} \left(N_i(1-\delta_i)\right)^f \omega_{ia}}{D} \tag{3.5}$$

$$D = 1 + \sum_{i=1,2} \left[a_{ij} h_{ij} J_i^f + a_{ia} h_{ia} \left(N_i(1-\delta_i)\right)^f\right] + a_{1a} h_{1a} \eta \tag{3.6}$$

where $f = 1$ for a Type 2 functional response, and 2 for Type 3 (always Type 2 for moose). I partitioned a_{ik} (i is *sp.*, $k = j$ for juvenile and a is adult) into search, encounter and kill success. Assuming that wolf travel is independent of prey type, the rate of encounter and the rate of successful attack determine the maximum capture rate for a prey class:

$$a_{ik} = \lambda_{ik} \xi_i a_i^*, \quad k = j, a \tag{3.7}$$

Here λ_{ik} is the kill success rate, ξ_i is the encounter rate scaling factor and a_i^* is the search rate of wolves on species i. The search rate reflects travel

Table 3.1: Parameters and symbols used in predator-prey models.

Parameter	Symbol
Adult caribou density	N_1
Juvenile caribou density	J_1
Adult moose density	N_2
Juvenile moose density	J_2
Wolf density	W
Other prey biomass	η
Caribou intrinsic growth rate	r_1
Caribou carrying capacity	K_1
Adult caribou mortality	m_1
Caribou harvest rate	δ_1
Effective rate of search on adult caribou	a_{1a}
Effective rate of search on caribou calves	a_{1j}
Moose intrinsic growth rate	r_2
Moose carrying capacity	K_2
Adult moose mortality	m_2
Moose harvest rate	δ_2
Effective rate of search on adult moose	a_{2a}
Effective rate of search on moose calves	a_{2j}
Attack success probability	λ_{ik}
Encounter probability	e_{ik}
Conversion efficiency	ε
Wolf mortality rate	m_w
Handling time for one adult caribou	$h = 2$ days
Handling time for ungulates	$h_{ik} = \omega_{ik}h$
Relative weight calf:adult caribou	ω_{1j}
Relative weight caribou	$\omega_{1a} = 1$
Relative weight juvenile moose:caribou	ω_{2j}
Relative weight adult moose:caribou	ω_{2a}
Probability of dying in the day following x	$q_{x,t}$
Probability of surviving until x+t given alive at x	$p_{x,t}$

speed of wolves and the detection radius of a particular prey type. I assume that the effective rate of search on a species is scaled by the kill success and the encounter rate.

I calculate the spatial correlation of wolves and ungulates using Equation 3.8. Caribou are not found in the same areas with wolves as often as are moose (see Figure 3.2), providing the impetus to model the encounter rate explicitly. Hereafter, I assume that there exists a parameter ξ_i that describes an encounter rate that is related to $C_{x,y}$, where x and y represent coordinates on a two dimensional grid.

$$C_{x,y} = \sum_i \sum_j \frac{(X_{i,j} - \mu_x)(Y_{i,j} - \mu_y)}{\sigma_x \sigma_y} \tag{3.8}$$

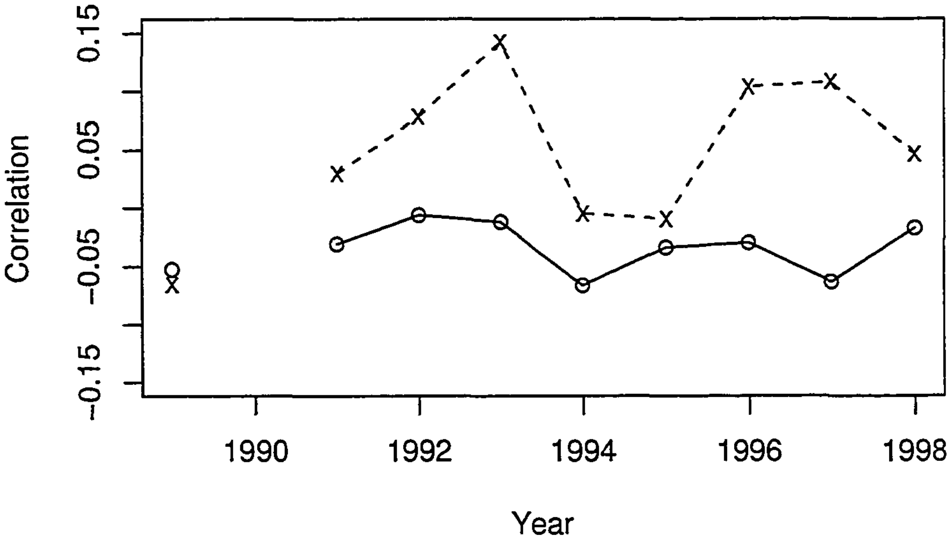


Figure 3.2: Plot of spatial correlation between snow tracks of caribou, moose and wolves. Solid line shows the wolf-caribou correlation. Dashed line shows the wolf-moose correlation. No correlation between wolves and ungulates is shown in 1990 because no wolf tracks were observed in that year.

I assume that the handling time for a single caribou is 2 days and the handling times for other prey classes is proportional to their relative weights ω_{ik}. I do not assume that wolves encounter ungulates in equal proportion to their

Table 3.2: Encounter rate scaling factors for Models 1, 2 and 3

Model	Encounter rate
1	ξ
2	ξN for caribou, 1 for moose
3	$\xi(1 - M/\varphi_M)$

Table 3.3: Attack success probability of wolves on each prey class

Stage	Caribou	Moose
Calf	0.65	0.25
Adult	0.45	0.05

densities. I assume that there are behavioural reasons that explain differences in how prey are *effectively* accessible, spatially and temporally, to predation by wolves. $\xi_{ik} = t_{ik}p_{ik}$ implies that prey are not equally distributed, with t_{ik} being the proportion of time prey spent within the searched area and p_{ik} being the proportion of the predators territory occupied by prey. I can make use of these distinctions to estimate fewer parameters by scaling the search rate a^* with prey class specific spatial and temporal components. Given some knowledge about λ_{ik}, and assuming that ξ_i is roughly the same for adults and juveniles, I can estimate a_i^*. Essentially, this involves using the temporal overlap information to scale the search rate between species, and the kill success rate to further scale adults relative to juveniles. Table 3.3 shows ungulate kill success rates derived from observed ungulate kills from two wolf packs in Denali, Alaska recorded by (Haber 1977). Carrying capacities are $K_1 = 3$ for caribou and $K_2 = 2$ for moose. The caribou value is reduced to 3 from 5 found in (Skogland 1985) because that figure pertained to domesticated reindeer that receive supplemental feeding. The moose value comes from (Crete 1989).

I use data from a wolf recovery study in the Yukon (Hayes and Harestad 2000a) to estimate the value of ε by minimizing the objective function in Equation 3.9. The study documented wolf recovery trends as well as kill rates and densities of moose. ε thus represents the recruitment of wolves purely in response to moose biomass consumed. To account for recruitment in response to unrecorded biomass, I add another parameter η, which represents a density of unknown biomass in the wolves diet. I assume that it is effectively searched and handled with the same rates as caribou. It is accounted for in wolf energetics and time budget each year.

$$SS = \left(\frac{W_{t+1}}{W_t} - e^{\varepsilon F - m_w}\right)^2 \tag{3.9}$$

I calculated $m_w = \log(1 - s_w)$ where s_w are annual survival rates from collared wolves. Yearly kill rates were estimated by multiplying 100-day rates by 3.65. The estimated value of ε is 0.08967 in moose units, which converts to 0.036 in caribou units (assuming 2.5 caribou = 1 moose by weight).

Table 3.4: Wolf conversion efficiency parameters

Parameter	Symbol
Wolf densities in year t	W_t
Estimated kills/predator/year	F
Mortality rate	m_w

Given these, I have only to estimate two a_i^*'s instead of four a_{ik}^*'s. A single search rate cannot apply to both species because the total area searched by predators must incorporate both distance travelled and detection radius or prey. Since we know nothing about the relative detection radii of caribou and moose, I assume that area searched is relative to individual detection radii. I also assume that ξ_i is proportional to a spatial overlap *and* a detection radius, meaning that empirical data can be used to scale the ξ_i further so that the only remaining variation comes from the detection radius.

Model 4 assumes a structure of *foraging arenas* (Abrams and Walters 1996; Walters et al. 1997) where prey biomass is effectively divided into two states:

vulnerable and invulnerable. This has numerous behavioural interpretations, but any avoidance, encounter rate or refuge can be thought to contribute to the parameters that determine predator access to prey: the mixing, or exchange rate parameters ν_{in} and ν_{out}. Invulnerable prey can move into the vulnerable state with a rate ν_{in}. They can also move out of a vulnerable state with rate ν_{out}. We assume that this behaviour occurs on a much faster time scale than population dynamics and predation, and reaches an equilibrium vulnerable pool of prey V (see Walters et al. (1997) for a discussion of variable-speed-splitting). The functional response thus pertains to V instead of N since predators only see that quantity. In the case of ungulate-wolf behaviour, this refuging behaviour is reflected by prey detection and predator avoidance (and evasion) occurring over very short time scales.

$$F = \frac{aVW}{1 + ahV} \tag{3.10}$$

where

$$V = \frac{\nu_{in} N}{\nu_{in} + \nu_{out} + \frac{aW}{1+ahV}} \tag{3.11}$$

is the equilibrium vulnerable biomass that comes from solving Equation (3.12) when $dV/dt = 0$ (i.e., V reaches its equilibrium).

$$\frac{dV}{dt} = \nu_{in}(N - V) - \nu_{out} V - \frac{aVW}{1 + ahV} \tag{3.12}$$

The equivalent two-prey system is as follows:

$$F_i = \frac{a_i V_i W}{1 + a_1 h_1 V_1 + a_2 h_2 V_2} \tag{3.13}$$

where

$$V_i = \frac{\nu_{i,in} N_i}{\nu_{i,in} + \nu_{i,out} + \frac{aW}{1+a_1 h_1 V_1 + a_2 h_2 V_2}} \tag{3.14}$$

Substituting the vulnerable biomass into a two species model with a single age class gives:

$$\frac{dN_i}{dt} = r_i N_i (1 - \frac{N_i}{K_i}) - \frac{a_i V_i W}{1 + a_1 h_1 V_1 + a_2 h_2 V_2} - m_i N_i \tag{3.15}$$

$$\frac{dW}{dt} = \varepsilon W \frac{\omega_1 a_1 V_1 + \omega_2 a_2 V_2}{1 + a_1 h_1 V_1 + a_2 h_2 V_2} - mW \tag{3.16}$$

For convenience, I set ν_{in}=10 and divide the top and bottom of equation 3.14 by ν_{in}. This allows estimation of only a single parameter, ν_{out}. It turns out that ν_{in} need only be sufficiently large such that picking a wide range of values of ν_{out} causes the vulnerable biomass to range from 0 to the total prey density. Figure 3.3 shows the relationship between the exchange rate out of the foraging arena and the effective vulnerable biomass when Equation 3.12 is solved iteratively.

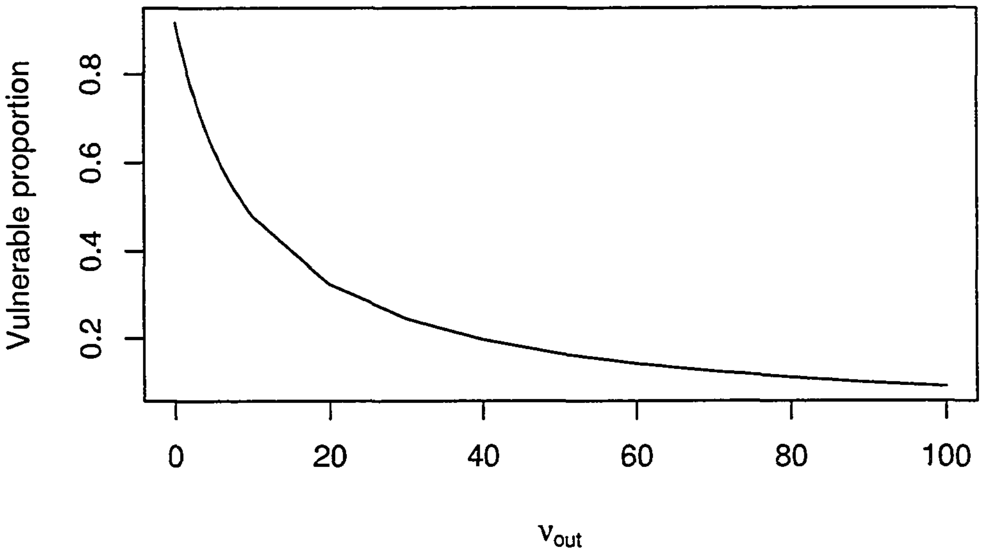


Figure 3.3: The reduction in the amount of vulnerable biomass as the parameter ν_{out} increases shows the decline in the amount of vulnerable biomass as behaviour forces a greater proportion into an invulnerable state. Shown for case where ν_{in}=10, a=1, h=1, N=1, W=1.

3.3.2 Parameter estimation

Parameters are estimated in two stages. Some come from fitting sub-models and others from fitting dynamic models. The parameters estimated from fitting sub-models are then used in the dynamic fitting. A survival model (see Section below on survival modelling) is used to estimate caribou mortality rate from natural (non-predatory) causes. This survival rate is then assumed in Models 1 to 4, which are then used to predict abundance trends and estimate the other dynamic parameters. At this stage, other parameters are also assumed from various literature sources, such as the conversion efficiency ε (see Equation 3.9) and attack success rates from Haber (1977). The list of assumed parameter values is shown in Table 3.5. Dynamic model predictions are compared to empirical abundance trends and a statistical fitting procedure was used to estimate the remainder of the parameters that provided to best fit. The logic of this process is shown in Figure 3.4.

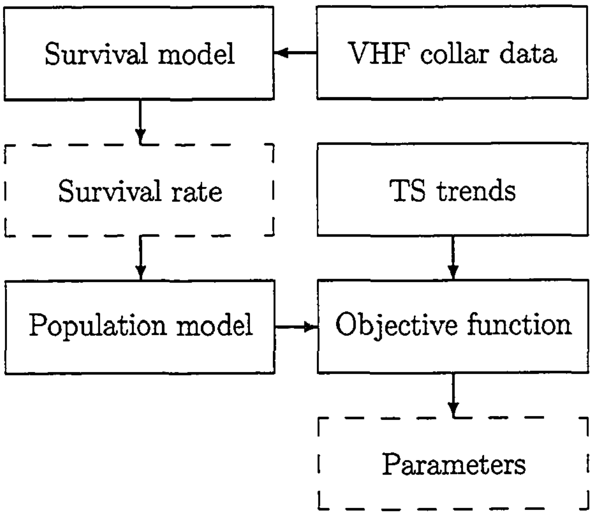


Figure 3.4: Logical flow of analysis and simulation methods.

Table 3.5: Parameter values assumed during estimation procedures (see also Table 3.3). This shows parameter values that were taken from literature sources or assumed by analyzing literature data.

Parameter	Value used	Reference
δ_1	0	This study
K_1	3	Reduced from 5 in Skogland (1985)
K_2	2	Crete (1989)
m_1	0.089	Estimated from VHF data in this study.
m_2	0.14	Anonymous (1998)
m_w	0.4925	Kuzyk (2002)
h	2 days	Dale et al. (1994)
ω_{11}	0.5	This study
ω_{12}	1	–
ω_{22}	2.5	This study
ω_{21}	1	This study
$\nu_{1,in}$	10	This study
$\nu_{2,in}$	10	This study

I use relative ungulate weights from the literature, but scale to caribou units instead of deer units (Fuller 1989; Bergerud 1990). I also assume that the $\nu_{i,in}$'s are equal to 100 and I estimate the value of $\nu'_{i,out}$'s between 0.1 and 10000. This allows the vulnerable biomass to reach near zero values as well as approaching maxima near N_i.

Adult caribou survival model

If available records include the time since death, I use that figure to calculate the date of death, otherwise I assume deaths occurred half way between last confirmed day alive and the date the death was recorded. The probability of each individual surviving t days is $p_{x,t} = p^t$ where x is the reference date of the first location for VHF collared caribou i. The probability of an animal dying is $p_{x,t-1}$ times $1 - p_{x+t-1,1}$, which reduces to $p^{t-1}(1-p)$.

$$p_{x,t} = e^{-mt/365} \tag{3.17}$$

is the probability of surviving from x to $x+t$, where m is the instantaneous mortality rate applied over an entire year and

$$q_{x,t} = 1 - e^{-mt/365} \tag{3.18}$$

is the probability of dying in the interval $(x, x+t)$.

3.3.3 Dynamic models

I fit models to empirical data, such that likelihood functions are maximized so that the probability of observing the data is highest compared to any other parameter choice. VHF relocations of adult caribou from 1988-2001 provide records of know periods of survival as well as mortalities and are used to estimate the natural mortality rate of caribou. I estimate the instantaneous mortality rate that would maximize the likelihood of observing the data. Where mortality was due to predation, I include only the information up to the date of the last observation prior to death. The mortality rate estimate therefore reflects sources known not to be predation.

The likelihood of the data given δ is:

$$L(Y|m) = \prod_i p_{x_i^*,t-1}\,(1-p)\;p_{x_i} \tag{3.19}$$

where x_i^* are the individuals that died and so are only alive for $t-1$ days. My objective is to maximize this probability or more conveniently, to minimize the negative log-likelihood

$$\mathbf{L} = -\sum_i \log\left(p_{x_i^*,t-1}\right) \;-\sum_i log(1-p) \;-\sum_i \log\left(p_{x_i,t}\right) \tag{3.20}$$

Population dynamics models are fit to empirical trends using a Generalized Reduced Gradient algorithm that minimizes the negative log-likelihood of the observation error model shown in Equation 3.21:

$$Y_i = qN_ie^{\beta} \quad where \quad \beta \sim N(0, \sigma_\beta) \tag{3.21}$$

$\{Y_i\}$ represent empirical quantities (snow track counts, abundance estimates, etc...). q is a scaling quantity used to describe the relationship between the actual values $\{N_i\}$ and the set of observed quantities $\{Y_i\}$. β is a gaussian random variable with mean 0 and standard deviation σ_W. Taking the log of both sides we get:

$$\log(\frac{Y_i}{N_i}) = \log(q) + \beta \tag{3.22}$$

Setting $Z_i = \log(Y_i/N_i)$ and using the MLE $\hat{q}' = \widehat{log(q)} = \frac{1}{n}\sum_i^n {Z_i}^2$ minimises the following negative log-likelihood function:

$$L = \frac{(n-1)}{2} \log \sum_i^n (Z_i - \hat{q}')^2 \tag{3.23}$$

This generic likelihood kernel will self-weight to the reciprocal of the variance of the observation process (Walters and Ludwig 1994).

For all models, I use the error structure in Equation 3.21 to explain the observation of relative abundance indices. I assume that the scaling parameter q describes the *observability*, which can take on any value in the interval $[0, y_i/u_i)$, where y_i is the maximum number of tracks observed per 10 km of transect and u_i is the upper range of densities for species i. This parameter scales prey density to the number of tracks observed per 10 km of transect flown. The likelihoods of caribou, moose and wolf track observations are each treated the same way and can be summed to a single likelihood. When observing calf-at-heel rates, predation rates and diet composition, I assume that $q = 1$, which means that there is no scaling because they are ratios, but that there is still log-normal error in the observation. This assumes that calves and female adults are equally *observable*. In those cases, the likelihoods become:

$$L = \frac{n}{2} \log \sum_i^n {Z_i}^2 \tag{3.24}$$

These likelihoods are also summed and added to the likelihood of the snowtrack observations. This total likelihood objective function across all data sources

$$L = \sum_{j}^{n} L_j \tag{3.25}$$

is minimized to find the set of parameters Θ_i that provide the best fit to time series data. This predicts the best fit of the model to *all* the data *simultaneously.*

To minimize Equation 3.25, I code Equations 3.1 - 3.6 in C^{++} and use a non-linear optimization algorithm to minimize (3.25). The equations are integrated using the Adams-Bashforth numerical integrator $X_t = X_{t-\Delta t} + \frac{\Delta t}{2}[3\frac{dX_{t-\Delta t}}{dt} - 2\frac{dX_{t-2\Delta t}}{dt}]$, where X_t represents the state variable being integrated (i.e. either one of the N_i or W). At each time step $\Delta t = 0.05$, the values $\frac{dN_i}{dt}$ and $\frac{dW}{dt}$ are calculated and $N_1(t)$, $N_2(t)$ and $W(t)$ were calculated. The individual likelihoods are evaluated using 3.21 and 3.23 for the snowtrack data and 3.24 for comparison with abundance estimates. Minimization of the likelihood yields the maximum likelihood estimates, which are then used to project trends 100 years into the future.

3.3.4 Uncertainty

By assuming an observation error model, I can use the likelihood to perform Markov Chain Monte Carlo simulations (MCMC's) using the Metropolis Hastings algorithm (Gelman et al. 1995). The covariance matrix is obtained and used to build a multivariate normal distribution that acts as a random generator of candidate parameter values. The method starts with an initial candidate, draws a new one at random from the candidate generating distribution, accepts the new point as a sample if its likelihood evaluates higher than the first point, or accepts it with a probability that is the ratio of the likelihoods if the new point has a lower likelihood than the first point. Repeating these steps has the effect of selecting unlikely parameter combinations less frequently than more likely ones. The end result is that the list, or *chain*, of accepted parameters converges to a distribution that is the true probability distribution for each parameter. This Bayesian technique is widely used to estimate posterior distributions when integration over marginal posteriors is not possible (Chib and Greenberg 1995; Brooks 1998). Sampling randomly from parameter space distributes parameter values around the maximum likelihood estimates of the means with estimated variances. These samples are then used to project time series. The result is a probability distribution of predictions that describes how likely the predicted events are to occur. I sample parameters from the distribution, project trends 100 years into the future and record the elapsed time until caribou became extinct.

I simulate chains of 2,200,000 samples for each model. To display the distributions I draw every 200^{th} value from the posterior samples, after skipping the first 100,000 samples. Skipping the first 100,000 avoids including the samples that may still bear the weight of initial conditions. Skipping 200 between samples merely spreads the sample out across a longer portion of the chain.

I use a Gelman-Rubin statistic to test for convergence (Gelman and Rubin 1992). This statistic examines the the sampling distributions of the independent chains and determines whether they are converging to the same distribution relative to continuing simulation indefinitely from a single chain. I produce 3 chains of 2,000,000 samples each for this test.

3.3.5 Stability analysis

I analyse Model 1 for tendencies toward stable densities. I do this only for Model 1 because it has the most tractable assumptions. I look at how changing key parameters has a tendency to increase and decrease stable densities of each species. The assumptions made in the other models are merely modifications to the simpler assumptions of Model 1 and can be interpreted from these results. The analysis assumes that forest conditions do not change over time.

The first parameter of interest scales the wolf effective rate of search to mimic refuging behaviour and/or spatial separation by caribou (James et al. 2004). GPS collar data indicate that the RPC herd spent 31.8% of the year in the winter range overlapping wolf territories, whereas moose are present year-round. By assuming a spatial and temporal overlap scale factor of 1 for moose and varying the rate across a gradient for caribou, I can examine the relative impact of spatial and temporal separation on species equilibrium densities. Because I assume that moose are exposed to wolf predation year-round, I fix $a_{2,max}$ and assume that $a_{1,max} = \xi a_{2,max}$. For the purpose of the stability analysis, I treat variation in ξ as a change in predator avoidance behaviour. As $\xi \rightarrow 1$, caribou no longer avoid predators within wolf territories; they only differ from moose in temporal separation and attack success. When the temporal separation approaches the reciprocal of the attack success, there is no difference between the two species.

I calculate the equilibrium densities of each species using Equations 3.1 - 3.4. I calculate the equilibrium points using the equation solver in Maple© with different values of ξ and look at the eigenvalues of the equilibrium points to determine whether the points were stable. The stable equilibrium densities of caribou, moose and wolves are plotted as contours with respect to variations in the parameters r_2 and ξ (see Figures 3.14 - 3.18).

I also test for evidence of benefits to controlling moose densities. The system of equations is reduced such that moose were treated as a parameter (i.e., a fixed density). Wolves still consumed moose and responded numerically, but I assume the moose population could be held constant at a managed density. Repeating the stability analysis with wolves and caribou populations increasing naturally while maintaining moose at a constant density, I find the equilibrium points of of both caribou and wolves.

3.4 Results

The maximum likelihood estimate of the instantaneous caribou mortality from causes other than predation is 0.089 (see Figure 3.5). This is close to figures found in other systems. McLoughlin et al. (2003) found survival rates between 0.86 and 0.93 for boreal caribou in northern Alberta. Smith (2004) calculated a mean adult female survival rate of 0.873 for the RPC herd, but that estimate came from 1998-2003 data and did not remove known predation kills. An adult natural mortality rate of 0.089 is used to parameterize the population dynamics models and estimate the remaining parameters. The maximum likelihood estimates from fitting the dynamic model to empirical trends are shown in Table 3.6. I use these parameters in Equations 3.1 - 3.4 to predict long-term trends. The $a_{i,max}$ shown in Table 3.6 are the species specific search rates. The effective rates of search a_{ik} come from multiplying $a_{i,max}$ by the encounter rates and kill success rates. The adult moose effective rate of search becomes $a_{2a} \simeq 6$ when we apply the rates in Table 3.3. This is lower than the rate estimated from the Messier (1994) data, owing perhaps to differences in diet compositions.

A visual account of the quality of each model fit to empirical trends is shown in Figure 3.6, which shows the model prediction of the actual observed data (number of tracks per 10 km transect) rather than the densities that the models predict for each species. The predicted densities are shown in Figure 3.7. Long term projections of predicted dynamics are shown in Figure 3.8. All models predict roughly the same number of moose and wolves. Model 2 predicts more caribou than the other models due to model assumptions, which diminish predation on caribou at lower densities. There is insufficient

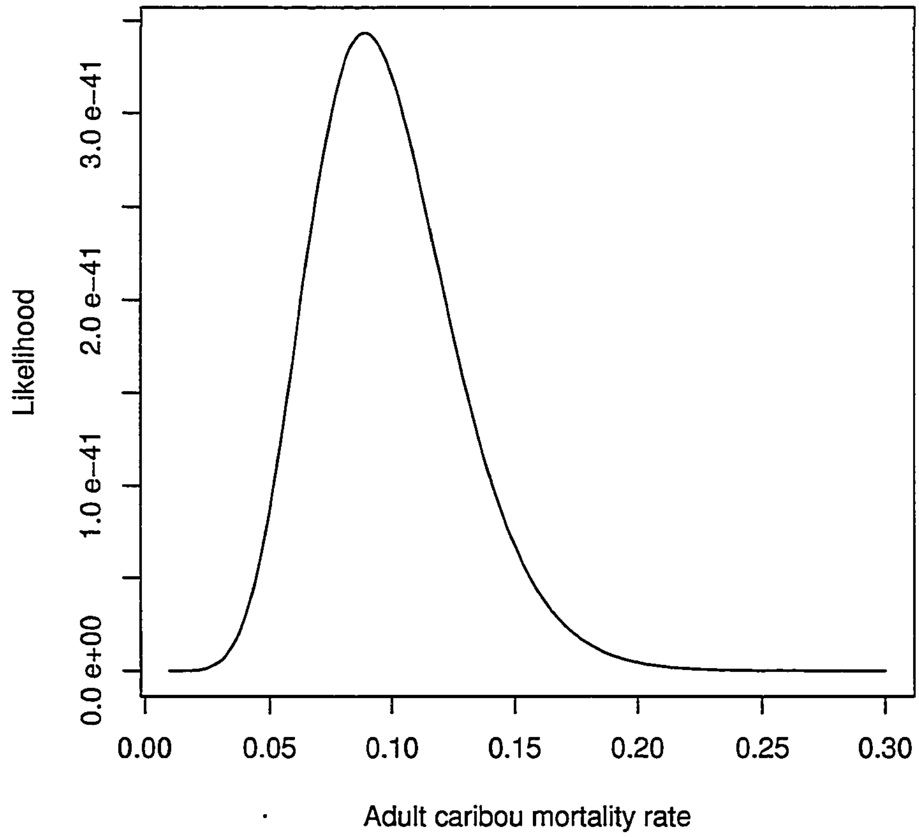


Figure 3.5: This shows the likelihood of observing the data over a range of instantaneous mortality rates.

Table 3.6: Maximum likelihood parameter estimates for Models 1-4 obtained from minimizing observation error likelihood.

Parameter	Model 1	Model 2	Model 3	Model 4
c_0	0.0952	0.0954	0.1361	0.1836
m_0	0.0756	0.0756	0.1143	0.0822
w_0	0.0035	0.0036	0.0174	0.0051
r_1	0.1588	0.1588	0.2082	0.1544
$a_{1,max}$	74.761	687.67	36.089	436.2
r_2	0.7155	0.7170	0.8838	0.6209
$a_{2,max}$	117	114	77	436
η	0.0025	0.0003	0.0835	-
δ_1	0.0462	0.0460	0.0435	0
$\nu_{1,in}$	–	–	–	10
$\nu_{1,out}$	–	–	–	227
$\nu_{2,in}$	–	–	–	10
$\nu'_{2,out}$	–	–	–	275

empirical evidence for the fitting procedure to force lower caribou densities while still satisfying empirical evidence for the moose and wolf trends. In Figure 3.8 the long-term patterns are visible. The most consistent pattern is that caribou densities decline or go locally extinct within roughly 50 years as the system becomes driven by the interactions between moose and wolves. Under present conditions, the numerical response of wolves to high moose densities increases the predation rate on caribou sufficiently for caribou to be driven to low densities or to local extinction.

3.4.1 Uncertainty

Markov Chain Monte Carlo (MCMC) simulations tested positively for convergence. A scaling factor close to 1 is obtained for all parameters, indicating that the distributions converged. Histograms of these posterior samples of the MCMC chains for each model are shown in Figures 3.9 - 3.11. The figures all show that ungulate growth rate parameters are well defined. This is because time series data that show population fluctuations inform the algorithm about what rate would be required to produce observed increases. There is also no

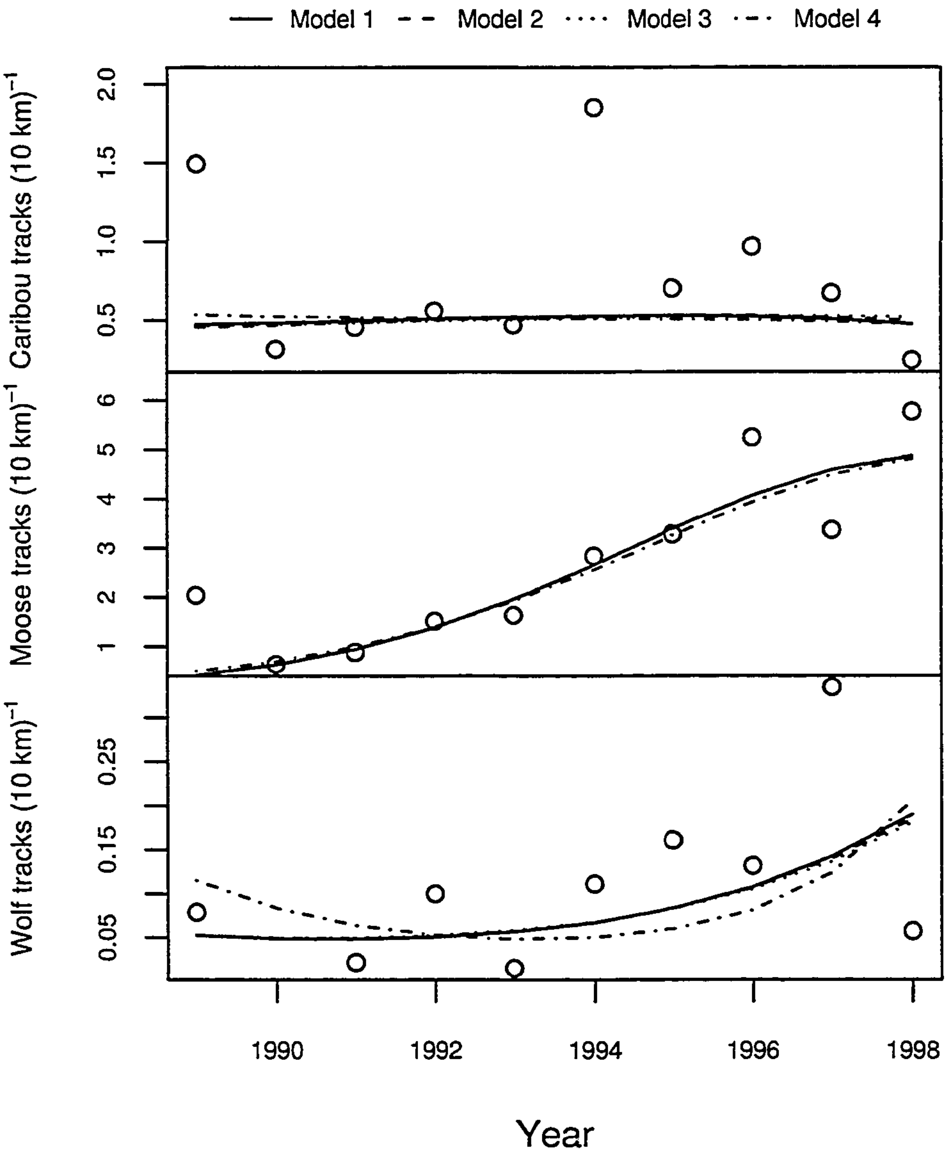


Figure 3.6: Fit of Models 1-4 to empirical snow track densities. Circles represent the number of tracks observed per 10 kilometers flown. Lines shows the predicted number of tracks for each model during the period of time that snow track densities were collected.

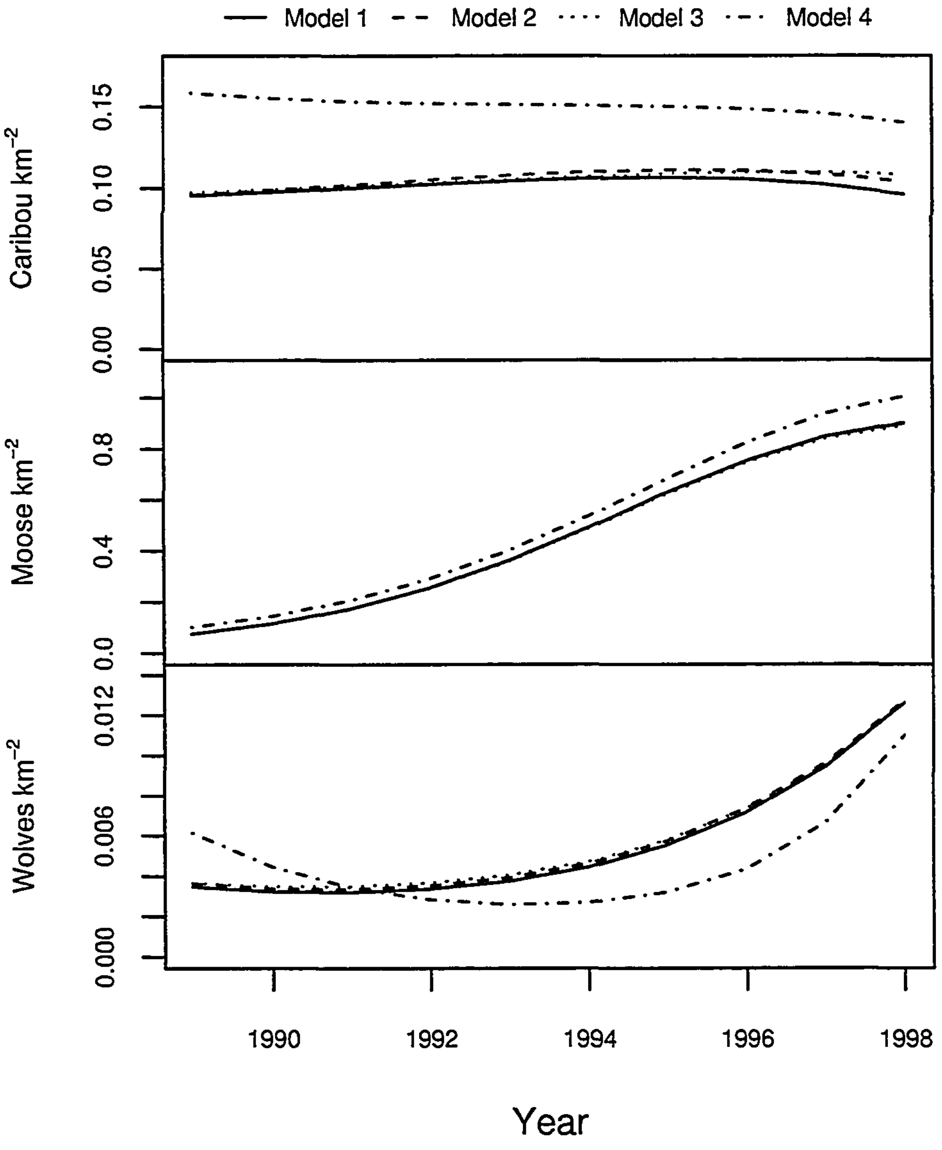


Figure 3.7: Maximum likelihood prediction of population trends using Models 1-4. Figure shows the predicted densities of each species during the 10 year period that snow track densities were collected.

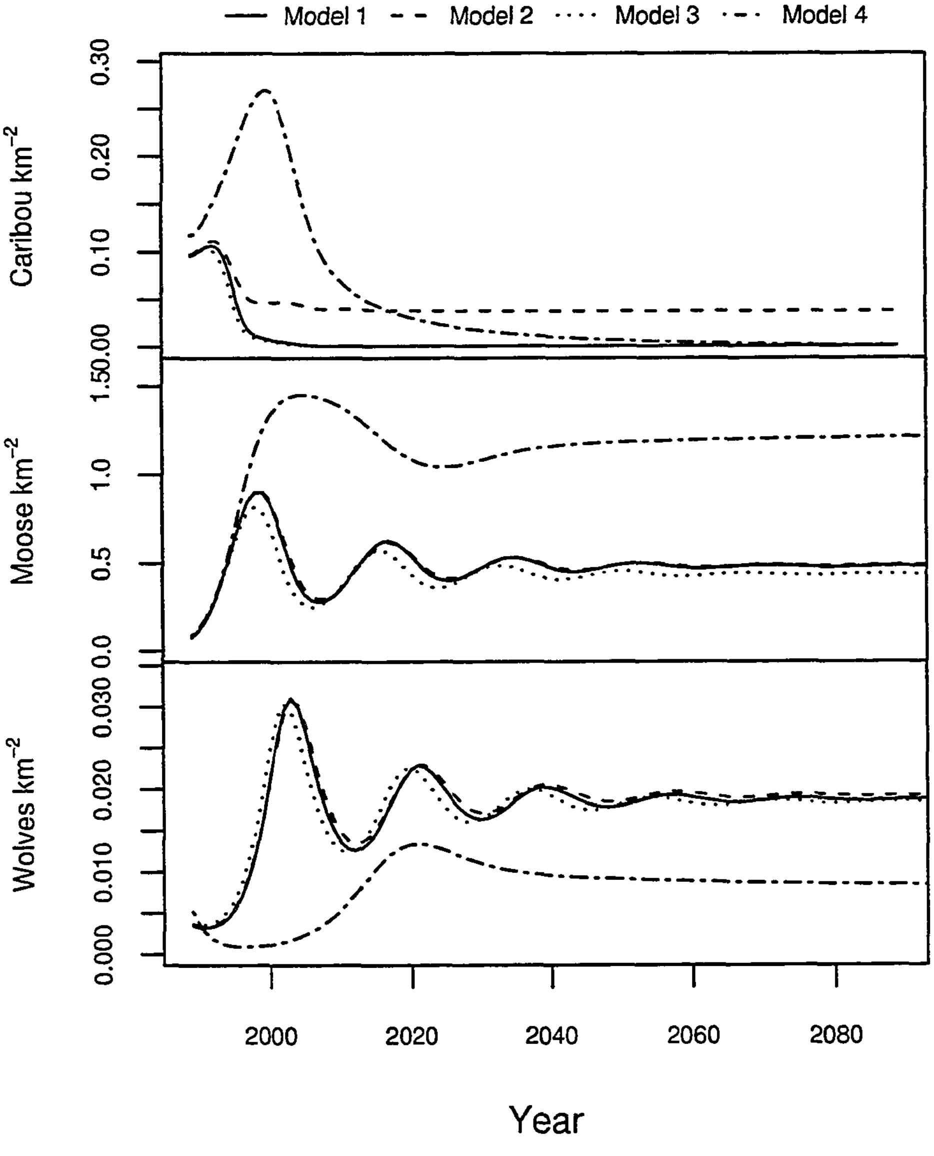


Figure 3.8: Predicted 100-year population trends using maximum likelihood parameter estimates.

confounding between these parameters and the way the models are structured. Conversely, the wolf conversion efficiency parameter ε resolves wolf population growth trends in conjunction with the capture rates a_{ij} of ungulate biomass. These two parameters are *confounded.* Nonetheless, estimates of the posterior densities of parameters are valuable in providing a sense of probable future outcomes. To predict the probability of a future event, one can draw at random a set of parameters from saved MCMC simulation values, run the model with those parameters and record the predicted trend. Repeating this process hundreds (or thousands) of times produces a sample of predicted time series that can be analysed for statistical properties. I produce such time series and analyse them to determine the extinction probability of the RPC caribou herd. Ten thousand random draws from the joint posterior densities were used to predict the year at which caribou densities declined to zero. The histograms of these predicted extinction years are shown in Figure 3.13 for Models 1 and 3. Drawing from the posterior densities of Models 2 and 4 do not predict any extinctions at all and thus the histograms are not shown.

Model 1 extinctions rates are lower than the maximum likelihood projected trends suggest. The distribution of extinction times from randomly drawn parameter values show that there is a 50% probability of extinction within $\simeq$70 years. Model 3 predicts extinction within $\simeq$50 years with 95% probability. Models 2 and 4 do not predict extinctions because empirical parameter estimates of search rates and vulnerability exchange parameters do not permit sufficient predation mortality to extirpate caribou. Random draws from the joint posterior of Model 2 produces not a single extinction. This is inherent in the model structure. Prey will escape predation at low densities when a Type 3 functional response is used. The only thing that will cause the prey population to decline is if the predation-independent productivity and mortality rates do not favour growth. $r_c \simeq 0.17$ exceeds $m_c \simeq 0.089$ however, which is insufficient to cause the population to decline.

3.4.2 Stability analysis

Figures 3.14 to 3.16 show the effect that spatial separation has on each species. Caribou decline as a result of increasing spatial overlap with wolves. Caribou densities decrease and wolf densities increase since the wolves respond numerically to increased food that is supplied by more freely available prey resources. Figure 3.14 shows caribou equilibrium densities when the spatial overlap with wolves is allowed to increase. Decreases along the productivity gradient of moose (r_M) are much more gradual than along the caribou-wolf spatial overlap gradient (ξ). If we imagine manipulating the system so as to increase stable caribou densities, we would either want to reduce r_M or reduce ξ. The figure clearly shows that small reductions in ξ result in much larger gains than corresponding reductions in r_M. This is perhaps the most telling result of all, implying that ξ strongly influences the behaviour of the system, and more so at low values of r_M. This suggests that to mitigate caribou declines, management should address factors that affect caribou-wolf encounter rates.

The surprising result is that the wolf equilibrium density peaks at approximately 20 wolves per 1000 km^2 when the spatial overlap is still quite low (approximately 0.30). Moose reach a local equilibrium density at that value. It is also the point at which the equilibrium density of caribou declines the most for each additional increase in the spatial overlap. This means that near a spatial separation value (ξ) of 0.3, caribou become accessible enough at the assumed wolf search rate that predation causes a decline. It also means that predation on caribou becomes sufficient to cause a numerical response in wolves and a subsequent decline in moose. Following the arrow in Figure 3.15, we see the decrease in moose densities, which follows the same pattern as the decrease in caribou densities in Figure 3.14. At the point corresponding to the

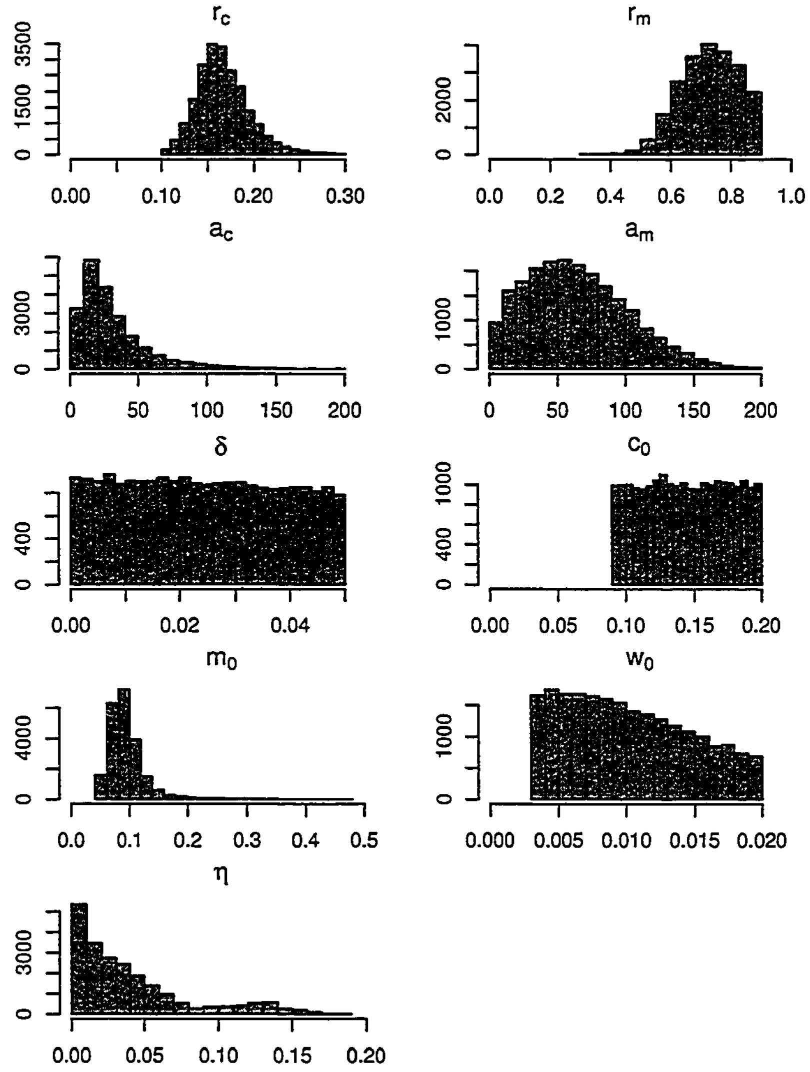


Figure 3.9: Estimated posterior densities for the parameters using Model 1. The X-axis shows the value of the estimated parameter. The Y-axis shows the relative frequency of occurrence in MCMC sample of the parameter indicated above plot. Figures show the estimated probability distributions of parameter values. Narrow distributions indicate that parameter is well defined under model assumptions and with the data available.

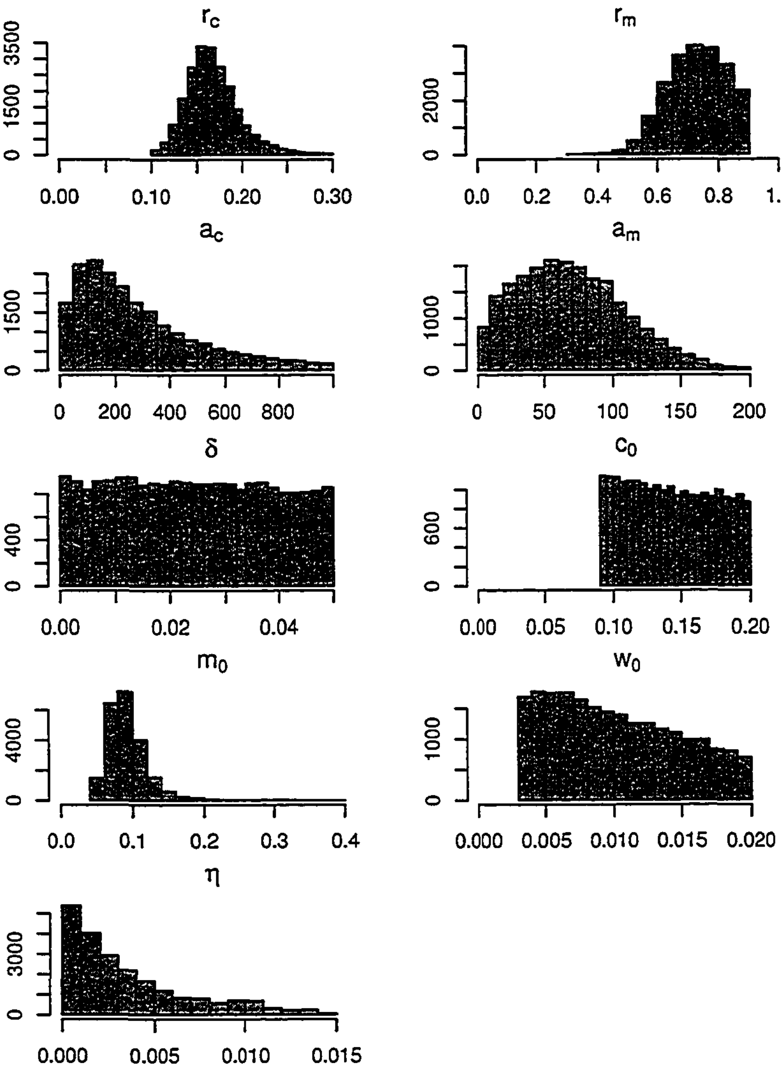


Figure 3.10: Estimated posterior densities for the parameters using Model 2. The X-axis shows the value of the estimated parameter. The Y-axis shows the relative frequency of occurrence in MCMC sample of the parameter indicated above plot. Figures show the estimated probability distributions of parameter values. Narrow distributions indicate that parameter is well defined under model assumptions and with the data available.

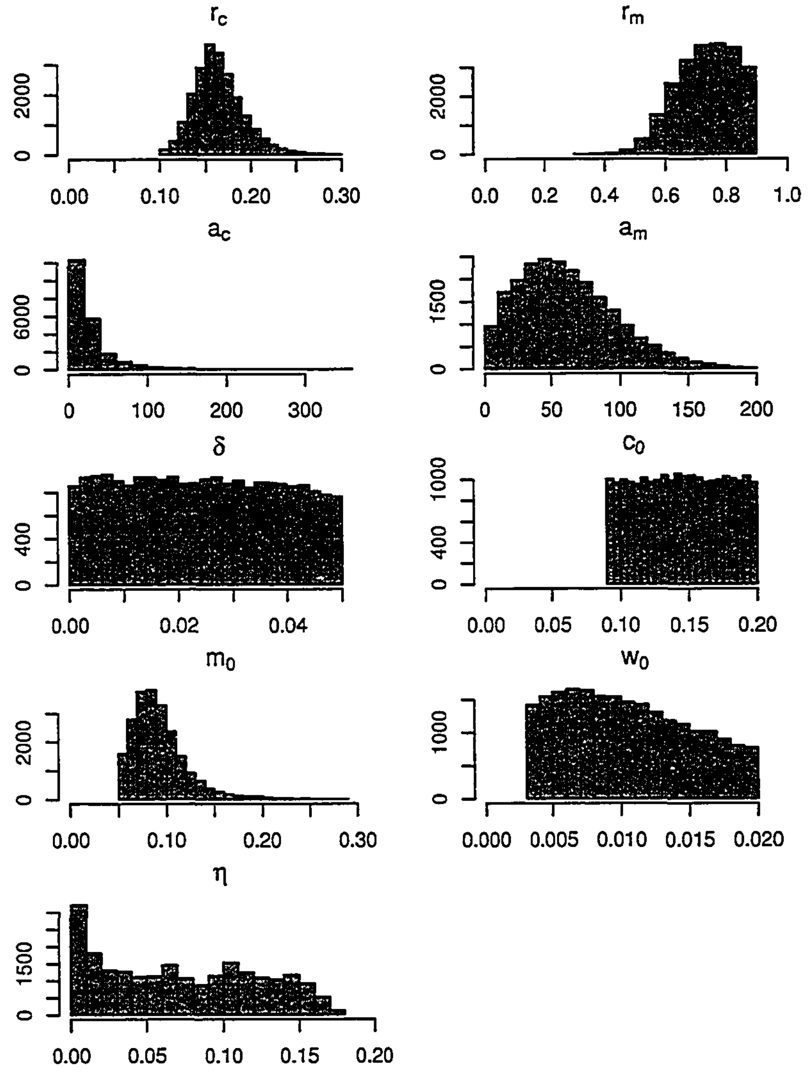


Figure 3.11: Estimated posterior densities for the parameters using Model 2. The X-axis shows the value of the estimated parameter. The Y-axis shows the relative frequency of occurrence in MCMC sample of the parameter indicated above plot. Figures show the estimated probability distributions of parameter values. Narrow distributions indicate that parameter is well defined under model assumptions and with the data available.

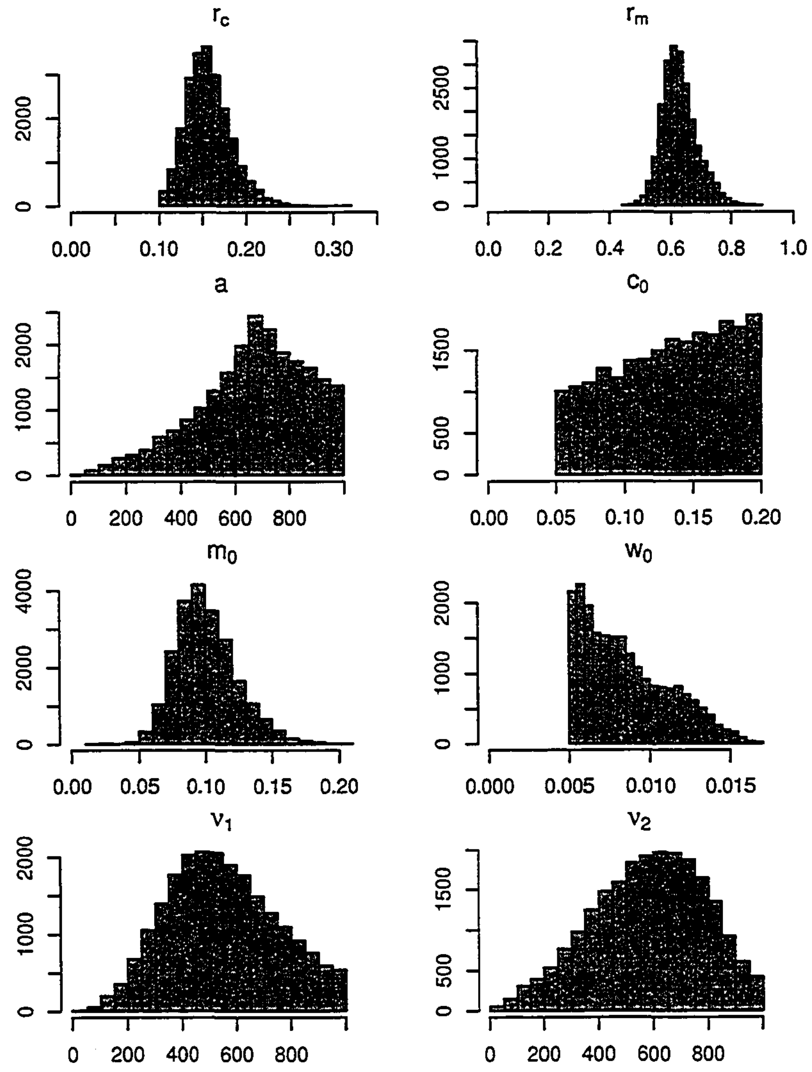
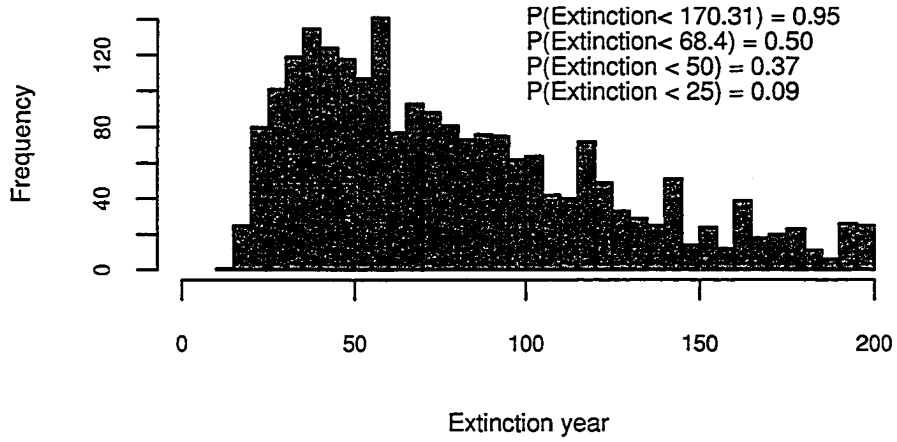


Figure 3.12: Estimated posterior densities for the parameters using Model 2. The X-axis shows the value of the estimated parameter. The Y-axis shows the relative frequency of occurrence in MCMC sample of the parameter indicated above plot. Figures show the estimated probability distributions of parameter values. Narrow distributions indicate that parameter is well defined under model assumptions and with the data available.

Model 1



Model 3

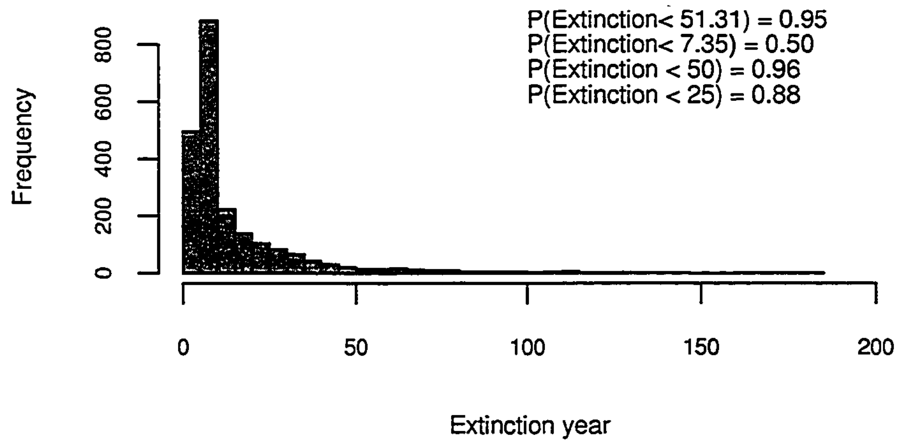


Figure 3.13: Plot of relative probabilities of extinction in a given year using random draws from the posterior estimate to predict trends.

end of the arrow, caribou are accessible enough and still numerous enough to have this effect. When the overlap is higher than 0.3, fewer caribou can persist and there is a lower numerical response in wolves. The reverse logic applies to lowering the spatial separation.

Figures 3.17 and 3.18 show the densities of caribou and wolves that would result from a system with fixed densities of moose. This shows the qualitative behaviour of a system where moose are maintained at fixed densities through direct control of species abundance to prevent strong numerical responses in wolves. Notice that caribou densities increase when moose densities are reduced. This is also true of lowering the encounter rate, but there is an important difference. Encounter rates are the product of animal behaviour, animal densities and spatial structure of the forest. Effecting changes to the forest are only slowly realized.

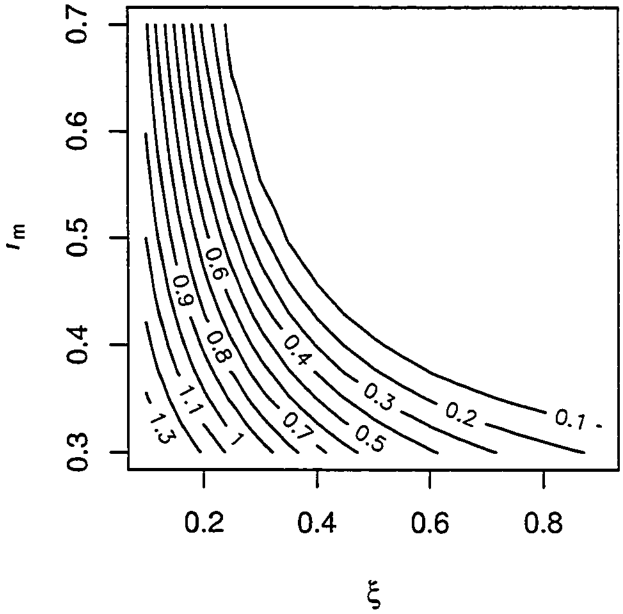


Figure 3.14: Plot of the equilibrium density of caribou when moose rate of change r_M and caribou-wolf encounter rate ξ are varied across a range of values. Contours are in units of animals/km^2.

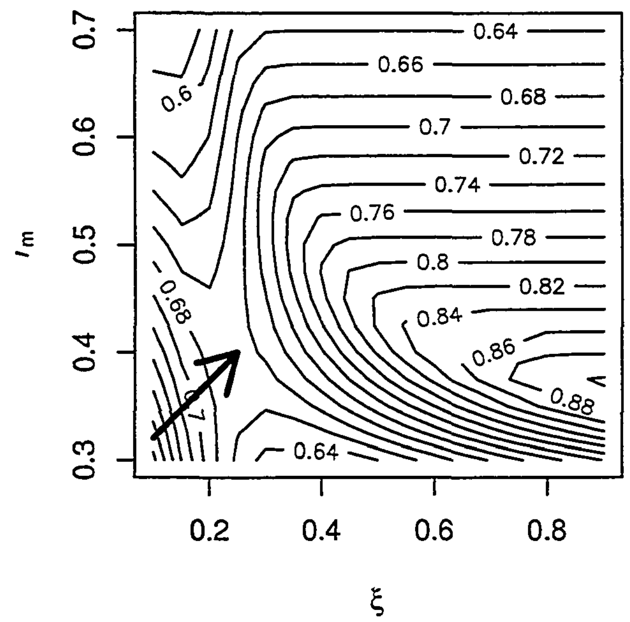


Figure 3.15: Plot of the equilibrium density of moose when moose rate of change r_M and caribou-wolf encounter rate ξ are varied across a range of values. Contours are in units of animals/km^2.

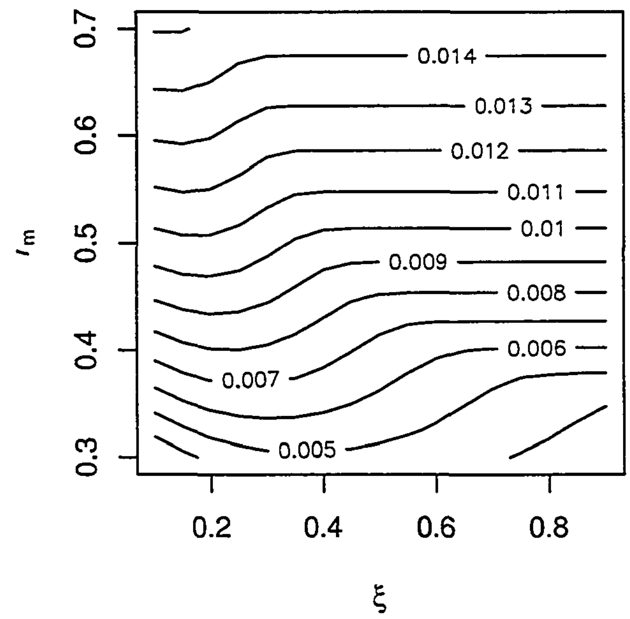


Figure 3.16: Plot of the equilibrium density of wolves when moose rate of change r_M and caribou-wolf encounter rate ξ are varied across a range of values. Contours are in units of animals/km^2.

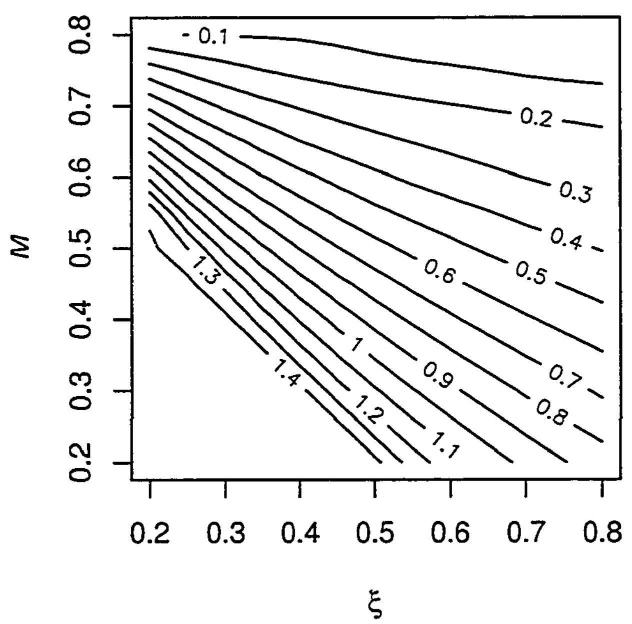


Figure 3.17: Contour plot of equilibrium density of caribou with fixed moose densities. This figure shows effects of varying the managed density of moose (M animals/km^2) and the encounter rate between wolves and caribou (ξ).

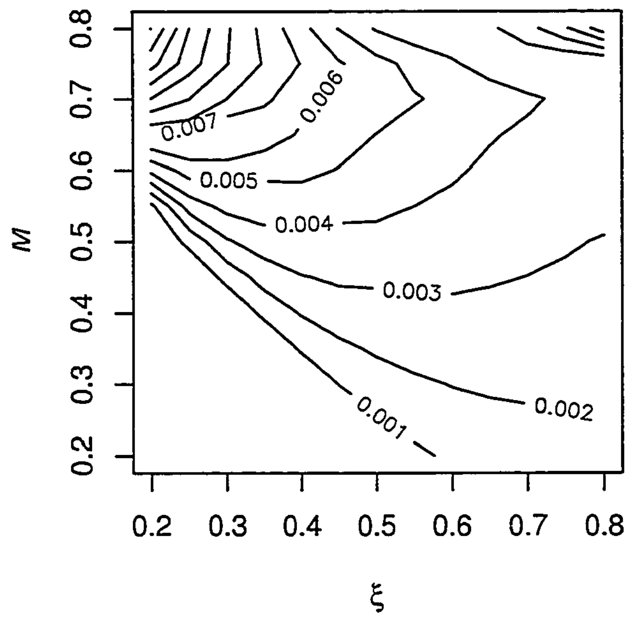


Figure 3.18: Contour plot of the equilibrium density of wolves with fixed moose densities. This figure shows effects of varying the managed density of moose (M animals/km^2) and the encounter rate between wolves and caribou (ξ).

3.5 Discussion

The analysis in this chapter reconstructs population trends by assuming four different models. I project trends into the future and perform a qualitative analysis of the interactions between predation rates and demographic rates. The models describe four hypotheses on how caribou can co-exist (or not) in a system where wolves prey predominantly on moose. I find that all four models fit the data equally well, but that two models predict extirpation of caribou within approximately 100 years. I do not compare the model fits statistically because small variation in parameter values can cause large enough changes to the likelihood objective function that an examination of the qualitative behaviour of the models is more meaningful. In addition, the uncertainty shown in Figures 3.9-3.12 demonstrates that a range of variation should be considered.

Model 1 only allows caribou to persist if the effective rate of search is low enough, which implies some low encounter rate (ξ) value. It requires high spatial and/or temporal separation of caribou from wolves. Once caribou are extirpated, wolves and moose either stabilize or enter a periodic cycle. The empirical model fit suggests that separation is not currently occurring adequately enough to sustain caribou densities.

Model 2 does not allow a species to go extinct unless the natural mortality rate of adults is higher than recruitment. This occurs because predation rates under Type 3 functional responses are very low at low densities. It implies switching away from caribou when they are at low densities, which precludes allowing incidental encounters to result in a kill. Given the precedence of high predation rates of wolves on caribou when caribou are at low densities (Wittmer 2004), this does not seem reasonable. It is possible, however, that a strict Type 3 form may relax predation too much at low densities. It may be reasonable to assume lower search rates at lower densities but it may not be reasonable to assume that they decline to zero so quickly. Rather that using a zero intercept in the relationship between caribou density and the effective rate of search, we might consider using an intercept above zero, such that the search rate never declines to zero. This would allow the model to predict extirpation of caribou and still demonstrate switching within certain density ranges.

Model 3 differs from Model 2 in that low caribou densities will not guarantee that predation rates will decline. If there are insufficient moose, wolves will maintain high search rates on caribou. It does not predict drastically different dynamics from Model 1, perhaps owing to the fact that the slope is not very steep. Since there is little information to draw upon to characterize a relationship between the search rate and moose densities, I used the inverse relationship to moose capacity (K_2). To fully test this relationship, we would need to monitor the kill rates on caribou as moose densities were controlled. Since we currently have no moose density estimates, much less any kill rate data, this is not possible.

Model 4 reduces to Model 1 when the exchange rate between invulnerable and vulnerable states favours foraging so strongly that the exchange rate between vulnerable and invulnerable states forces all prey into the vulnerable state. Model 4 can easily predict caribou persistence since a portion of the animals can always be inaccessible to wolves. It only requires that the there is sufficient habitat such that the carrying capacity is high enough for recruitment to balance natural mortality.

The models presented herein have subtly different parameter interpretations. Models 1 to 3 consistently interpret r_i as the rate of recruitment into a pool of juveniles subject to predation by wolves before recruitment into the adult population. Model 4, on the other hand, interprets r_i as the rate of recruitment into the adult population, with predation on juveniles already accounted for. This means the parameter value will be lower than if juveniles were preyed upon explicitly after entering the population. Also, predation does not occur the same way among the models (i.e., effective rate of search is subject to different assumptions). It is therefore not surprising that r_i's and a_i's vary so much among models. Additionally, parameters can be *confounded* (i.e., two or more parameters have the same general effect on an aspect of the system and are difficult to disentangle). The most obvious examples of confounded variables are a_{ij} and ε: a_{ij} determines the capture rate of prey and is multiplied by ε to generate wolf recruitment.

The parameter ε, which describes the relationship between consumed prey biomass and wolf recruitment, should be bounded by what we know about maximum observed rates of increase and known consumption rates. Turchin (2002) approximates ε at 0.1 per moose unit, which is equal to 0.04 per caribou unit if we assume a weighting of 2.5 caribou units per moose. When it was left as an estimated parameter in a preliminary analysis, the algorithm forced the value to be ≈ 0.09, indicating that some unaccounted biomass was finding its way into the wolves diet. If the data indicate an increase in wolf densities that can't be accounted for by the consumption of known ungulate biomass, it may mean that wolves are responding numerically to other sources of biomass not included in the data. The fitting routine associates the increase with a higher than expected conversion efficiency. I took this as an indication that wolf dynamics were being influenced by prey resources not considered by the model and added the parameter η. The degree to which the search rate parameters are overestimated should correspond roughly to the caribou units of biomass that are lacking in the energetic budget of the model. Further modelling efforts should consider including other prey species such as deer or elk.

The estimated effective rates of search of moose in all models fall short of the estimates obtained from the reanalysis of Messier (1994)'s data in Chapter 2 ($\simeq$6 here vs. $\simeq$31 the meta-analysis of the previous chapter). There are a few possible causes. If the spatial distribution of prey in the RPC is such that the encounter rates with moose are very low, the capture rate and functional response would be biased such that effective rate of search would be low. This would result if the wolf packs did not cover the entire winter range over which the estimates were made. If wolves only preyed over 75% of the range for example, we should expect the estimate to be biased downward by that amount. If the success rate killing moose is higher than 5%, it would also be biased downward. It is also possible that the estimated moose density is too high, causing the gradient search algorithm to lower effective rates of search to explain the low capture rate. Another cause could be that the high growth rate is a result of twinning, which is common when moose are well nourished (Schwartz 1997).

Not a single simulated long-term prediction shows periodic behaviour when the maximum likelihood parameter estimates were applied. Given that habitat conditions appear to be productive for moose, this is surprising. There is evidence that wolves and moose can cycle with a period of $\simeq$30 years (Peterson et al. 1984; Turchin 2002). Estimates of a_{2k} were lower than other empirical findings (Messier 1994; Hayes and Harestad 2000b), which may be caused by the rapid growth in the moose population forcing the fitting algorithm to find values of a_{2k} that allowed the population to increase. A substantial portion of wolf diet may also have come from other prey species not accounted for in the model. In this case, the functional response would have an inadequate number of satiating terms in the denominator, causing the search routines to look for lower values of a_{2k} instead of accounting for the fact that a lot of time was spent handling other prey items. If, in fact, a_{2k} is higher, the projected trends would likely show periodicity. The lack of periodicity in projected empirical fits may also be a product of the short time series from which the parameter estimates were obtained. It is also possible that empirically observed cycles come from systems different than the one studied here. Wolf pack sizes, average body weights of both predators and prey, and habitat can all play a role.

In all the long-term projections, models predict caribou densities that are relatively stable or increasing in the first 10 years. Serious declines only begin after 10 or 20 years when wolf densities increase to more than 20 per 1000 km^2 . This is more optimistic than the observations BC herds (Bergerud and Elliot 1986), where caribou populations began to decline when wolf densities exceeded 6.5 per 1000 km^2. Since caribou have been considered relatively stable in recent years (Brown and Hobson 1998; Dzus 2001) and wolves are known to have been at 11 per 1000 km^2, it is possible that conditions in the RPC have allowed caribou to remain relatively separated from wolves compared to the BC herds. *Status quo* conditions in the RPC may tolerate higher densities of wolves at present. Increased moose and wolf densities are nonetheless predicted by all models. This corresponds to an inflection point in the decline of caribou, which occurs sharply at about 15 year from the start of simulations.

The maximum likelihood parameter estimates of all four models predict caribou will further decline or go extinct. The population viability analyses of Models 1 and 3 both suggest that caribou will be driven to extinction within roughly 100 years if conditions remain as they are currently estimated. Modelling declining caribou/wolf encounter rates with elevated moose densities (Model 3) does not appear to provide sufficient relief from predation. At best this provides a brief reprieve from predation before wolf densities get too high, after which the sheer number of wolves ensures a high enough predation rate to exceed recruitment. Model 2 predicts persistence of caribou at densities just below 0.1 animals/km^2, assuming that caribou predation declines linearly to zero when densities are low (Type 3 functional response). Model 2 fits the data as well as other models, but empirical observations in British Columbia (Wittmer 2004) suggest that wolf predation rates may not decline at low caribou densities. Rather, it seems that survival rates decline at low densities, even when densities are measured with respect to quantities of suitable habitat. This suggests that even if wolves (and in some cases cougars) are switching to other more prevalent prey species when caribou are declining, incidental encounters may still be sufficient to result in depensatory mortality on caribou. This evidence makes it difficult to trust a model that uses a Type 3 functional response on caribou.

Declining populations of caribou have generally been associated with reductions in the amount of old growth forests. Large patches of 140+ year old forests are currently the target of caribou conservation strategies in British Columbia (Wittmer 2004). While it is true that increasing the proportion of old growth forest mitigate declines, caribou may decline much further during the time it takes to recover an adequate quantity of large old patches. The stability analysis of a Model 1 system shows that caribou can reach higher densities if encounter rates with wolves are lower, or if the birth rate of moose is lower. Moose birth rates may currently be high because of favourable habitat conditions or low juvenile mortality from causes other than wolf predation (such as bear predation). Habitat management options for reducing r_M involve regenerating forests to have less young stands. This may be impractical because waiting for forests to regrow may allow caribou to decline to very low densities by the time habitat conditions cause a sufficient decrease in r_M. Managing encounter rates may be even more problematic. Encounter rates between predators and prey can involve complex density dependent spatial behaviour. The details are beyond the scope of Model 1 (see Chapter 5 for details on modelling encounter rates), but a similar practical argument exists against managing their causes. Encounter rates can increase because lower quantities of habitat can force prey to inhabit area that have higher predation risks. Caribou habitat takes time to replace (typically on the order of 140 years), so policies aimed at managing the ultimate cause of encounter rates involve waiting for habitat supply and spatial structure to return a state consistent with older natural forests. I therefore turn to the direct management of moose densities as a means to manage the system.

In theory, direct reductions in moose densities can be used to increase caribou densities. I have shown that when moose densities were reduced and maintained at lower densities, we observe lower wolf densities and therefore higher caribou densities because of reduced wolf predation on caribou. The preference for managing moose densities is predicated on the fact that it is a fast manipulation to implement relative to other options.

There is a long history of research into the effects of wolf reductions on moose and caribou densities (Gasaway et al. 1983; Gasaway et al. 1992; Seip 1992a; Bergerud and Elliott 1998; Hayes et al. 2003). There has been comparatively less research on the effect of reducing one ungulate species to increase the density of another. The idea has long been recognized as a form of competition mediated by predator numerical responses to other prey (Holt 1977; Holt 1984). The danger of reducing moose densities is that wolf populations may then spend more time searching for alternate prey and thus encounter caribou more often. Though wolf densities may ultimately decline, predation on caribou may, in the interim, be sufficient to cause further declines. Simultaneous reductions of wolf populations could offset this. Populations could be monitored and further reductions in moose and wolf populations could be implemented until caribou populations begin to increase. Empirical results provide an indication of the typical predator densities above which we observe declines in caribou (i.e., 0.065 wolves/km^2) (Bergerud and Elliott 1998).

Moose should therefore be reduced to a density that maintains wolves below 0.065 wolves/km^2. The policies that could bring about these reductions in moose would require further information on harvest rates in the area. Further details would also be required on the number of kills per hunter day as well as the number of hunters that can reasonably be expected to participate in a given year. The same type of data would be required to monitor wolf trapping effort. The specifics related to these policies are beyond the scope of this thesis, but the modelled implication indicate potential effectiveness in reversing caribou declines. Management options are examined in more detail in Chapters 4 and 6.

Conditions are likely to change in the RPC. Based on conditions that prevailed during 1989-1998, however, best estimates of past trends predict declines in caribou. Deleterious changes to forest composition and structure in the ensuing years could have a negative impact on the population dynamics of this system. Parameters that are sensitive to environmental conditions may vary such that the outcome may be worse for caribou than under current conditions. The following chapter explores the behaviour of such changes.

Lack of data was a serious drawback in this analysis. Important parameters are a_{ij}, ε and m_W. If kill rate data had been available, the methods use here would have produced more accurate estimates of a_{ij} and ε, making it easier to distinguish between the models. Absence of estimates of the initial densities further hampered the estimation process. The chapter that follows explores the importance of each parameter in determining the dynamics of the system. This provides an indication of qualitative differences between models as well as suggesting which parameters matter the most. These parameters share an important characteristic: they can be obtained from monitoring wolf activities, not ungulate activities.

Chapter 4

Population response to environmental variation

Introduction

Woodland caribou conservation in Alberta and elsewhere is concerned with long term viability of caribou populations in the presence of forestry (Hervieux et al. 1996; Smith et al. 2000; Dzus 2001) and energy sector activities (James 1999; Dyer et al. 2001). The task at hand is to understand how caribou populations may respond to the changes imposed by those activities. The loss of old growth forests is of concern because it reduces the overall quantity of lichens, the primary food source of caribou. Forestry activities also alter the spatial structure of forests. *Mountain* ecotypes in British Columbia experienced reduced adult female survival rates with decreases in the proportion of old forest (Wittmer 2004). Oil and gas exploration leaves linear swaths of cleared forest after seismic devices are used to detect oil and gas deposits. These *seismic lines* vary in width, cover enormous areas in central and northern Alberta, and are the subject of many caribou conservation studies (James 1999; Dyer et al. 2001; Oberg et al. 2002). Cumulative impact assessments have shown that current practices and anticipated demands for natural resources will likely lead to further declines in boreal caribou populations (Schneider et al. 2003).

Thus far I have not attempted to capture dynamic changes in environmental conditions. In Chapter 3, I estimated parameters in relation to observed changes in animal abundances over a period of time. I assumed that the parameters represented implicit averages representative of the environmental conditions of the period. An alternative is to construct mathematical expressions that describe how population parameters scale in relation to changing environmental conditions. This can be accomplished for demographic as well as behavioural parameters. In this chapter, I extend the previous models with such scaling relationships for key parameters. The effective rate of search of caribou a_1, a behavioural parameter, is scaled to forest spatial structure, and the density dependent parameters K_i are scaled to forest age.

I augment Models 1 to 4 from the previous chapter with sensitivities to forest landscape conditions, but rather than estimate parameters anew, I use the parameter estimates from Chapter 3 and determine the qualitative differences that occur when forest aging and fires are simulated. There was not enough variation in environmental conditions within the time scale of the data to estimate parameters within the new model designs. However, because of the uncertainty in the estimated values of parameters (see Section 3.4.1), I also look at the qualitative differences arising from variations to the parameters not explicitly affected by changing forest conditions. Looking at the qualitative behaviour of models across ranges of parameter values is essential for two reasons: 1) the parameter estimates have uncertainty and may take on new values when environmental conditions change, and 2) it reveals the components to which the system is very sensitive. Sensitivity analysis helps anticipate the consequences of biases in parameter estimates and the effects of environmental change.

The recruitment capacities K_i and the caribou effective rates of search a_{1k} are recalculated every year in relation to the current state of the forest. Trends are simulated 400 years into the future using a common starting point and a range of relationships among parameters and forest structure. I compare the qualitative behaviour of the models across a gradient of parameter values and look for management options that could reverse caribou population declines. I then search for robust strategies across models and parameter values.

4.1 Methods

This is a sensitivity analysis where *sensitivity* implies two things. It is both an examination of the effects of temporal fluctuations in environmental conditions, as well as a test of the consequences of assuming higher or lower values of specific parameters.

Sensitivity to changing environmental conditions examines the effect of environmental fluctuations on specific parameters and the consequences to population dynamics (e.g., what are the population consequences of fluctuations in the age distribution of the forest as manifested in fluctuating recruitment?).

Sensitivity to individual parameters examines system behaviour as a consequence of assuming different fixed parameter values (e.g., what if the parameter estimates were wrong?). Note that we can perform a sensitivity analysis of this nature in addition to examining the consequences of fluctuations in environmental conditions.

Four new models were developed. Models 5, 6, 7 and 8 have the same structure as Models 1, 2, 3 and 4 from Chapter 3, respectively, except that some parameters vary with spatial variables that are measured each year over the RPC winter range. The parameters that are altered are K_1, K_2, a_{11} and a_{12}. The models were augmented with the ability to read ESRI© ASCII grid files. I used forest ages in 2 km × 2 km grids. With this information, the models can read forest ages at the beginning of a simulation and increase the forest age each year thereafter. I used forest data from the Redrock Prairie Creek (RPC) as *bottom-up* forcing on recruitment capacity by creating a mathematical relationship between the two. Caribou carrying capacity increases sigmoidally with forest age, reaching its maximum at some specified age. Moose carrying capacity decreases sigmoidally with forest age in a similar fashion. I also vary the effective rate of search to simulate relationships to proportion of large old growth patches. In all cases, I choose scaling rates and asymptotes that allow parameters to equate to the same values as their non-dynamic counterparts when evaluated at the initial forest conditions.

Alternative models

I modified the basic equations of Models 1, 2, 3 and 4, to create relationships between forest age, spatial structure and population dynamic parameters. The relationship of these parameters to landscape change are described by Equations 4.1 - 4.4 and shown in Figure 4.1. The biological, environmental and management interpretations of the parameters follow.

$$
\begin{aligned}
K_1 &= \frac{1}{n}\sum_{j=1}^{n}\frac{K_{1,max}A_j^3}{K_{1,half}^3 + A_j^3} && (4.1)\\
K_2 &= \frac{1}{n}\sum_{j=1}^{n}K_{2,max}\left(1 - \frac{A_j^5}{K_{2,half}^5 + A_j^5}\right) && (4.2)\\
a_{1j} &= a_{1j,max}\left(1 - \frac{G^3}{g_{half}^3 + G^3}\right) && (4.3)\\
a_{1j} &= a_{1j,max}\left(1 - M/\varphi_M\right) && (4.4)
\end{aligned}
$$

Model 5 re-calculates carrying capacities as a function of forest age. This explores sensitivity of model prediction to $K_{1,max}$ and $K_{2,max}$. Models 6, 7, and 8 have mechanisms whereby forest conditions scale the value of the effective rate of search on caribou. This explores the sensitivity of model predictions to

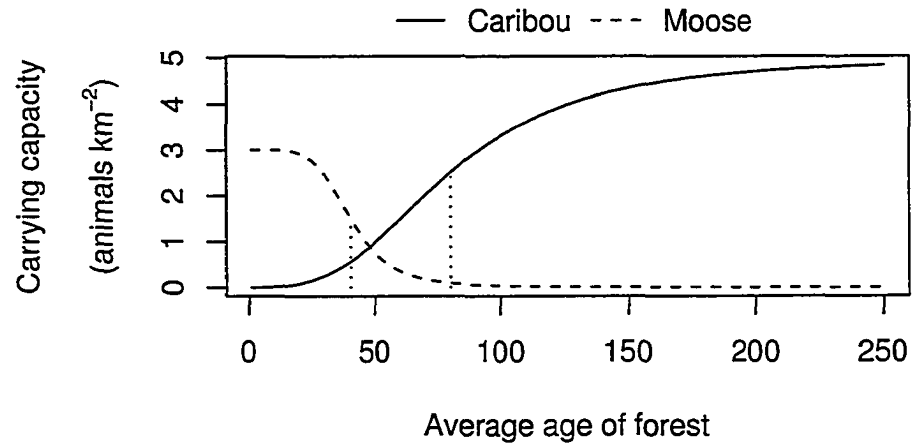


Figure 4.1: Plot of change in carrying capacity of caribou (solid line) and moose (dashed line) with changes in forest age. Vertical dotted lines are drawn at the age of half maximum carrying capacities.

assumptions about predation mechanisms. The models each provide a mechanism that makes it easier for caribou to co-exist with moose and wolves. Model 6 is a Type 3 functional response, allowing caribou to escape predation at low densities. Model 7 represents a prey switching mechanism whereby caribou encounters with wolves decline linearly with moose density while moose still encounter wolves in proportion to availability. Model 8 includes a mechanism whereby caribou and moose populations are divided into vulnerable and invulnerable states.

Model 5 Wolves prey on ungulate calves and adults with distinct effective rates of search for each prey species and age class. Wolves prey on caribou and moose with a Type 2 functional response. a_{1j} and $K_{i,max}$ are varied with forest conditions using Equations 4.1, 4.2 and 4.3.

Model 6 Same as Model 5 but wolves prey on caribou with a Type 3 functional response and moose with a Type 2 functional response.

Model 7 Same as Model 5 except that search rate on caribou declines when moose densities are higher. a_{1j} and $K_{i,max}$ are varied with forest conditions using Equations 4.1, 4.2 and 4.4.

Model 8 Predator-prey interactions are structured such that a portion of the prey population is invulnerable to predators at any given time. (See description of Model 4). a_{1j} and $K_{i,max}$ are varied with forest conditions using Equations 4.1, 4.2 and 4.3.

Parameter variation

I vary parameters that can alter the behaviour of the system, using a range of values (see Table 4.1). The range reflects reasonable limits to assumed values. It is meant to address the possibility that parameter estimates may be wrong as well as the possibility that the system may undergo change. I look at the effect of different assumed values of the following parameters:

$a_{ij,max}$ By looking at system behaviour across a range of $a_{ij,max}$ values we see the potential effect of factors such as wolf travel speeds, prey detection radius and attack success rates. These can be affected by road and seismic line densities, topography, stand density, snow depth and patch sizes. Obviously there is no management action possible for topography or snow depth, but we can directly manage $a_{ij,max}$ by not creating more land features that we suspect cause it to increase.

$K_{i,max}$ These parameters describe density dependent recruitment in relation to habitat quality. System dynamics are sensitive to this parameter when densities are high. Average forest age determines this for each species. We cannot manage $K_{i,max}$ but we can manage the age distribution of the forest, which has a direct bearing on it (see Equations 4.1 and 4.2).

g_{half} This parameters scales the rate at which encounters between wolves and caribou decline as the landscape becomes dominated by large old growth patches. It is the proportion of large old patches at which a_{ij} is half the maximum possible value (i.e., $a_{ij} = 0.5a_{ij,max}$ when the proportion of large old growth = g_{half}). A very low value means that $a_{ij} \rightarrow 0$ with very little large old forest patches. We cannot manage the value of g_{half} but we can manage the proportion of large old growth patches, thereby reducing the effective value of a_{ij}.

ε The conversion efficiency describes the relationship between consumed prey biomass and wolf recruitment. It cannot be managed, but it is important to consider. If wolves are responding numerically to prey biomass not accounted for in the models we can manage the alternate prey biomass.

m_w The mortality rate of wolves can be directly manipulated. Wolf control can be implemented on a yearly basis.

δ_2 The harvest rate of moose can be directly manipulated on a yearly basis with harvest regulation and monitoring.

φ_M I looked at the sensitivity of $a_{ij} = a_{ij,max}(1 - M/\varphi_M)$ to φ_M. Although the parameter φ_M cannot be directly managed, we can see the effect that moose reductions can have on caribou predation mortality. It has been suggested that in the short term, moose control, although aimed at reducing the number of wolves, can have the effect of increasing predation rates on caribou if wolves are forced to search for alternatives to moose.

A is the forest age in a given cell, and G is the proportion of the landscape covered by large (> 1200 hectares) old (>140 years) forest patches. I vary $K_{1,max}$ and $K_{2,max}$ such that the calculated K_i fall between 1 and 5 (Skogland 1985; Van Ballenberghe and Ballard 1997). I set the exponent in A^3 to cause

Table 4.1: Summary of the range of variation applied to each parameter. This shows how variation was applied to test sensitivity of model performance to each parameter. Parameters that show percentages of variation apply the same percent variation regardless of the estimated value of the parameter.

Parameter	Values assumed
$a_{1,max}$	50%, 100%†, 150%
$a_{2,max}$	50%, 100%†, 150%
$K_{1,max}$	3†, 5, 7
g_{half}	0.05, 0.10†, 0.15
ε	0.025, 0.035†, 0.045
m_w	0.4925†, 0.70‡
δ_2	0.14†, 0.24‡
φ_M	0.5, 1.0†, 1.5

$\dagger$: estimated or assumed value from non-spatial model
$\ddagger$: value used to simulate moose or wolf management controls

K_1 to increase quickly from 0 to $K_{1,max}$ in a short interval around $K_{1,half}$, which assumes that recruitment would decline quickly as the average forest age drops. I chose $K_{1,half} = 80$ because it is the age point at which caribou avoid stands Szkorupa (2001). Young patches will bring the landscape average calculation of K_1 down. I chose $K_{2,half} = 40$ because moose are found at highest densities around 20 yrs post fire (Schwartz and Franzmann 1989; Loranger et al. 1991) but quickly thereafter are found at much lower densities. The $K_{i,max}$ are not so important as the $K_{i,half}$ values. What is more important is how recruitment fluctuates with changes in forest age as a result of Equations 4.1 and 4.2, which is explored in this chapter.

A fire regime is emulated by mimicking lightning strike and fire spread events. An ignition rate represents the probability that an individual cell will ignite as a result of a lighting strike. A spread rate represents the probability that any burning cell can spread to adjacent cells. Forest fires are simulated by igniting a cell with draws from a uniform random number generator and initiating a fire if the draw is less than or equal to the value of the ignition rate being applied. Neighbouring cells are ignited if further random draws are less than or equal to the spread rate. Every cell that burns draws uniform random numbers to spread to all adjacent cells, whether the burn initiated from a lightning ignition or because of spread from an adjacent cell. I simulate different forest fire regimes by changing the ignition and spread rates. The maximum ignition rate is 0.003 and the maximum spread rate is 0.21. The ignition rate is further scaled to forest age such that it had a sigmoidal growth rate to its maximum, reaching half of its maximum at 20 years. The spread rates grows to its maximum value similarly, reaching half of the maximum value by 60 years. These parameters produce forests that fluctuate between 80 and 100 years of age as fires burn and maintain approximately the proportion of large old forests as the starting conditions. I also vary the combinations of ignition and spread rates to reflect shifts in average age and patch size composition. I use a base case (case 0 in Table 4.2) to produce all simulations with the exception of the simulations where I specifically test the effect of fire cases 1, 2 and 3 against each other.

Table 4.2: Fire regime parameters. Up and down arrows indicate the effect of ignition and spread rate parameters on the size (S) and frequency (F) of fires relative to the base case (0).

Case	Ignition rate	Spread rate	Description	Portion large old
0	0.003	0.21	Natural	$\simeq$11%
1	0.002	0.23	S↑ , F↓	$\simeq$15%
2	0.006	0.19	S↓ , F↑	$\simeq$5%

I do not explicitly model forest harvest, but it can be interpreted in the context of natural disturbance rates. Forest age distribution and patch size distributions arising from particular ignition and spread rates can be thought of as analogs to harvest rates and cut sizes. Anthropogenic disturbances are, of course, not the same thing as natural disturbances. For the purposes of this analysis however, I assume that forest age and patch size have similar effects on population parameters whether they arise from natural or anthropogenic causes. During the course of simulating various disturbance regimes, the model recalculates relevant landscape measures and adjusts parameter values accordingly.

Consider Equation 4.3, which describes the effective rate of search of wolves on caribou decreasing dramatically as old growth patches dominate landscapes. This predicts that caribou in forests with large old growth patches will have lower predation mortality, consistent with trends observed in 16 subpopulations of mountain caribou, where adult female survival rates increased with the *proportion* of old forest (Wittmer 2004). I model it here to be the proportion of *large* patches of old growth because, as a conservation strategy, building up the supply of large old patches is widely discussed as a means to simultaneously provide habitat and spatial refuge (Hervieux et al. 1996; Seip 1998; Smith et al. 2000; Szkorupa 2001; Wittmer 2004).

We can also assume that certain factors will act to increase the search rate of wolves on caribou. Seismic lines are purported to increase travel rates of wolves, making it likely that search rates also increase (James 1999). This is true mainly of younger and wider seismic lines but this comes with the caveat that caribou are known to partially avoid larger seismic lines (Dyer et al. 2001; Oberg et al. 2002). There are already substantial densities of seismic lines in the RPC winter range, but as of 1998, the majority originated in 1975 (see Figure 4.2). Seismic lines distributions were evaluated by Oberg (2001) using 5m resolution satellite imagery. Using the reported age, length and width of the seismic lines, I calculate the distribution of km and km^2 of seismic lines in the RPC winter range among seismic line origin dates (Figure 4.3). I choose not to include the effect of changes in seismic line density explicitly because there was no large change in density during the time period over which parameters were estimated. Any hypothesis about the effect of increased seismic line density can be inferred from increases in a_{ij}, increases in K_2 and decreases in K_1.

Figure 4.2: Map of the distribution seismic lines in the RPC caribou winter range. Seismic lines of all widths and age are shown.

Using the parameter estimates from Models 1, 2, 3, and 4 as a starting point, and using the forest age data from year 2000 forest inventory maps, I simulate population dynamics simultaneously with forest growth and disturbance. I use fire ignition and spread rates to produce patch sizes and age composition consistent with starting conditions (see Figure 4.4). Population trends are then simulated using a range of parameter combinations for a_{ij}, K_1 and K_2. I simulate for 400 years because it was long enough to allow simulated conditions to cover a range of forest age compositions and spatial structures. Covering a wide range of conditions in a single simulation is a practical compromise to looking at multiple simulations starting at random starting points. In addition, the exact same fire regime was applied to every

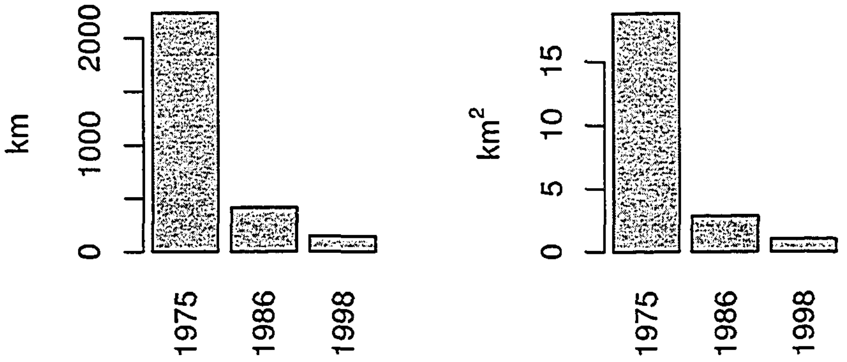


Figure 4.3: Length in km and km^2 of area covered by seismic lines of each age class in the RPC caribou winter range in west-central Alberta.

scenario because the same sequence of random numbers was drawn each simulation. This caused the forest to undergo the same succession at precisely the same time, and the disturbances were of the same size as well. Further, forest age fluctuated over a wide range in a quasi-cyclic pattern. Sensitivities to ranges of spatial structure and age could addressed within the time-frame of the simulations. Long simulation runs of 400 years were chosen because the long period acts as a surrogate for repetition, allowing most dynamics to occur by virtue of the fact that most types of conditions prevailed for a significant portion of simulation run. I examine the simulations for any prevailing patterns as well as for consistency with important empirically observed trends. Ideally, this analysis would be more robust if it included a statistical summary of the outcome of simulating each scenario 100 or 1000 times. Because of the volume of simulation involved, I chose to do single long simulation runs designed to span a full range of conditions.

For each of the models, I fix the values of all other parameters while viewing the qualitative differences of varying a focal parameter. To begin with, $K_{2,max}$ are fixed at a value of 2. The parameters that scale K_1, K_2 and a_1 to landscape change are set such that K_1, K_2 and a_1 are the same as the estimated parameters at the beginning of the simulations. The proportion of the landscape covered by patches greater than 1200 hectares and greater than 140 years at the beginning of the simulations was 0.11. Since a_1 varies with this proportion, I choose a value of $a_{1,max}$ that makes a_1 equal to the value estimated in Chapter 3. Assuming $g_{half} = 0.1$, $a_{1,max}$ is set to approximately 2.2 times the value estimated. Varying g_{half} on $\{0.05, 0.1, 0.15\}$ thus means approximately ±50% variation on the effective rate of search.

Sensitivity analysis

I explore the sensitivity of model predictions to chosen values of specific parameters by simulating population dynamics while simultaneously aging the forest and simulating forest fires. I repeat this for three combinations of ignition and spread rates to show the relative effects of forest age and patch size structure as they pertain to forest harvest and natural disturbance assumptions. Calculation of sensitivity is described for each model in Table 4.3.

I test for changes in system behaviour when parameters are varied. This can identify obvious management considerations as well as sensitivity to estimated parameter values. If parameters can be manipulated in favour of identified management goals, policies can then be developed to realize those goals. When interpreting the results of the simulations, it is important to distinguish the parameters that have management potential from those that do not. The sensitivity of each parameter to known aspects of the system is summarized in Table 4.4.

Table 4.3: Methods used to calculate the parameters as environmental conditions change over time. A and G are calculated from forest conditions. $K_{1,max} = 5$, $K_{2,max} = 3$, $K_{1,half} = 80$, $K_{2,half} = 40$ and $g_{half} = 0.1$ and $\varphi_M = 2$ are baseline values for scaling parameters.

	Expression	Sensitivity	Models
K_1	$\frac{K_{1,max}A^3}{K^3_{1,half}+A^3}$	$K_{1,max} \in \{1, 3^{\dagger}, 5\}$	5, 6, 7, 8
K_2	$K_{2,max}\left(1 - \frac{A^5}{K^5_{2,half}+A^5}\right)$	$K_{2,max} = 5$	5, 6, 7, 8
a_1	$a_{1,max}\left(1 - \frac{G^3}{g^3_{half}+G^3}\right)$	$g_{half} \in \{0.05, 0.1^{\ddagger}, 0.15\}$	5, 6, 8
a_1	$a_{1,max}\left(1 - \frac{G^3}{g^3_{half}+G^3}\right)\left(1 - \frac{N_1}{\varphi_M}\right)$	$\varphi_M \in \{0.5, 1.0^{\S}, 1.5\}$	7

†: value at which $K_{1,max}$ held constant while $K_{2,max}$ is varied
‡: value at which g_{half} held constant while other parameters are varied
§: value at which τ held constant while other parameters are varied

Table 4.4: Summary of key parameter sensitivities and associated causes of variation.

Parameter	Manageable causes	Unmanageable causes
$a_{1,max}$	Road and seismic line densities	Topography, stand density
g_{half}	–	Wolf behaviour
$K_{i,max}$	Tree species composition	–
δ_2	Moose harvest	–
m_w	Wolf control	Natural mortality
ε	–	Unaccounted alternate prey
r_c	Unaccounted predation	Disease

4.2 Results

The simulations presented in Figures 4.5-4.23 are the product of a single random forest disturbance scenario spanning 400 years. Caribou abundances consistently decline when wolf densities are above approximately 8 animals per 1000 km^2. This is consistent with Bergerud and Elliott (1998), where 6.5 animals per 1000 km^2 was the density where caribou declines were consistently seen in multiple prey systems in northern BC. This observation predominates regardless of the model. The only caveat to this rule is that caribou tolerate

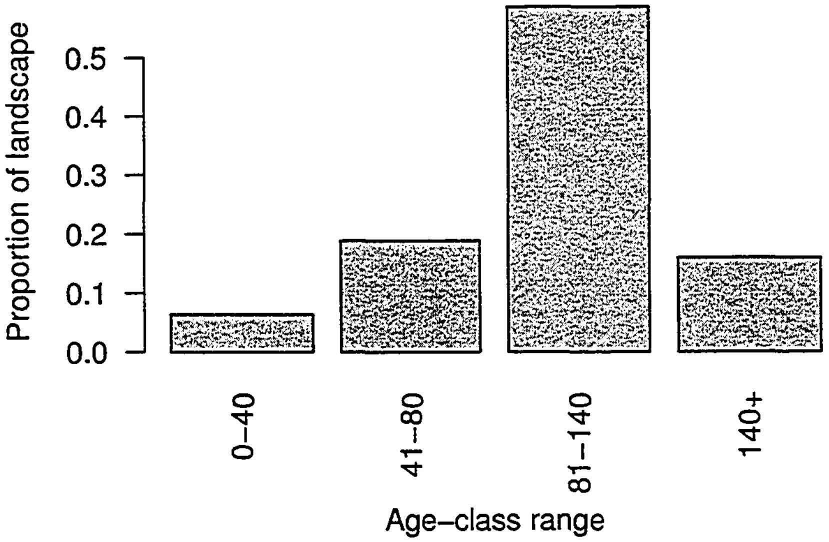


Figure 4.4: Proportion of stands in four major age-class ranges of Redrock Prarie Creek X-axis units are ranges of age in years. Distribution calculated from forest age data.

higher densities of wolves when mechanisms are in place to simulate avoidance, or when parameters are set to more optimistic levels for caribou. The results are summarized by individual model in Table 4.5 and by parameter sensitivity in Table 4.6.

Simulations predict a gradual decline in K_1 and an increase in K_2 followed by fluctuations around 2±0.2 and 3±0.5 respectively. These result in initial declines in caribou followed by a brief increase, and ultimately a decline leading to extirpation at around 120 years after the start of simulations. Some parameter values facilitate caribou reaching higher densities before the declines occur, but the declines occur nonetheless and caribou are locally extirpated in all but a few exceptions. High moose densities and a wolf numerical response to moose are the cause in all cases.

Notably, when $g_{half} = 0.05$, a_{1k} (both juvenile and adult) are low enough under simulated forest age and patch size structures that caribou nearly escape extirpation. When τ is set to 0.5 in Model 7, caribou predation rates are sufficiently low at the beginning of the simulations that caribou populations are able to reach high densities (0.8/km^2) and then continued low a_{1k} results in caribou populations fluctuating between 0.2 and 0.8/km^2 (see Figure 4.10). This is only possible because moose densities are consistently fluctuating around 0.5±0.1. This outcome assumes that wolves will not prey on caribou when moose are at densities above 0.5. When different fire regimes are simulated, g_{half} plays a role (see Figures 4.20 - 4.23). The fire scenario that produces the larger older patches results in the highest caribou densities because the landscape structure decreases $a_{1,max}$ with the relationship to g_{half}. The different fire regimes also affect K_1 and K_2 because they lead to different average ages as a result of differences in ignition and spread rates. Since simulated variation in K_1 and K_2 produced very little change in the overall results, I assume that the main effect of different fire regimes is the effect on $a_{1,max}$, but the effect is not significant enough to permit caribou to persist.

An interesting observation is that in many cases, elevated caribou densities appear to induce cycling between moose and wolves (see Figures 4.12, 4.13, 4.5, 4.7 and 4.8) but only while caribou densities are relatively high. A cyclic pattern is produced when $g_{half} = 0.05$, following elevated caribou densities. There was also some apparent periodic behaviour in wolves and moose in Model 8 (Figures 4.14 and 4.15). It followed fluctuations of K_2 very closely, however, suggesting that it is not cyclic behaviour from predator-prey interactions, but rather a response to fluctuating prey resources.

I consider the *status quo* to be a system with a level of moose harvest consistent with maximum likelihood parameter estimates and no wolf control. Figures 4.16 - 4.19 illustrate a very exceptional situation: a contrast between the *status-quo* and a dual-control management option where moose are harvested at a rate 0.1 greater than the estimated value as well as culling wolves. The figures show the results of simulations where $m_2 = 0.24$, $m_w = 0.7$ and

$a_{1,max}$ was set to 50% lower than the estimated value. I show this to illustrate that under the *status-quo* set of parameters, even the management actions prescribed do not prevent extirpation of the RPC herd. The reason for setting the value of $a_{1,max}$ to 50% lower than estimated is because the moose harvest and wolf reductions were not sufficient to prevent the caribou decline.

The simulated results show how difficult it is to find parameter combinations that allow caribou to co-exist with moose. In multiple prey systems, predator-prey interactions can easily lead to the extirpation of one prey type. The more vulnerable of the two prey types needs to have adapted a behavioural mechanism to avoid predation as predators respond numerically to the other prey, unless the predator mortality rates increase with their densities through intra-specific strife (Holt 1984). Simulations show that caribou only persist when effective rates of search on caribou are very low, or when wolf densities are below roughly 8 animals per 1000 km^2. Predominantly, caribou populations go locally extinct within about 120 years. Only very large changes to the base parameters allow the system to escape this pattern. Figures 4.5 - 4.23 show the abundance trends across ranges of values of key parameters.

Table 4.5: Model result summary, describing general simulation results by individual models. Results that pertain to specific parameters are indicated.

	Key result
Model 5	- Caribou go locally extinct after $\approx$120 years. Populations decrease at first, increase for 30 years during low wolf density years, but then decline when wolves respond to higher moose densities. - Moose densities remain around 0.5 animals/km^2. Wolf densities attain 20 animals per 1000 square kilometers.
Model 6	- Caribou do not go locally extinct. - $a_{2,max}$+50% causes high amplitude cycle ($\approx$20 yrs) in moose with corresponding low amplitude cycle in caribou (see Figure 4.12). - $a_{1,max}$-50% increases caribou densities (see Figure 4.11). - g_{half}=0.05 causes a cycle in caribou to be driven by the proportion of large old growth patches, which is coincident with fluctuating age structure. Fire regime driven by bigger, less frequent fires increases the amplitude of the cycle (see Figure 4.7).
Model 7	- Caribou go locally extinct after $\simeq$120 years in all but one case. - Caribou persist when $a_{2,max}$ is decreased by 50% (see Figure 4.13). - Decline of moose when g_{half} = 0.05. High caribou densities causes numerical response in wolves (0.10-0.15/km^2) and high mortality in moose (see Figure 4.8). Caribou reach 0.2 animals/km^2 when g_{half} = 0.05.
Model 8	- Large fluctuations occur when g_{half} = 0.05. Caribou begin to recover after $\approx$350 years (see Figure 4.9). - Wolf populations appear to cycle, possibly being induced by small fluctuations in moose densities. This occurs when moose fluctuate between 1.2 and 1.5/km^2.

Table 4.6: Summary of the effects of varying parameter values on simulated population trends in Models 5, 6, 7, and 8. This describes general simulation results, summarized by parameter. Results that pertain to specific models are indicated.

	Observed effect
$K_{1,max}$	Very little effect.
g_{half}	Causes large fluctuations in moose populations when $g_{half} = 0.05$. Caribou nearly persist in Models 5, 7 and 8.
$a_{1,max}$	Little effect at ±50%.
$a_{2,max}$	$a_{2,max} + 50\%$ induces cycles in moose and wolf populations in Model 6 (see Figure 4.12).
ε	When $\varepsilon = 0.025$, caribou increase to a higher density before collapsing when Model 8 is used (see Figure 4.15). Otherwise, caribou are not sensitive to this parameter.
m_w	Increasing m_w from 0.4925 to 0.7 has the most significant effect on increasing caribou densities as well as moose, and wolves are found at their lowest densities.
δ_2	Increasing the harvest rate to 15% increases caribou densities and decreases wolf densities. It has little effect on moose densities.
τ	When $\tau = 0.5$, caribou persist (see Figure 4.10).
r_1	Allows caribou to reach higher densities but still collapse in 120 years. No effect on moose. Increases wolf densities slightly in Model 6.

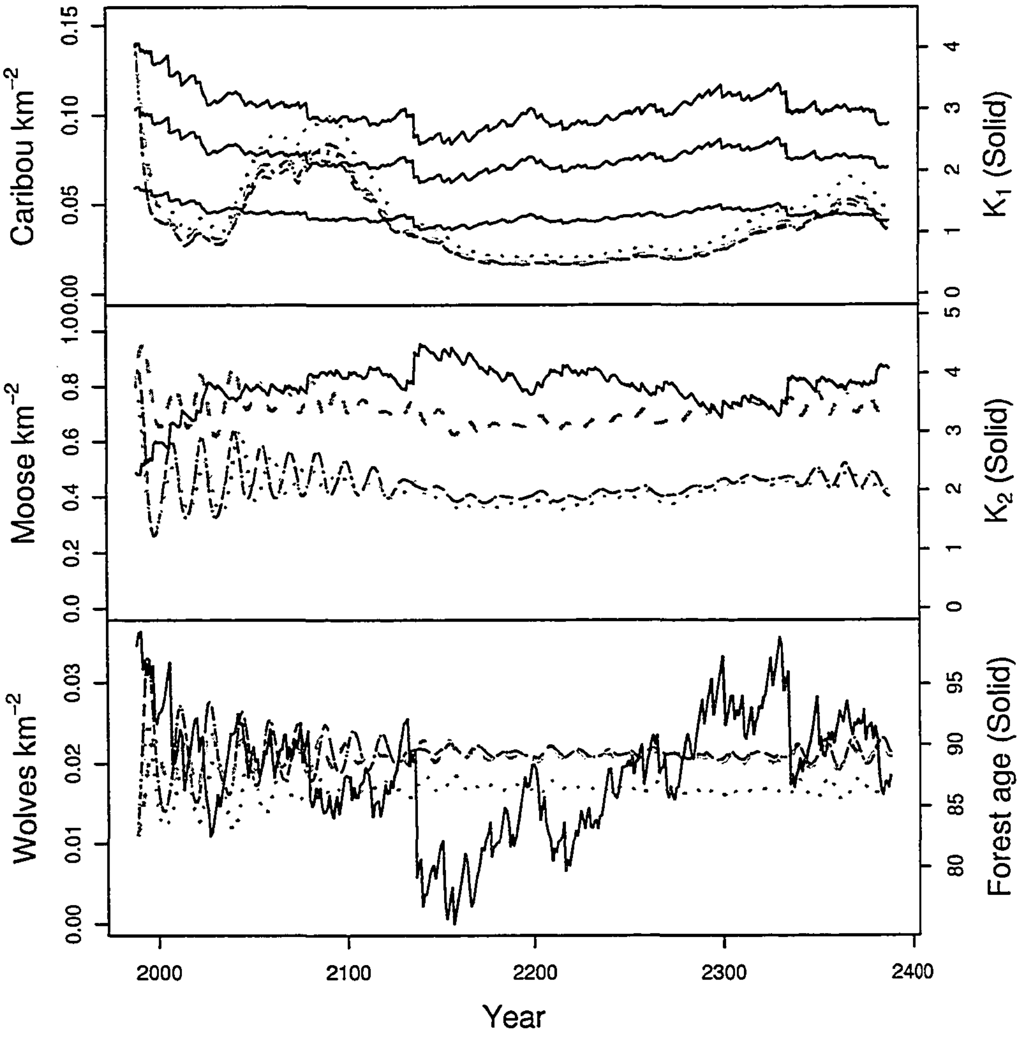


Figure 4.5: Model 6 projected trends with $K_{1,max}$ varying on (3,5,7). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $K_{1,max}$ = 3, 5 and 7 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

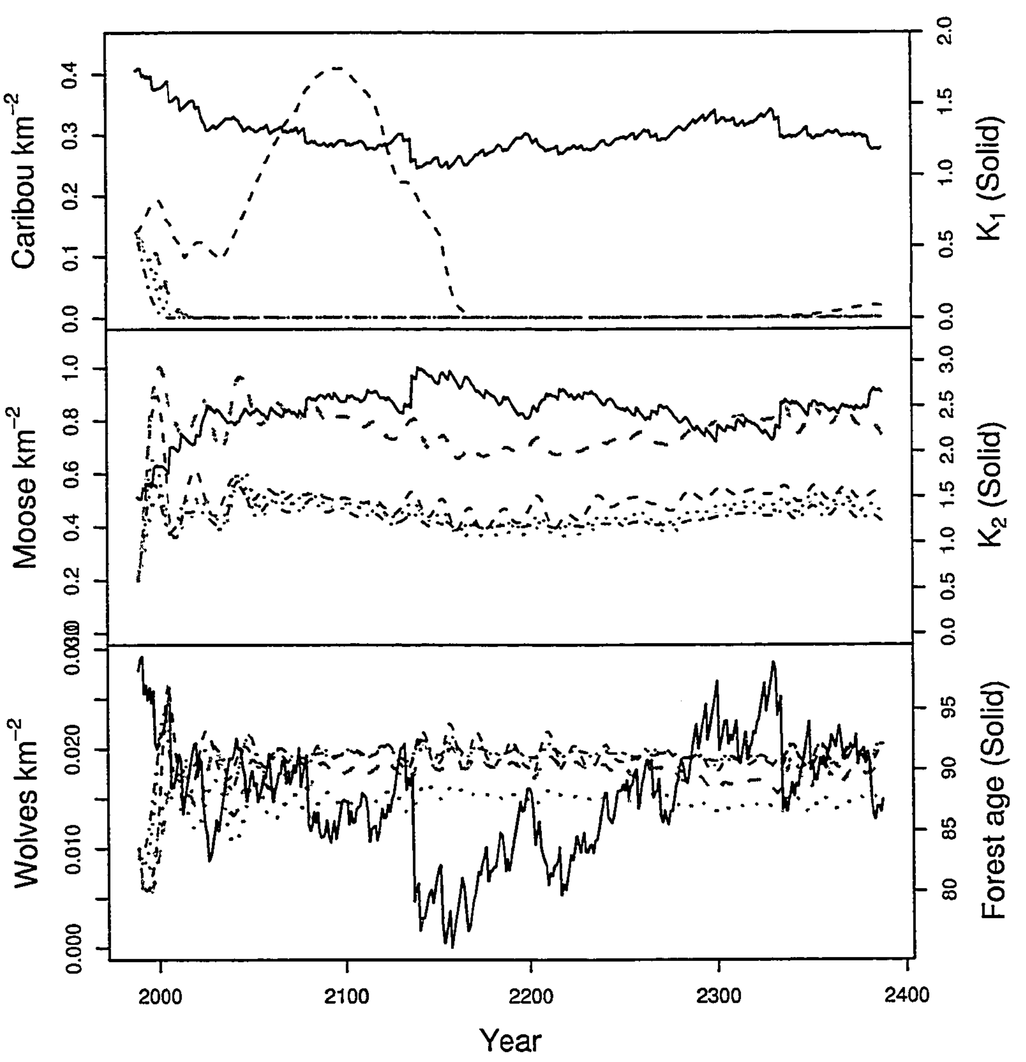


Figure 4.6: Model 5 projected trends with g_{half} varying on (0.05, 0.1, 0.15). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $g_{half} = 0.05, 0.1$ and 0.15 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

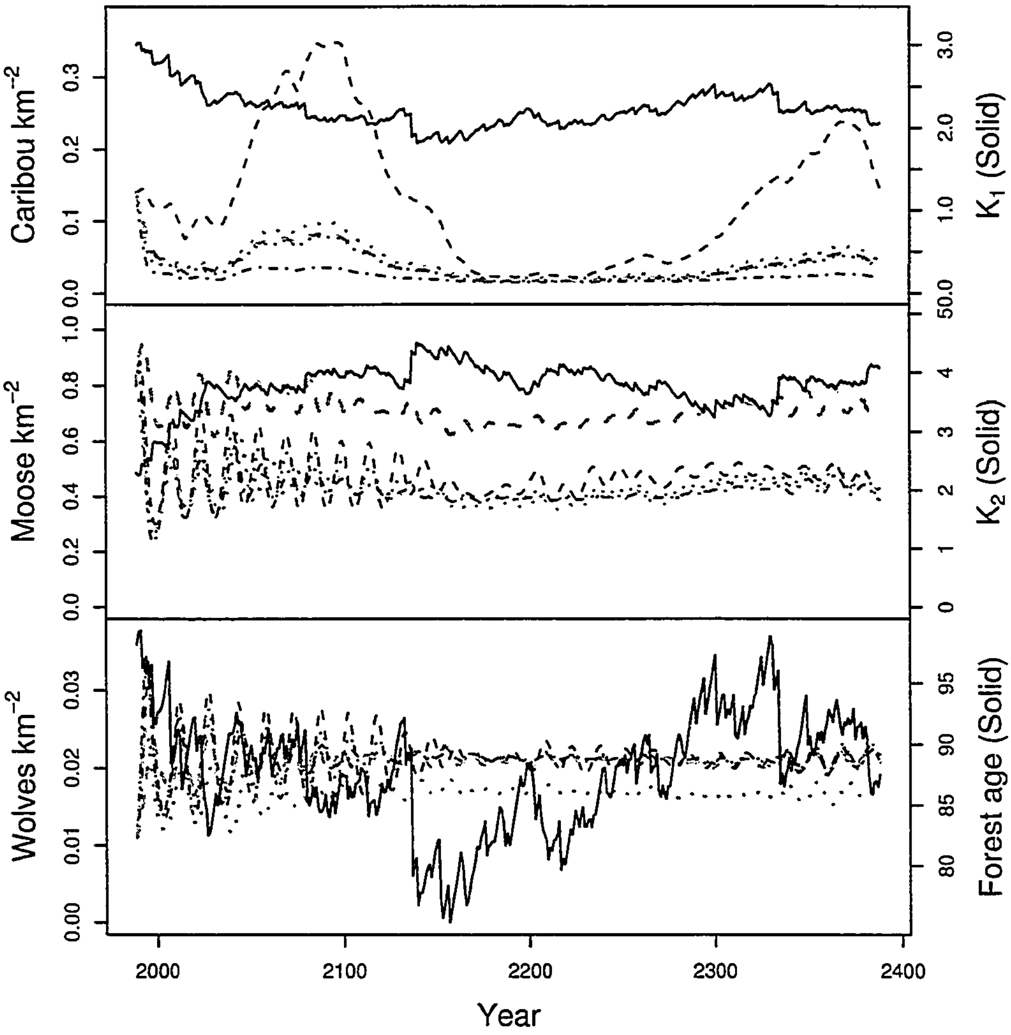


Figure 4.7: Model 6 projected trends with g_{half} varying on (0.05, 0.1, 0.15). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $g_{half} = 0.05, 0.1$ and 0.15 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

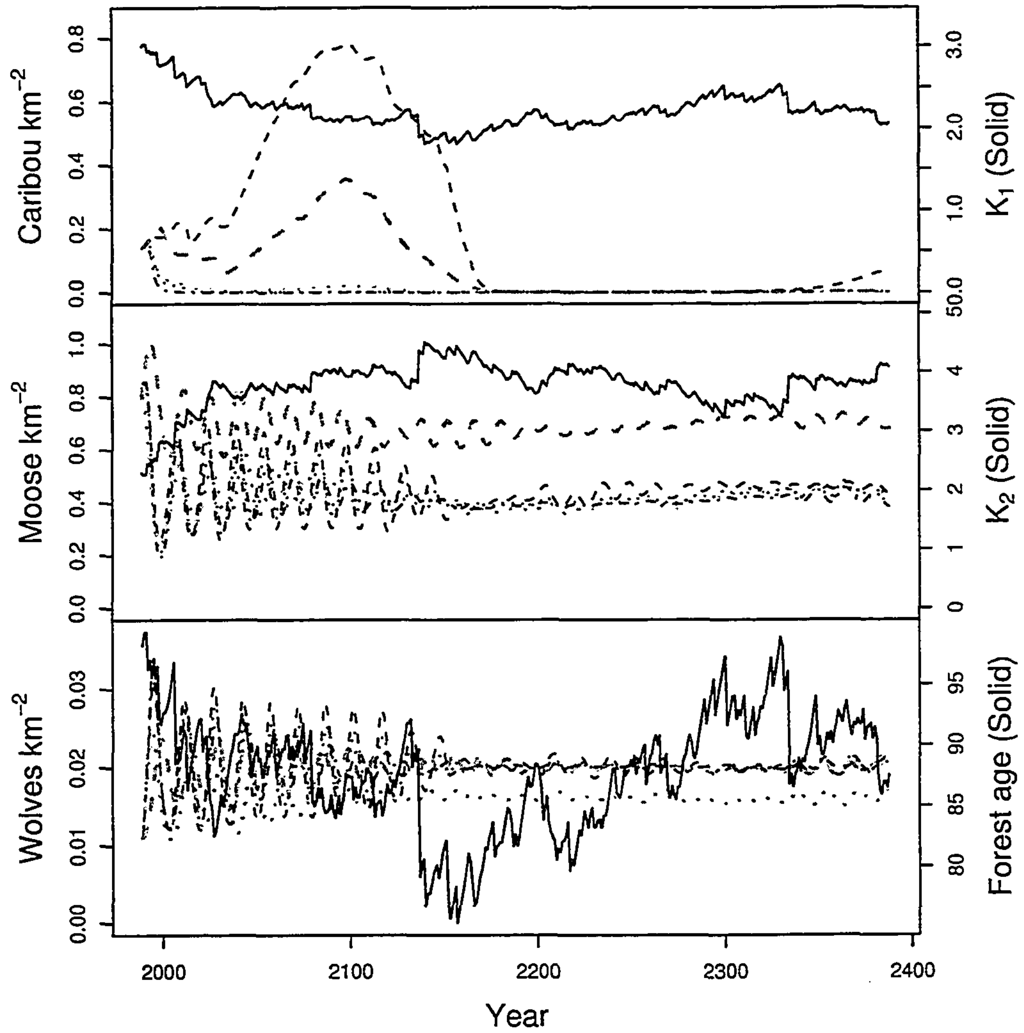


Figure 4.8: Model 7 projected trends with g_{half} varying on (0.05, 0.1, 0.15). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $g_{half} = 0.05, 0.1$ and 0.15 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

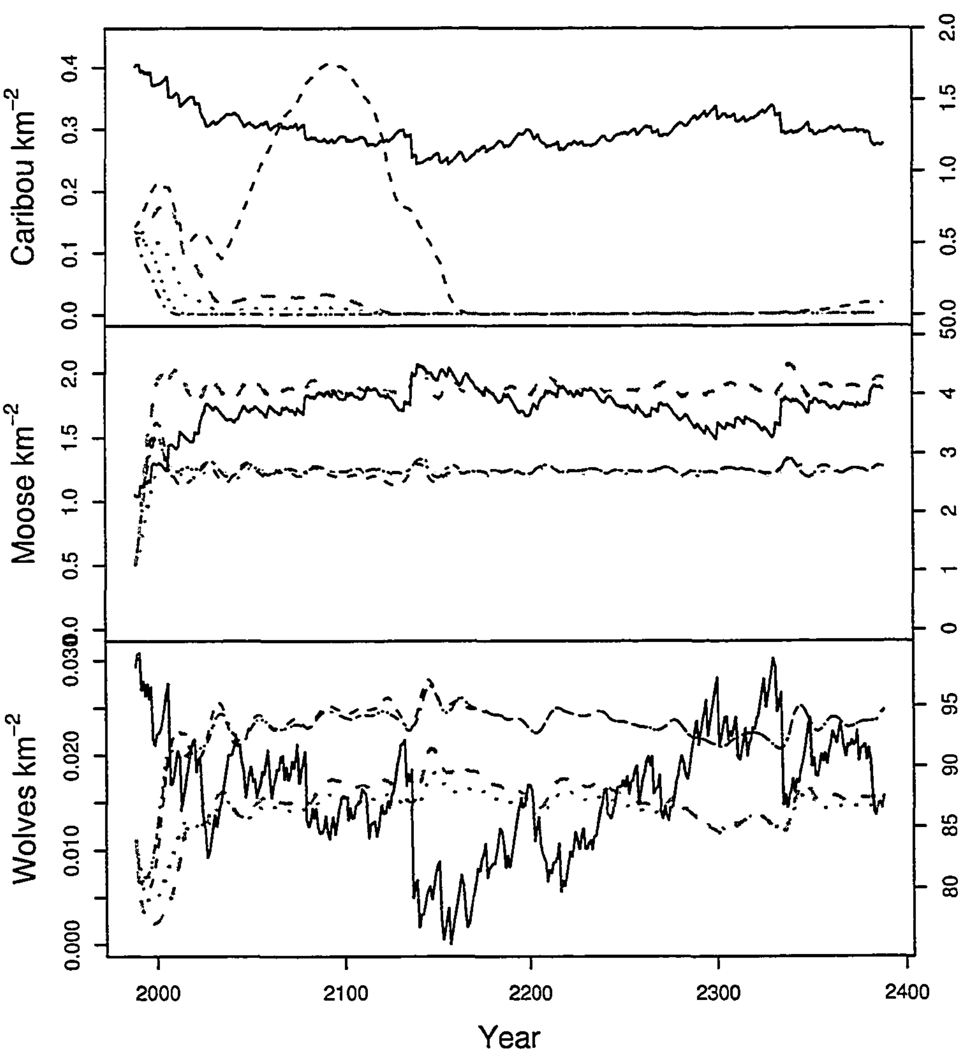


Figure 4.9: Model 8 projected trends with g_{half} varying on (0.05, 0.1, 0.15). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $g_{half} = 0.05, 0.1$ and 0.15 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

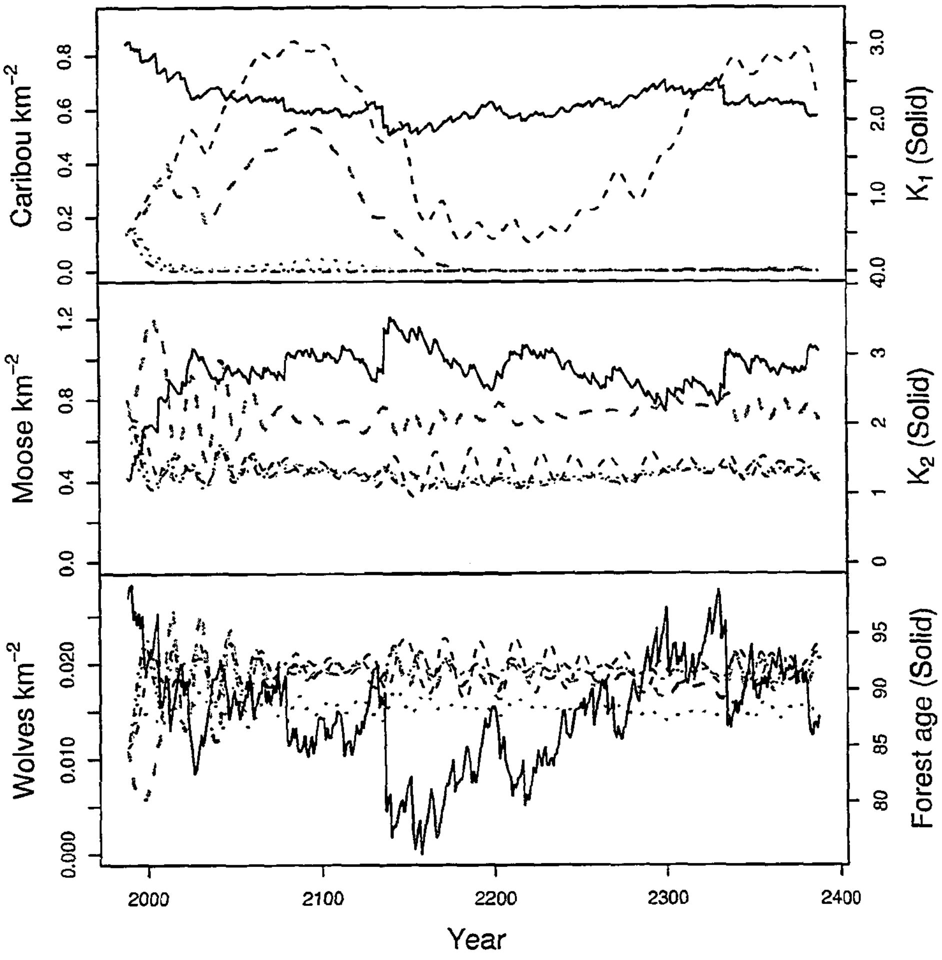


Figure 4.10: Model 7 projected trends with τ varying on (0.5, 1.0, 1.5). Solid line shows the average age of the forest. Dashed, dotted and dashed-dotted lines show species abundance prediction when $\tau = 0.5$, 1.0 and 1.5 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

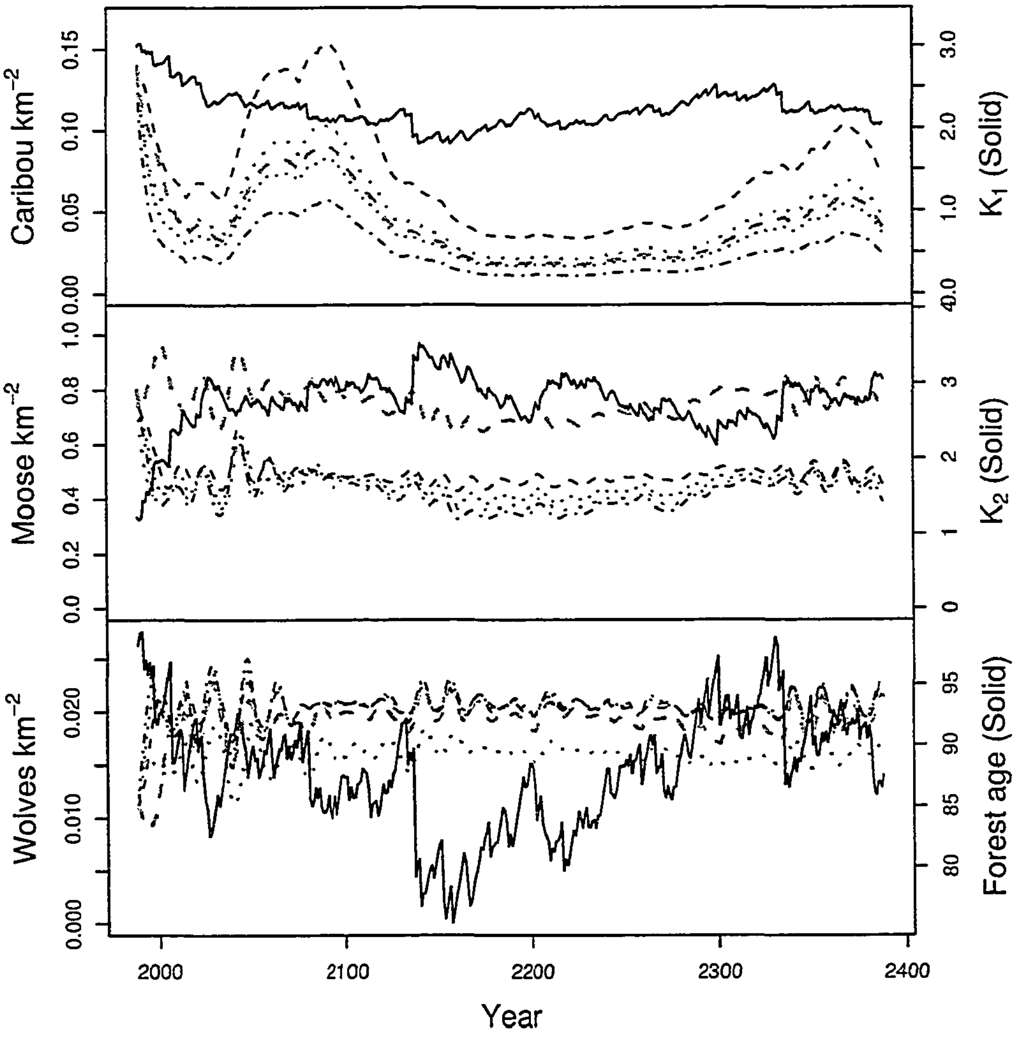


Figure 4.11: Model 6 projected trends with $a_{1,max}$ varying ±50%. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $a_{1,max}$ = 50%, 100% and 150% of its estimated value respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

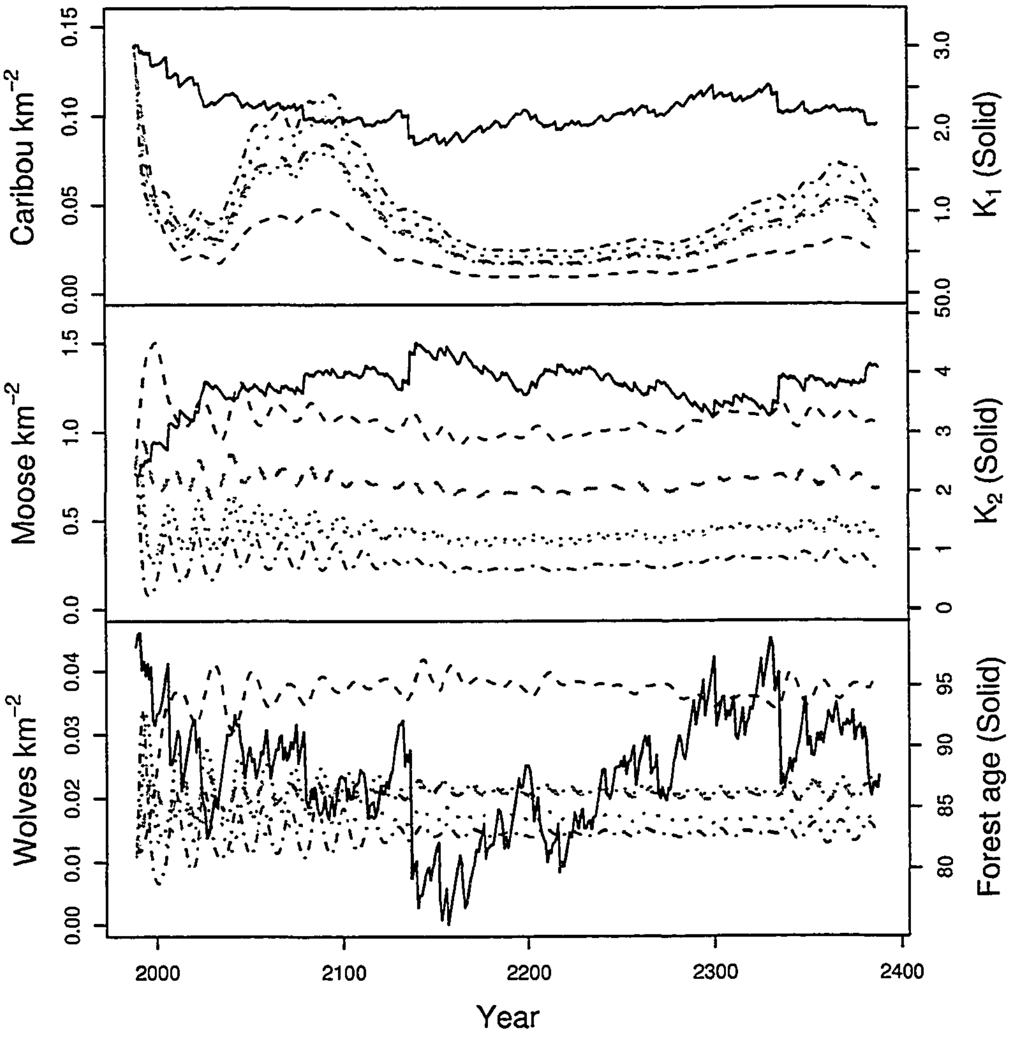


Figure 4.12: Model 6 projected trends with $a_{2,max}$ varying ±50%. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $a_{1,max}$ = 50%, 100% and 150% of its estimated value respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

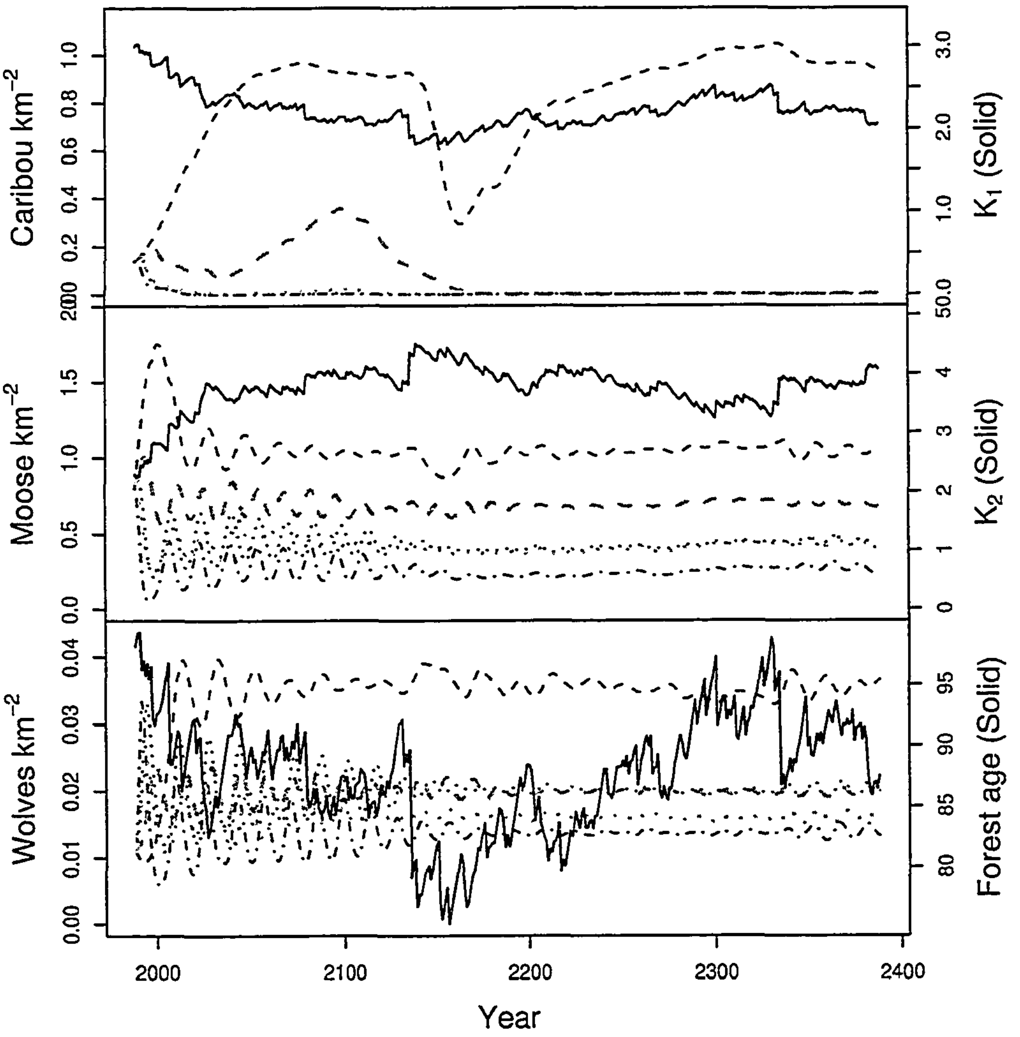


Figure 4.13: Model 7 projected trends with $a_{2,max}$ varying ±50%. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $a_{1,max}$ = 50%, 100% and 150% of its estimated value respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

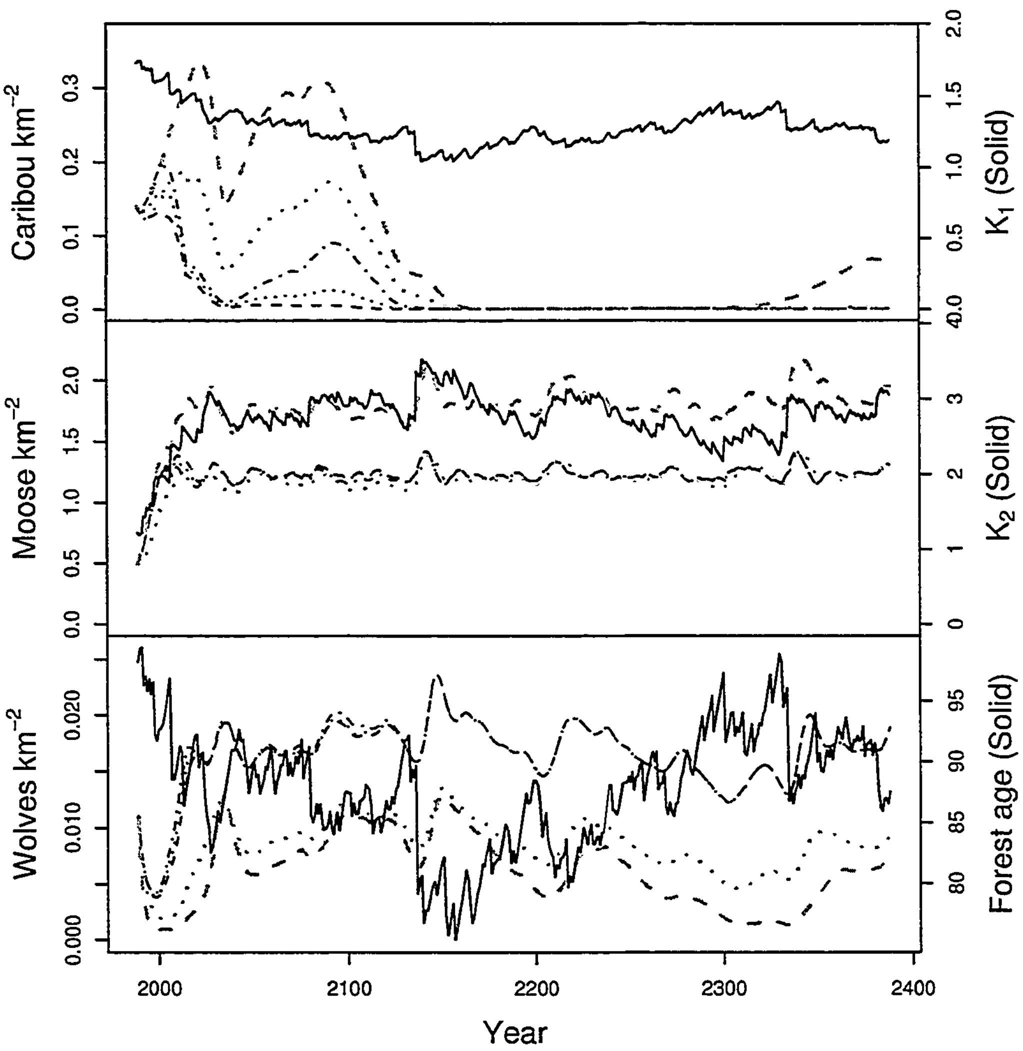


Figure 4.14: Model 8 projected trends with r_1 varying on (0.17, 0.19, 0.21). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when $r_1 = 0.17$, 0.19 and 0.21 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

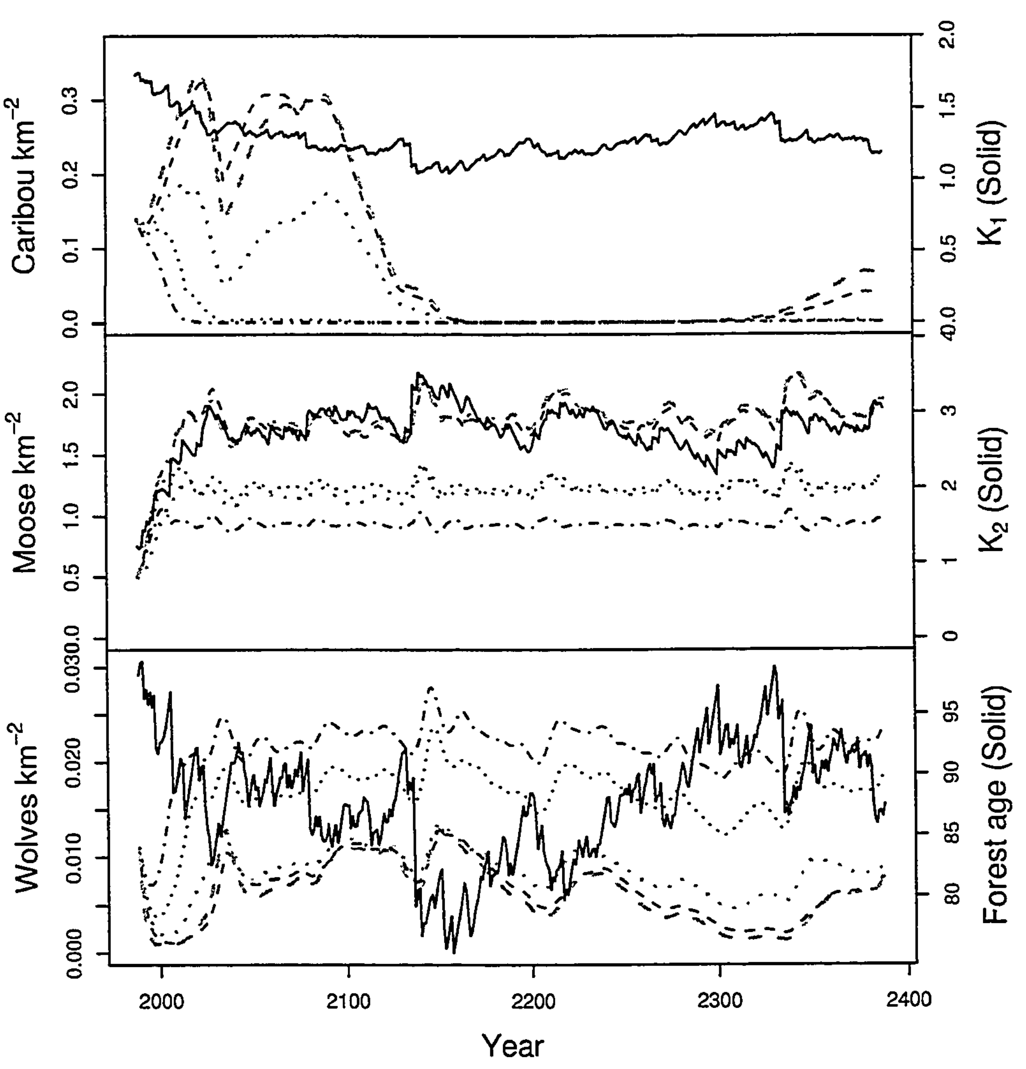


Figure 4.15: Model 8 projected trends with ε varying on (0.025, 0.035, 0.045). Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed, dotted and dashed-dotted lines show species abundance prediction when ε = 0.025, 0.055 and 0.045 respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest.

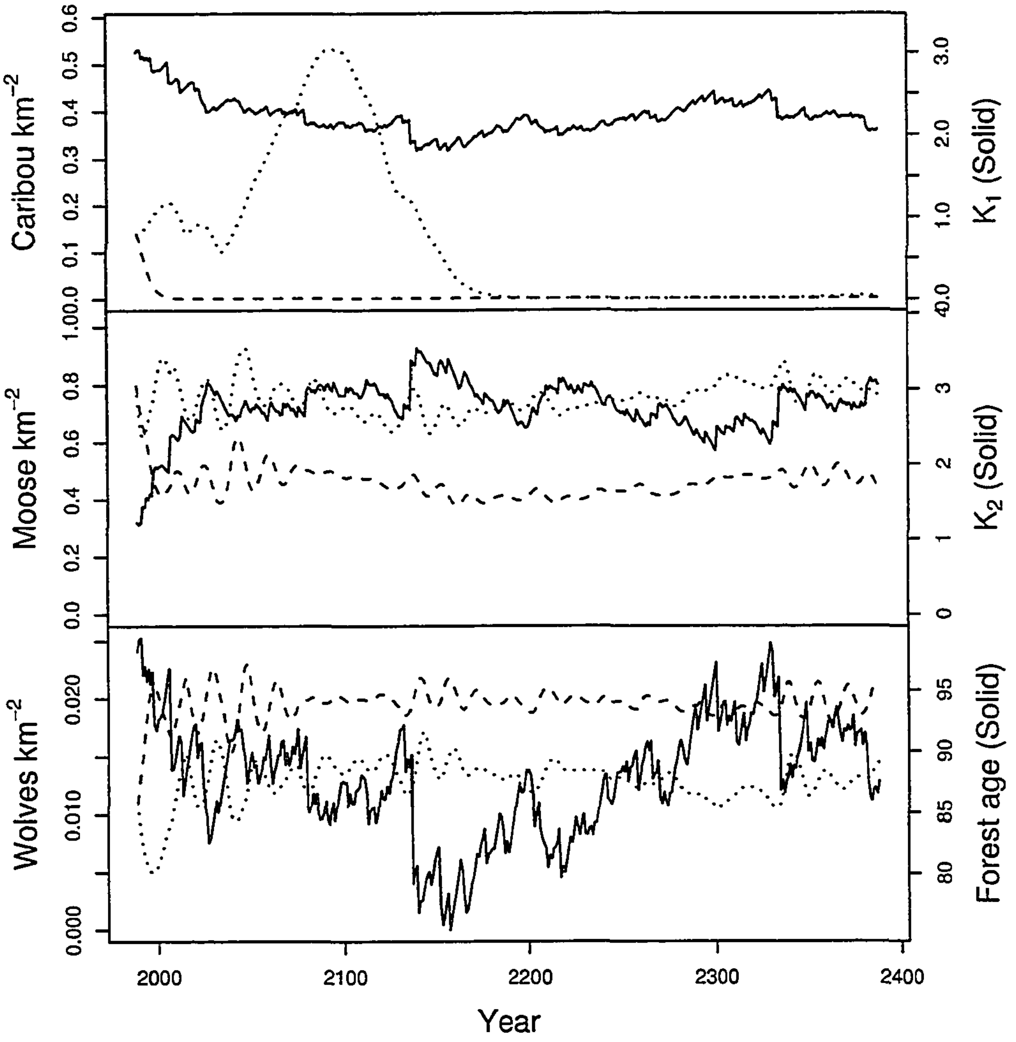


Figure 4.16: Model 5 performance when wolf control and moose harvest are simultaneously implemented. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed and dotted lines show species abundance prediction under status-quo and with dual-control respectively.

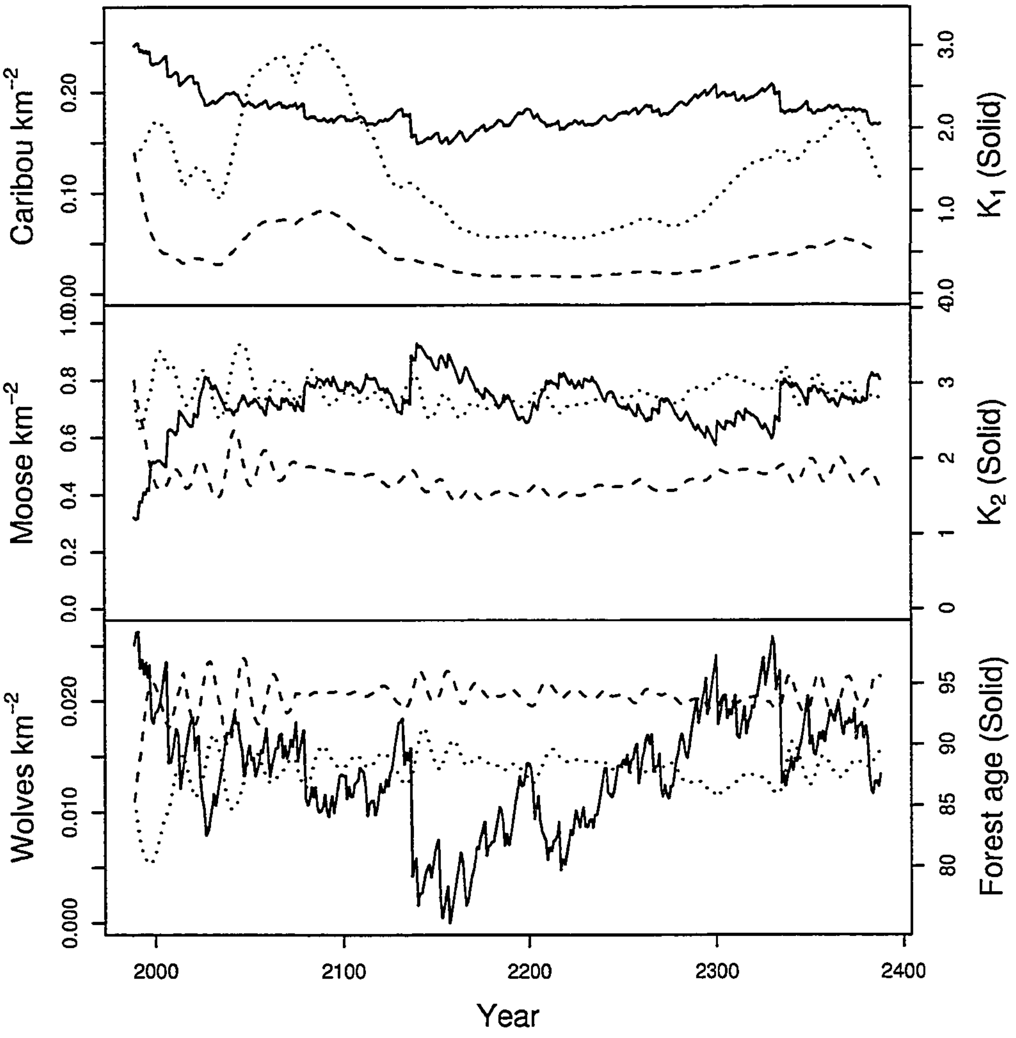


Figure 4.17: Model 6 performance when wolf control and moose harvest are simultaneously implemented. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed and dotted lines show species abundance prediction under status-quo and with dual-control respectively.

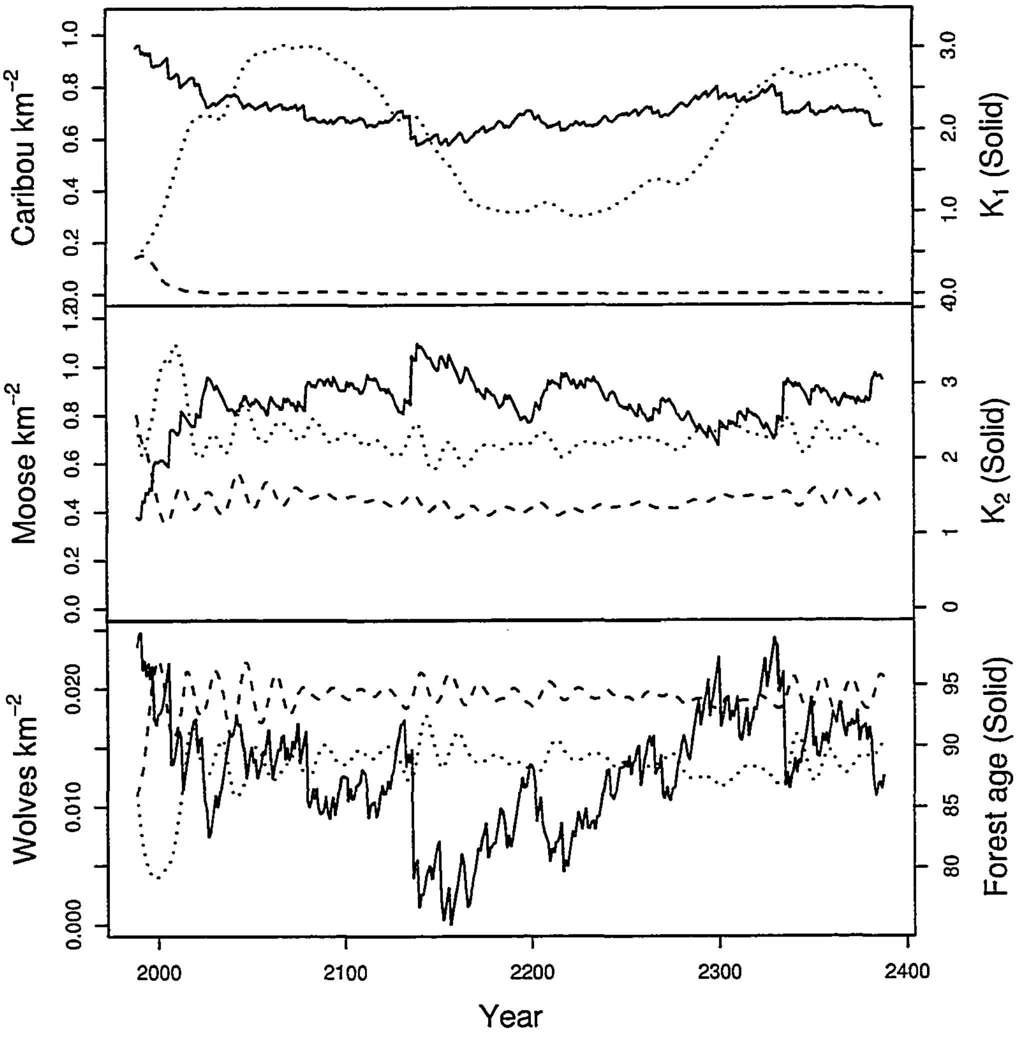


Figure 4.18: Model 7 performance when wolf control and moose harvest are simultaneously implemented. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed and dotted lines show species abundance prediction under status-quo and with dual-control respectively.

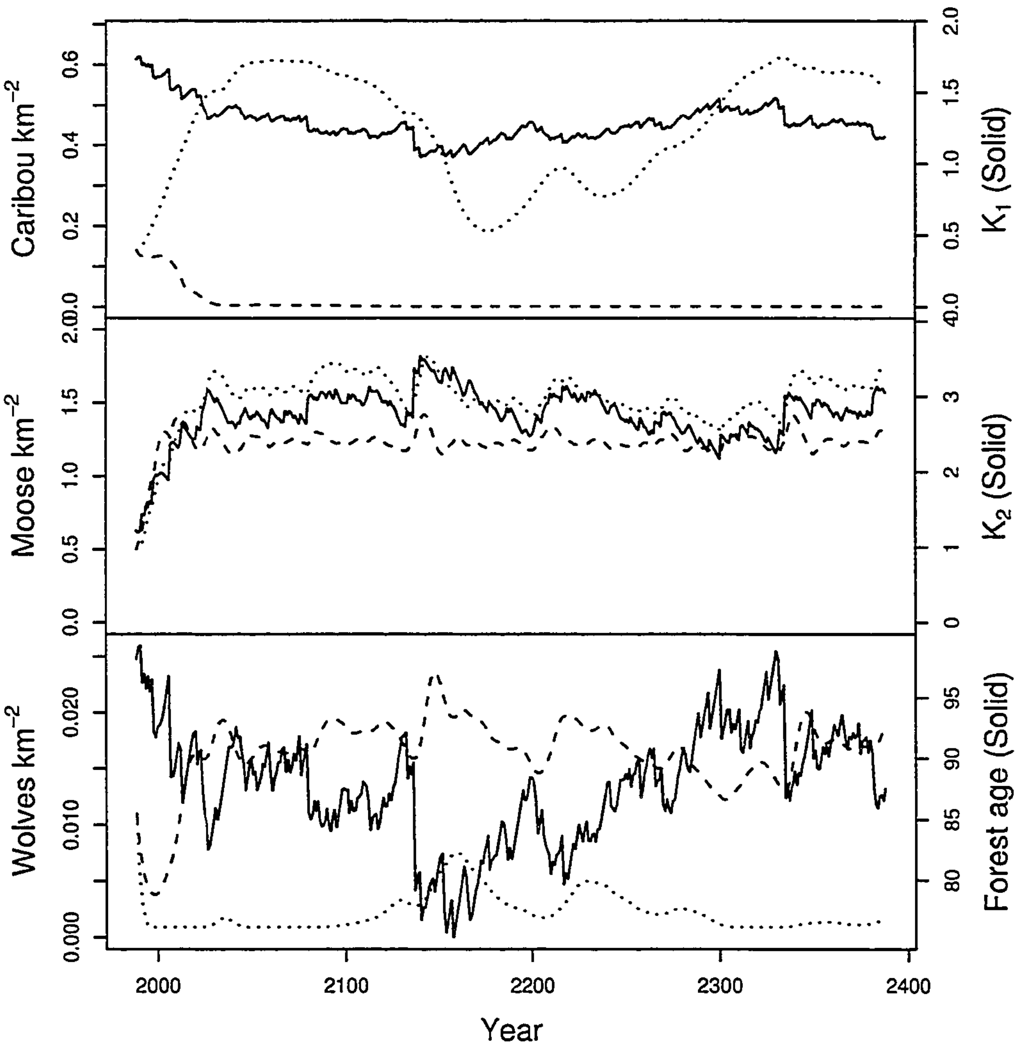


Figure 4.19: Model 8 performance when wolf control and moose harvest are simultaneously implemented. Solid lines show the values of K_i and the average age of the forest as fires are simulated over a 400 year period. Dashed and dotted lines show species abundance prediction under status-quo and with dual-control respectively.

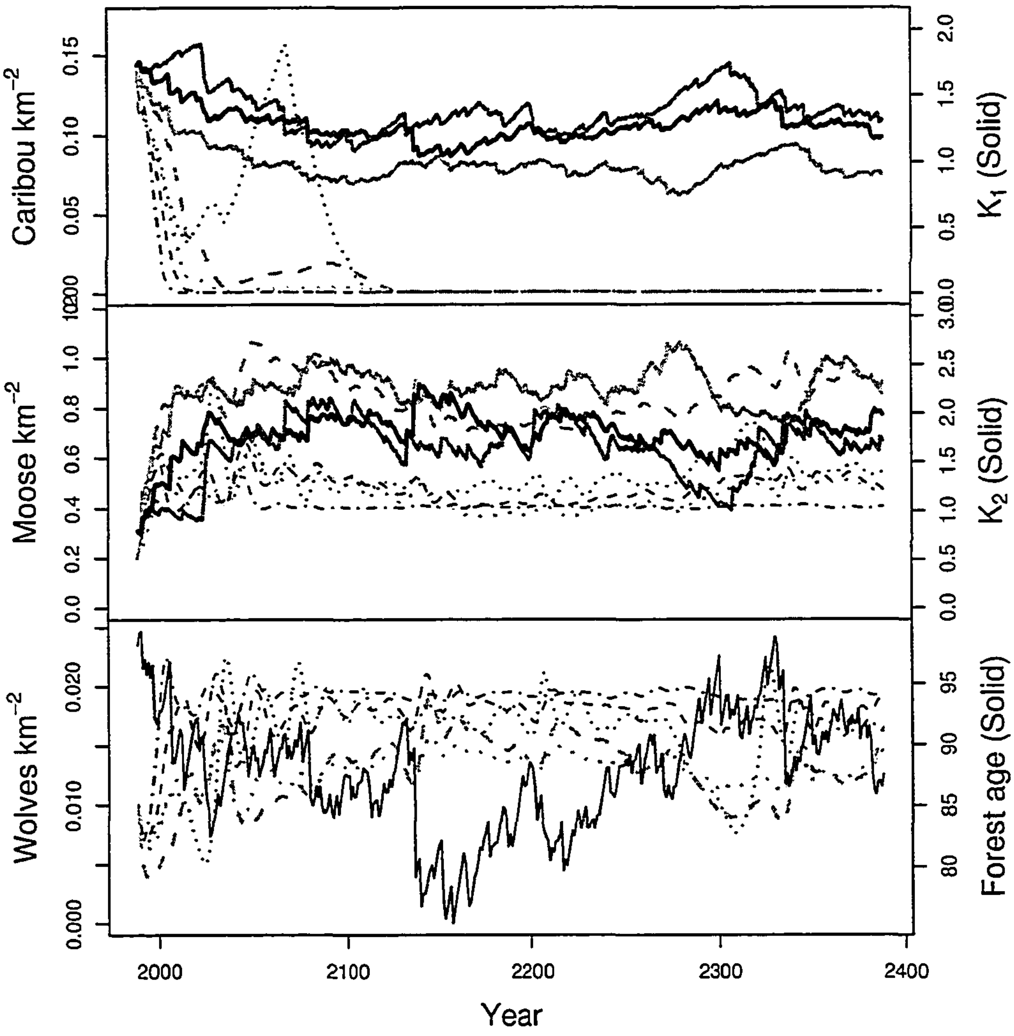


Figure 4.20: Model 5 fire regime sensitivity. Dashed, dotted and dashed-dotted lines show species abundance prediction when fire regimes produce status-quo, large-old and small-young patches respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest. Thick solid light, medium and dark grey lines represent K_i from fire regimes produced by status-quo, large-old and small-young patches respectively.

4.3 Discussion

The major objective of this chapter was to examine the effect of environmental variation on population dynamics. This was accomplished by examining the sensitivity of population trends to parameter values that changed with landscape conditions. This revealed the parameters to which system behaviour is most sensitive and the parameters that may have management potential for the recovery of caribou.

Only one modelled dynamic did not lead predominantly to the extirpation of caribou populations when environmental variation was added: a system with a Type 3 functional response of wolves preying on caribou (Model 6). I demonstrated that few manipulations in parameters compensate for declines in caribou in all other models. Fluctuations in landscape conditions had little effect on declining trends and recovery occurred in only a few cases. Predominantly, caribou populations only escaped extirpation if effective rates of search were low. This occurred either when the effective rate of search was systematically reduced by 50%, or when it was inversely scaled to the density of moose (Model 7).

Many of the simulated cases showed apparent cycling in moose and wolves. This occurred because the disturbances created slightly younger forests and increased the parameter K_2. This generally resulted in 20-year fluctuations of 0.2 to 0.4 moose/km^2. Cycles were often coincident with increases in caribou densities when parameter combinations favoured caribou persistence in the short-term. During such phases, wolves responded numerically to high caribou densities, which exacerbated the periodic behaviour between moose and wolves. Cycling was not a predominant pattern given the parameter values that were used, however; the parameters having been taken from maximum likelihood fits of models to short term data. Interestingly though, moose in-

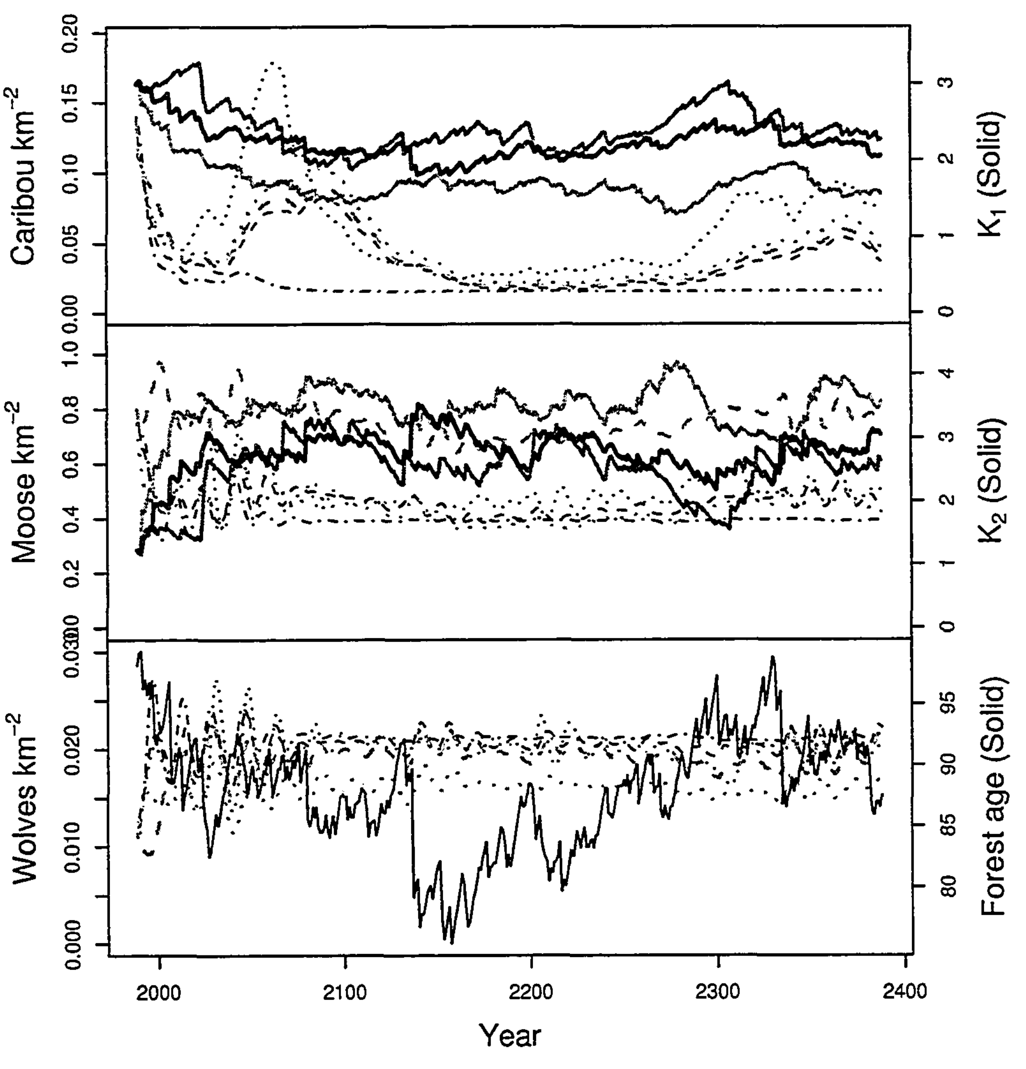


Figure 4.21: Model 6 fire regime sensitivity. Dashed, dotted and dashed-dotted lines show species abundance prediction when fire regimes produce status-quo, large-old and small-young patches respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest. Thick solid light, medium and dark grey lines represent K_i from fire regimes produced by status-quo, large-old and small-young patches respectively.

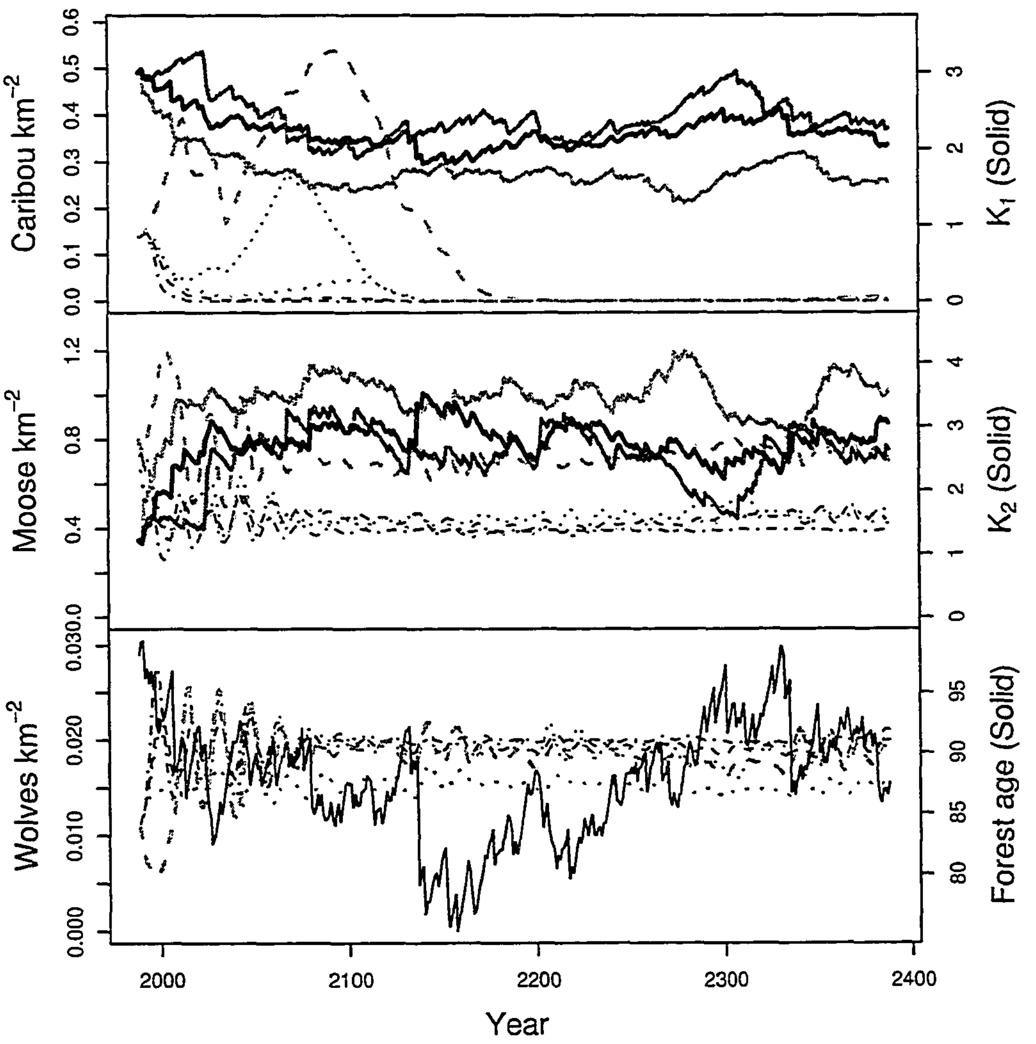


Figure 4.22: Model 7 fire regime sensitivity. Dashed, dotted and dashed-dotted lines show species abundance prediction when fire regimes produce status-quo, large-old and small-young patches respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest. Thick solid light, medium and dark grey lines represent K_i from fire regimes produced by status-quo, large-old and small-young patches respectively.

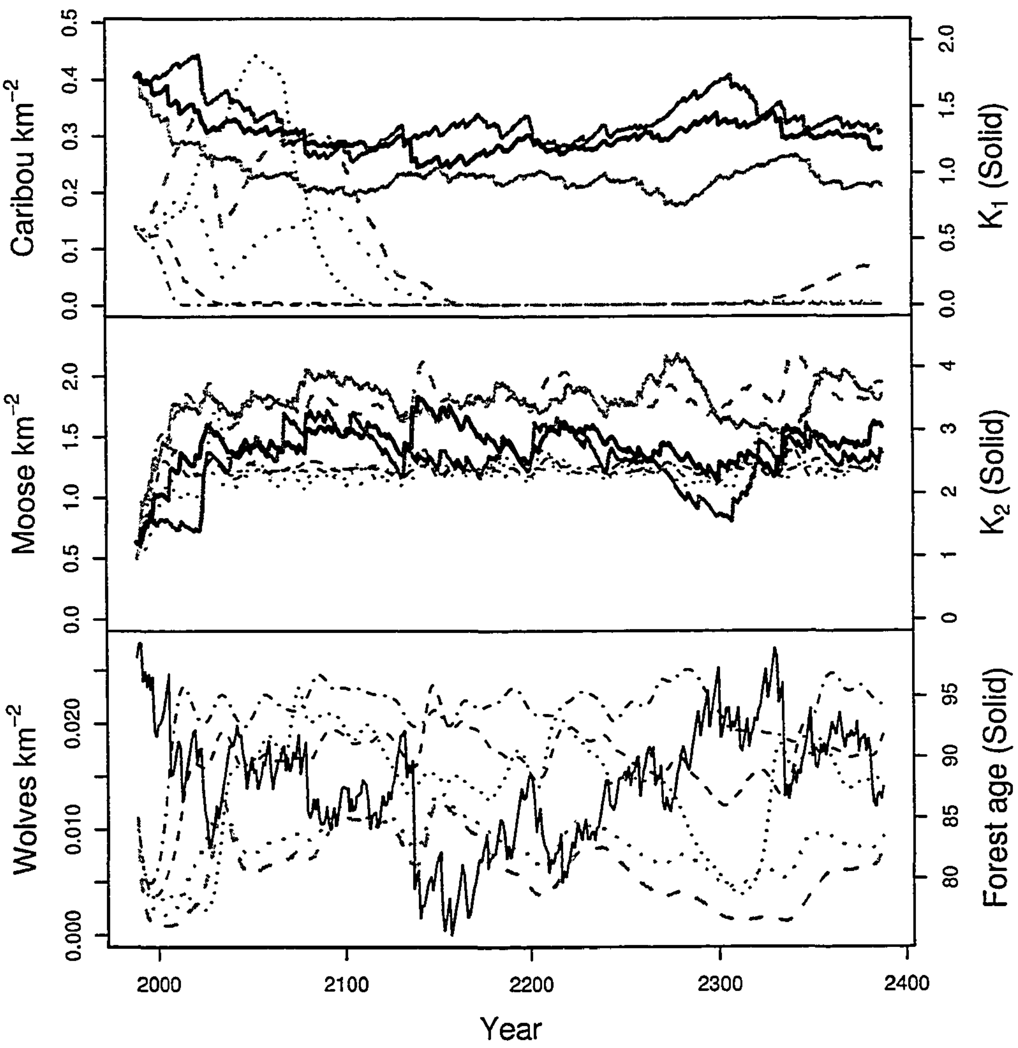


Figure 4.23: Model 8 fire regime sensitivity. Dashed, dotted and dashed-dotted lines show species abundance prediction when fire regimes produce status-quo, large-old and small-young patches respectively. Thick grey dashed and dotted lines represent wolf control and increased moose harvest. Thick solid light, medium and dark grey lines represent K_i from fire regimes produced by status-quo, large-old and small-young patches respectively.

crease phases produced roughly the same net increase in a decade as was seen in the empirical trends in the Redrock Prairie Creek empirical trends. Since the increases in moose were coincident with increases in K_2, this suggests that the observed moose increases between 1989 and 1998 in the RPC may also have been induced by an increase in K_2.

Model 5 demonstrates one of the more important issues that distinguishes caribou from moose. Because moose carrying capacity is at its highest in young forests, disturbances create pulses of habitat. Due to the higher reproductive rate and lower vulnerability to predation, this results in rapid increases in moose abundance soon after disturbance. Conversely, disturbances create instantaneous losses of caribou habitat, causing declines in caribou abundance. The fact that it takes $\approx$80 years to rebuild half of the caribou carrying capacity means that caribou are slow to regain high rates of increase following disturbance. This, compounded with the fact that caribou are more vulnerable to predation than moose, means that caribou recover very slowly following disturbances. The disturbances are normally also followed by increases in moose densities as well a numerical response in wolves, which further exacerbates the caribou decline.

If the relative reproductive rate of caribou relative to moose was higher, caribou populations could reproduce faster before wolves responded numerically to moose increases. If caribou preferred younger forests, they would not suddenly lose habitat after disturbances, whereas currently they face a long wait for it to rebuild. If they were less vulnerable, they would not face the same level of predation from wolves while trying to rebuild after a decline. In reality, all of these factors conspire against caribou simultaneously, making it very difficult for caribou to persist in the presence of wolves and moose.

Under natural conditions caribou herds have persisted despite this imbalance. This suggests two possibilities: 1) the estimated rates I used were not representative of a system undergoing natural fluctuations in landscape condition, or 2) the relationship I built caused the parameters to vary too much in relation to environmental change. I believe that because the parameters were estimated from a system where moose and wolves were increasing and caribou were decreasing, that some parameters may have been biased (case 1). The most likely biases would be the birth rate of moose and the effective rate of search on moose. The estimated values fit the data during a phase of rapid growth, but with a near three-fold increase in 10 years it is possible that the estimates were not representative. Recall that a_2 was estimated to be $\simeq 6$, which was much lower than the estimate from Messier (1994). It is possible that moose recruitment was high partly due to low capture rates by wolves; a situation that may not necessarily persist as wolf densities increase and territories expand. This is an important bias to consider. Higher a_2 and lower r_2 both predict higher stable densities of caribou.

In this chapter, I modelled forest succession, disturbance and the sensitivity of parameter values to age structure and patch size. I chose not to model the effect of seismic line explicitly because it can be easily interpreted from a sensitivity analysis of the effective rate of search as well as carrying capacities. Increases in the quantity and distribution of seismic lines should cause the effective rate of search of wolves to increase on both prey species. It is possible that prey species may avoid seismic lines, however (Oberg et al. 2002), causing lower encounter rates to compensate for increases in search rates. Any explicit accounting of seismic line development should include their effect in the calculation of the effective rate of search. Their effect can be included in two ways:

1. Include the seismic lines into forest age calculations by "netting-down" the total forest area to account for seismic disturbances (length×width

= area disturbed).

2. Include effect on travel rates such that the effective rate of search increases with D, the total length of seismic lines per km^2 (i.e., $a_{ij} = a_{i,max}\frac{d_{max}D}{d_{half}+D}$, where d_{max} is the maximum scaling factor and d_{half} is a half-saturation constant)

3. Include the fact that caribou avoid roads and high-impact seismic lines so the encounter rate in the immediate vicinity of these features is lower.

Regardless of which model structure is used to describe the population dynamics, caribou face imminent extirpation. Only extreme values on key variables let caribou survive increases in wolf populations and the resulting increase in predation on caribou. The exception is incorporation of Type 3 functional response, which is known to be incapable of causing extirpation of a prey species. The explicit assumption that predation rates fall to zero at low caribou densities may be optimistic, however. The Type 3 form does not account for explicit time budgets of predators targeting individual prey species (see Chapter 5 for the derivation of an explicit mechanism). The reason the Type 3 form has gained notoriety is that it addresses an issue of interest to biologists (i.e., prey switching), but it does not model the process explicitly in relation to the density and availability of each prey type. It erodes the predation rate in relation to the density of one species, but ignores the density of the other species.

This chapter demonstrated the dynamics that arise when different functional forms are used and different parameter ranges are applied to a dynamic system. Instances where caribou populations were capable of persisting were very few and required setting parameters to extremely "caribou-friendly" values. The prevailing trend is that wolves respond numerically to increases in moose densities. When wolves reach densities in excess of 8 animals /1000 km^2 , caribou declines ensue. I looked for situations where erroneous parameter estimates may have biased predictions toward a pessimistic view of expected caribou trends but found very few cases that predicted persistence. A few combinations of "caribou-friendly" parameter values in conjunction with moose harvest and wolf control permitted caribou persistence, but these were extreme cases of being optimistic on all fronts while applying management strategies that directly manipulate the proximate causes of caribou declines.

Clearly, the most significant mechanism is the functional response. Combined with the density of wolves, the *total response* is what drives caribou to extirpation. An examination of the sensitivity of lowering the effective rate of search by 50% showed that this was not sufficient when wolf densities were high - again because of total response factor. Wolf reductions (achieved by adding 0.2 to the wolf mortality rate) increased caribou survival in all cases. In conjunction with moose harvests, and assuming a few more optimistic parameters, caribou were able to avoid extirpation. In all cases, caribou persistence was accompanied by wolf densities below 8 per 1000 km^2. The only exception was Model 7, where the a_{1k}s were very low because τ was set at 0.5 (roughly the density range within which moose fluctuated). This allowed caribou to persist at slightly higher wolf densities.

The results did not show significant improvements to caribou persistence under any alternative fire regimes. One scenario was slightly older on average with larger patches; the other was slightly younger on average with smaller patches. Since the models were designed to be sensitive to the proportion of large old growth patches, the scenario with ignition rate = 0.002 and spread rate = 0.19 led to the highest caribou densities. Again, however, this was inadequate to allow caribou to persist despite the fact that conditions on average improved relative to the starting conditions, which were precisely the conditions present in the RPC in 2000.

It is possible that I have assumed base parameter values that do not favour caribou persistence. However, I argue that since I have calibrated the starting conditions so that simulations begin with parameters that are the same as the estimates, that the fluctuations are reasonably bounded. A notable example is g_{half}, for which I argue that spanning the values 0.05, 0.10 and 0.15 provides a good sense of the potential range of emergent behaviour. Still, the most optimistic value (0.05) did not allow caribou to persist except in Model 6, which already persisted without adopting a value of 0.05. The base values of $a_{1,max}$ used for the various models were scaled so that changes to the landscape would cause a_1 to fluctuate in proportion to relative quantities of large old growth patches. The initial proportion of large old patches was $\approx$11%, but disturbances caused the proportion to decline. Since a_1 appears to be the most important quantity determining the rate of caribou declines, its relationship to landscape conditions needs to be investigated further. That said, however, simulating with a 50% reduction to its base value did not bring about recovery of caribou.

I contend that the evidence presented here casts doubt on the possibility that caribou are capable of persisting. It remains possible that the estimated parameters reflect conditions that will not persist. There is also the possibility that the functional response that describes predation on caribou is Type 3. I have deliberately left this discussion until the end. There is much debate about the sigmoidal form of the functional response. Dale et al. (1994) claim that caribou kill rates appear to follow a Type 2 form, Messier (1994) concludes a Type 2 for wolves preying on moose, and others have shown that wolves continue to hunt caribou even when moose become far more abundant (Hayes and Harestad 2000a). Others have elected to use the Type 3 functional response because they felt that the presence of so many prey types virtually guaranteed that wolves would switch to another prey type when one became in short supply (Boyce and Anderson 1999). The Type 3 assumption of Model 6 requires further justification. The following chapter looks for mechanisms whereby predator and prey behaviour can occur such that fine scale interactions cause the use of space to lead to apparent switching.

Chapter 5

Population dynamics consequences of fine scale spatial interactions

Introduction

Functional responses can cause predator-prey models to predict wildly different qualitative behaviours, thus the choice of the functional response form is widely debated. The most frequently discussed in predator-ungulate ecology are the hyperbolic and sigmoidal functional responses, also known as the Type 2 and 3 forms (see Figure 5.1). The Type 2 form (Holling 1965) is solidly based on individual level mechanisms, simultaneously satisfing mass action and maximum physiological rate principles. Multiple-prey systems modelled with Type 2 functional responses predict instability and/or extirpation of one prey type in all but a narrow domain of conditions. Phenomenological forms, such as the ratio-dependent functional response (Arditi and Ginzburg 1989; Akcakaya 1992; Gutierrez 1992) and the Type 3 functional response have been used to stabilize predator prey models. However criticism against using them is that they are not mechanistically based (Abrams 1994; Abrams 1997; Turchin 2002). Nevertheless, the Type 3 has been used in a wolf-ungulate system, and considered to be consistent with empirical trends (Boyce 1992; Boyce and An-

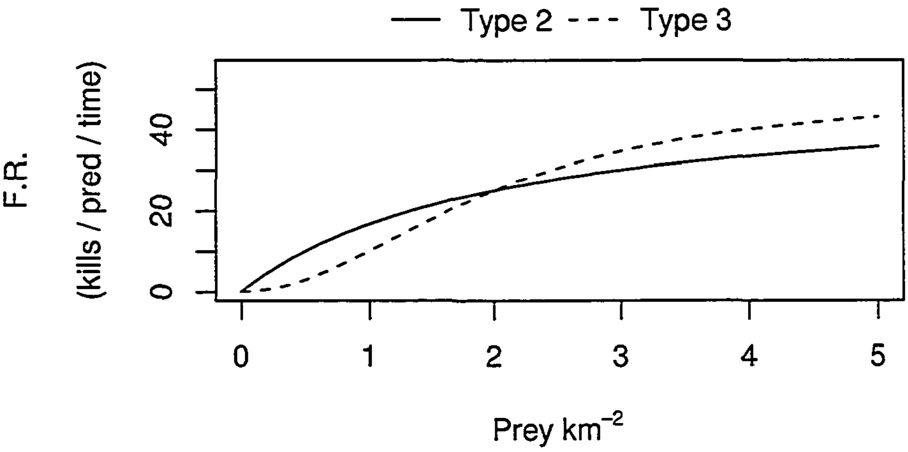


Figure 5.1: Plots of Type 2 & 3 functional responses. Functional response (F.R.) is in units of kills per predator per unit time.

derson 1999). The concave portion on left-hand side of the curve is attributed to predator search image formation and learning and remains intriguing, because the shape captures generalist predation in multiple prey systems, where *switching* among prey types has important consequences to broad scale population dynamics. Still, demonstration of a clear mechanistic basis for it is lacking. I believe that such a mechanistic basis can exist in explicit spatial habitat selection and foraging behaviour. In this chapter, I show how fine scale spatial behaviour can predict spatial distributions that give rise to "realized" switching when viewed at a broader spatial scale.

I use a model to predict the relative distribution of animals across a spatial grid. I assume that indistinguishable behavioural mechanisms operate at fine spatial scales, but that the aggregate sum of these small-scale events leads to empirically observed spatial distributions and trophic interactions. The mechanisms are made up of fine-scale decisions that balance energetic gains from feeding against risks of mortality. The functional response determines feeding rates for predators and predation rates for prey. I use a Type 2 functional response to calculate these rates across a spatial grid. A computer algorithm redistributes animals such that energetic gains and losses are equal for each animal in each cell. When the kills in each cell are aggregated, apparent prey switching can be an emergent pattern of spatial dynamics. This has important consequences to population dynamics.

5.1 Background

In pursuit of enhanced understanding, biologists are lured into exploring patterns with finer detailed data and at smaller spatial scales. Some would argue that modelling explicit spatial interactions gives no further perspective on population dynamics and the ecology of a system. The *Principle of Parsimony*, or *Occam's Razor*, suggests that we should look for a sufficiently predictive model that is as simple as possible to achieve the desired goal. This bounds the diversity of predictions possible from complex models. In addition, a system can get to the same end from different pathways (known as *equifinality* in systems theory). Looking at fine details should only be justified for two reasons: 1) a qualitative prediction cannot be reproduced without the detail, or 2) the more parsimonious explanation needs to be justified for lack of clear reasoning as to why the fine scale details can reasonably be ignored. In the case of predator-prey systems, I believe we need to demonstrate how explicit spatial interactions affect the functional responses of predators on their prey.

Stability and coexistence in predator and prey communities depend on many factors. If prey compete directly for resources, a dominant species can *competitively exclude* another (Gause's principle). *Apparent competition* between prey species is predator-mediated (Holt 1977), resulting from increased predation through a shared predator, when increased abundance of one prey lead to a higher abundance of predators and then more predation on the other prey. This favours neither coexistence nor stability. *Apparent mutualism* is the opposite phenomenon. Increased abundance of one prey type can alleviate predation pressure on another through satiation of the functional response (Abrams et al. 1998). By reducing densities of primary prey, predators also have been shown to reduce overall kill rates disproportionately as densities decline, known as *prey switching* (Murdoch 1969).

Theoretical work has shown that refuges can have a stabilizing effect on predator-prey interactions (Rosenzweig and MacArthur 1963; Hassel and May 1973). Optimally foraging predators, on the other hand, can destabilize dynamics (Krivan and Sikder 1999; Van Baalen et al. 2001; Bolker et al. 2003). When two prey species prefer different habitats, adaptive foraging may lead to prey switching when the primary prey declines in abundance (Murdoch et al. 1975; Oaten and Murdoch 1975; Fryxell and Doucet 1993), which tends to increase stability. Other stabilizing hypotheses have been proposed, including resource limitation in prey (Rosenzweig 1969; Gilpin 1972), interference among predators (Van der Meer and Ens 1997), and invulnerable pools of prey (i.e. refugia) (Abrams and Walters 1996).

A review by Briggs and Hoopes (2004) identifies three major cases whereby dispersal, combined with spatial and temporal heterogeneity, can promote increased population persistence and stability. They are:

1. An averaging across a number of out-of-phase unstable populations that gives rise to a stable global density.
2. Dispersal dynamics that result in apparent density dependence at local scales.
3. Spatial heterogeneity that arises from non-linear responses to local conditions.

I provide a mechanistic basis for the third case. It combines several concepts. I begin with the assumption that animals have evolved to maximize per-capita growth. I then assume that spatial distributions in heterogeneous environments come from behavioural decisions that are based on perceived growth rates in individual patches. Foraging by prey is based on food availability and predation risk. Foraging by predators depends on kill rates of prey and competition with other predators. Animals distribute spatially by balancing these factors across a spatial grid. This assumes that animals recognize the forage/risk tradeoffs among all cells in a grid, have full knowledge of the locations of other prey and predators, and that they effectively redistribute before any consumption of resources occurs.

Central to ecology and evolution is the concept that strategies favouring higher rates of reproductive success will predominate on evolutionary time scales. *Fitness*, or evolutionary success, is commonly accepted as the projection of progeny and genes into the future (Begon et al. 1990). I assume that if behaviour is determined by genes, and genes are passed on to future generations, then behaviour that improves the chance of passing on those genes must be favoured. In the following analysis, the measure of fitness is the per-capita rate of growth.

I build a behavioural model where each species evaluates fitness spatially and redistributes itself spatially such that no location is more fit than another (per-capita benefits are the same everywhere). This is known as an *Ideal Free Distribution* (IFD) (Fretwell and Lucas 1970). The IFD has gained notoriety as a method to test theories about the distribution of animals (Sutherland 1983; Kacelnik et al. 1992; Rozenzweig 1991; Van der Meer and Ens 1997). It has been used to used to study the effect of patch selection on competition (Grand and Dill 1999; Houston and Lang 1998), coexistence (Rozenzweig 1991; Grand 2002) and predation (Bernstein et al. 1999; Krivan and Vrokoc

2000). It is a logical choice for studying such problems because it has sound evolutionary, behavioural, and bioenergetic basis. What remains to be demonstrated is the effect that using a spatially explicit predator-prey IFD has on overall population dynamics. I show that an IFD of predators and prey using a Type 2 functional response can predict the spatial distribution of animals. Further, when kills are aggregated across all cells, a Type 3 functional response can emerge, thereby stabilizing population dynamics.

The rationale for this analysis is that it may demonstrate a mechanistic basis for a Type 3 functional response in a multi-prey system. Previously, this has been justified only on phenomenological grounds. This analysis also describes how habitat distribution and behavioural rates affect the shape of the sigmoidal functional response, which is critical to the conservation of woodland caribou populations. Forest management can benefit from these perspectives. Forestry objectives can target conditions that favour the emergence of the sigmoidal functional response. Thus, the results of this chapter have policy implications to forest harvest rates and the maintenance of spatial structure in forests. These are discussed in the context of key parameters that determine the relationship between population dynamics parameters, landscape spatial characteristics and predicted species distributions.

5.2 Methods

My goal is to show how spatial distributions can affect the functional response of wolves preying on moose and caribou. This is important because of the effect it has population dynamics. This is not an extension of the models produced in chapters 3 and 4. Those parameters implicitly captured fine-scale processes and averaged conditions. The parameters used to model explicit spatial behaviour in this chapter bear some resemblance to previous rates, but because conditions differ in each grid cell, they represent a reference point that each cell's conditions are measured against. Because of these differences, I now examine a generalized model involving one predator and two niche-differentiated prey.

The spatial distribution of animals is predicted with an IFD solution to spatially referenced equations of the rates of change of population abundances given local conditions. I build an algorithm that solves a system of fitness equations iteratively. The logic behind this is that animals will distribute themselves such that no particular location will have higher fitness given conditions and species abundances at all locations. The first step in the analysis is to define the fitness functions for each species. These are based on per capita rates of growth that are expressed by Equations 5.1 - 5.3 (see Table 5.1 for symbol definitions). We begin by assuming that fitness is the same in all cells for each species, or $\overline{F}_{N_i} = F_{ij} \forall j$.

$$\overline{F}_{N_1} = r_1\left(1 - \frac{N_{1j}}{K_{1j}}\right) - a_1 P_j \tag{5.1}$$

$$\overline{F}_{N_2} = r_2\left(1 - \frac{N_{2j}}{K_{2j}}\right) - a_2 P_j \tag{5.2}$$

$$\overline{F}_P = \varepsilon(a_1 N_{1j} + a_2 \omega_2 N_{2j}) e^{-\alpha P_j} - m \tag{5.3}$$

Rearranging Equations 5.1 - 5.3, we get:

$$N_{1j} = \frac{K_{1j}}{r_1}\left(r_1 - a_1 W_i - \overline{F}_{N_1}\right) \tag{5.4}$$

$$N_{2j} = \frac{K_{2j}}{r_2}\left(r_2 - a_2 W_i - \overline{F}_{N_2}\right) \tag{5.5}$$

$$P_i = \frac{1}{\alpha}\log\left(\frac{\varepsilon(a_1 N_{1j} + a_2 \omega N_{2j})}{\overline{F}_P + m}\right) \tag{5.6}$$

Prey fitness balances the relative energetic gains derived from food against the relative losses to predation. Gains have an upper limit set by carrying capacity and losses are proportional to the attack rate and density of predators.

Table 5.1: Symbols for state variables and parameters used in the calculation of the Ideal Free Distribution (IFD).

Parameter	Symbol
Density of prey i in cell j	N_{ij}
Density of predators in cell j	P_j
Intrinsic growth rate of Species i	r_i
Carrying capacity of prey Species i	K_{ij}
Effective rate of search on prey species i	a_i
Conversion efficiency	ε
Predator mortality rate	m
Relative weight Species 2:Species 1	ω
Predator competition rate	α
Fitness of species i in cell j	F_{ij}
Mean fitness across all cells	$\overline{F}_{sp.}$

Predator fitness is the energetic gain from captured prey minus the per-capita mortality rate. The term $e^{-\alpha W_j}$ describes interference between predators in cell j. Overcrowding reduces the potential energetic gain through mortality arising from intra-specific strife. Handling time is not included in the IFD calculation because the redistribution happens before the consumption actually occurs. The IFD is an intermediate step. Since the IFD produces animal distributions at an instantaneous point in time, it is reasonable to assume that behavioural decisions are made on the basis of perceived vegetation supply, prey abundance, and intra-specific competition. Handling time only plays a role on the time scale of demographic change. I assume that animals remain ideally and freely distributed long enough for instantaneous forage, recruitment and predation events to take place.

The calculation of the IFD assumes that a given mean fitness will lead to a relative activity level which can be interpreted as a density in each cell at a given point in time. Since we already know the total abundance, we can find the actual distribution by iterating over a range of possible mean fitnesses until the sum of all cell densities yields the known total. It uses and algorithm that follows the following 9 steps:

1. Assume $\overline{F}_{sp.} = 0$
2. Using $\overline{F}_{sp.}$ get $N_{sp.,j}$ at all cells i using (5.4)-(5.6)
3. Find the values of $N_{sp.} = \sum N_{sp.,j}$
4. Using $\overline{F}_{sp.} + 0.001$, get $N^*_{sp.,j}$ and $N^*_{sp.} = \sum N^*_{sp.,j}$
5. Calculate $dF_{sp.} = (N^*_{sp.} - N_{sp.})/0.001$
6. Let $\overline{F}^*_{sp.} = \overline{F}_{sp.} + \frac{(N_{sp.} - \sum N^*_{sp.,j})}{dF_{sp.}}$
7. Let $\epsilon = |F^*_{sp.} - F_{sp.}|$
8. If $\epsilon <= tol$ then assume stable strategy has been reached and $N^*_{sp.,j}$ is the density of a species in cell j.
9. If $\epsilon > tol$ then set $F_{sp.} = F^*_{sp.}$ and return to step 2.

This algorithm makes use of the fact that successive calculations of an iterative solution will necessarily be proportional to the former calculation. By assuming linearity in the progress from one step to the other, the algorithm "back-calculates" from the jump by assuming a small step and assuming that a straight line predicts the change from one iteration to the next. By continually assuming these small steps until relative change is very small, the algorithm will eventually stop. This is call a *Newton iteration* (Burden and Faires 1985).

If there were only one consumer, and if resources did not move, this algorithm would be sufficient. Because there are predators and alternate prey, and because each one depends on the other, numerical instabilities occur when the *inner loop* is performed (steps 1-9). To solve this problem, *successive over-relaxation* (Burden and Faires 1985) was added in an *outer loop.* The logic of the *outer loop* is as follows:

1. Distribute species such that $N_{sp.,j} = \frac{1}{n} N_{sp.}$ where n = number of cells

2. Get $N'_{sp.,j}$ using inner loop

3. Set $N_{sp.,j} = (1-\gamma)N_{sp.,j} + \gamma N^{new}_{sp.,i}$

4. Let $\epsilon = |\sum N'_{sp.,j} - \sum N_{sp.,j}|$

5. If $\epsilon <= tol$ then accept $N_{sp.,j}$ as the spatial distribution

6. If $\epsilon > tol$ then return to step 2.

Using both the inner and outer loops generally solves Equations (5.4) - (5.6) such that fitness is the same in all cells, but there is no guarantee that such a solution exists. The most effective way to reach an equilibrium solution is to set the value of γ very low; around 0.001 seems to work well. Also, it is better to perform an inner and outer loop on each species in sequence rather than performing an inner loop on all species followed by an outer loop. A visual inspection of many solutions over many different parameter sets indicated that even when a perfectly stable solution had not been reached, the numerical instabilities were insignificant compared with the overall trends. Despite some *chatter* (rounding error and numerical instability that comes from projecting trends on very steep curves), the trends still showed habitat selection patterns across a broad habitat gradient.

5.2.1 Sensitivity to habitat supply and niche overlap

I calculate IFDs across a range of habitat conditions to examine how predicted spatial distributions affected the functional responses. Conditions are chosen to span a range of niche differentiation, but rates and habitat niches are not meant to mimic any particular species, merely to mimic niche differentiation. For switching to occur, predators need to be drawn away from one prey type to locations where the other prey would predominate. If both species occupy the same habitat, both will still be encountered in proportion to availability since they will be in the same place too often. However, if they favour different habitats when one prey species becomes scarce, predators should see higher fitness in cells where the other prey resides. The alternate prey will therefore not come into contact with the predator. For the purpose of the analysis, I create a random forest with a mean age of 60 years and a standard deviation of 30 years. Habitat and demographic parameters are chosen so that prey are niche differentiated but overlapping near the mean age of the forest. Sensitivities on the relative position of each niche are therefore easier to manage.

I generalize the model to explore qualitative differences in spatial behaviour across a range of conditions. I retain the most important characteristic of the caribou-moose-wolf system: one species is modelled to prefer older forest, while the other prefers younger forest. The carrying capacity of Species 1 reaches a maximum with a sigmoidal pattern with a half-maximum saturation at b_1; Species 2 has an inverse sigmoidal relationship with a half-maximum at b_2. The relationships are shown in Figure 5.2 and in Equations (5.7) and (5.8). I use the following parameters to define the system:

Table 5.2: Parameters values used in sensitivity analysis.

Parameter	Symbol
Intrinsic growth rate of prey Species 1	$r_1 = 0.3$
Intrinsic growth rate of prey Species 2	$r_2 = 0.3$
Maximum carrying capacity of prey Species 1	$K_1 = 3$
Species 1 half-maximum saturation	$b_1 = 80$
Maximum carrying capacity of prey Species 2	$K_2 = 3$
Species 2 half-maximum saturation	$b_2 = 40$
Effective rate of search on prey Species 1	$a_1 = 20$
Effective rate of search on prey Species 2	$a_2 = 20$
Conversion efficiency	$\varepsilon = 0.035$
Predator mortality rate	$m_w = 0.5$
Relative weight Species 1:Species 2	$\omega = 1$
Predator interference	$\alpha = 2$
Averate age of forest	A

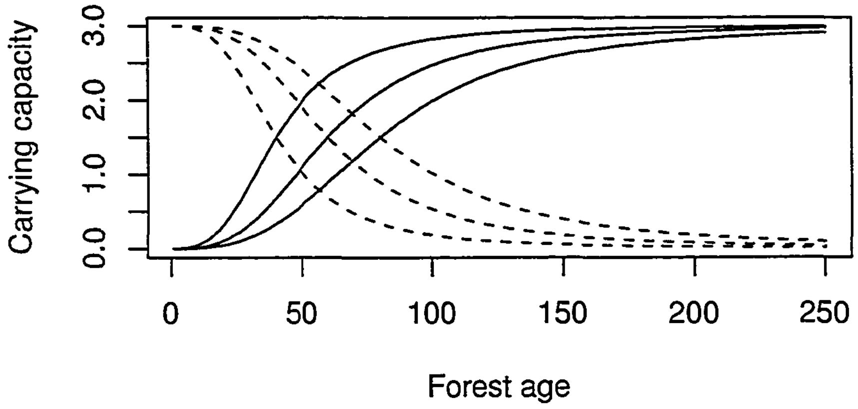


Figure 5.2: Plot of change in carrying capacity of prey Species 1 (solid line) and prey Species 2 (dashed line) with changes in forest age. One line for each species is drawn at half maximum rates of 40, 60, and 80 years.

$$K_1(A) = \frac{K_{1,max}A^3}{b_1^2 + A^2} \tag{5.7}$$

$$K_2(A) = 1 - \frac{K_{2,max}A^2}{b_2^2 + A^2} \tag{5.8}$$

I examine the sensitivity of switching in response to perceived changes across resource gradients. I construct an artificial forest to see how habitat supply affects the spatial distribution of all species, by simulating fires with fixed ignition probability rates of 0.004 and a mean patch sizes of 8000 hectares. This creates the forest conditions over which to run the IFD model. I then evaluate the functional responses when the half-maximum carrying capacity parameters b_1 and b_2 are varied to form all combinations of the values 40, 60 and 80. I calculate the functional responses across a range of densities of the primary species and examine how the kill rates are affected for three fixed values of the other prey species. This reflects the sensitivity of switching in response to variation in the habitat niche overlap as shown in Figure 5.2.

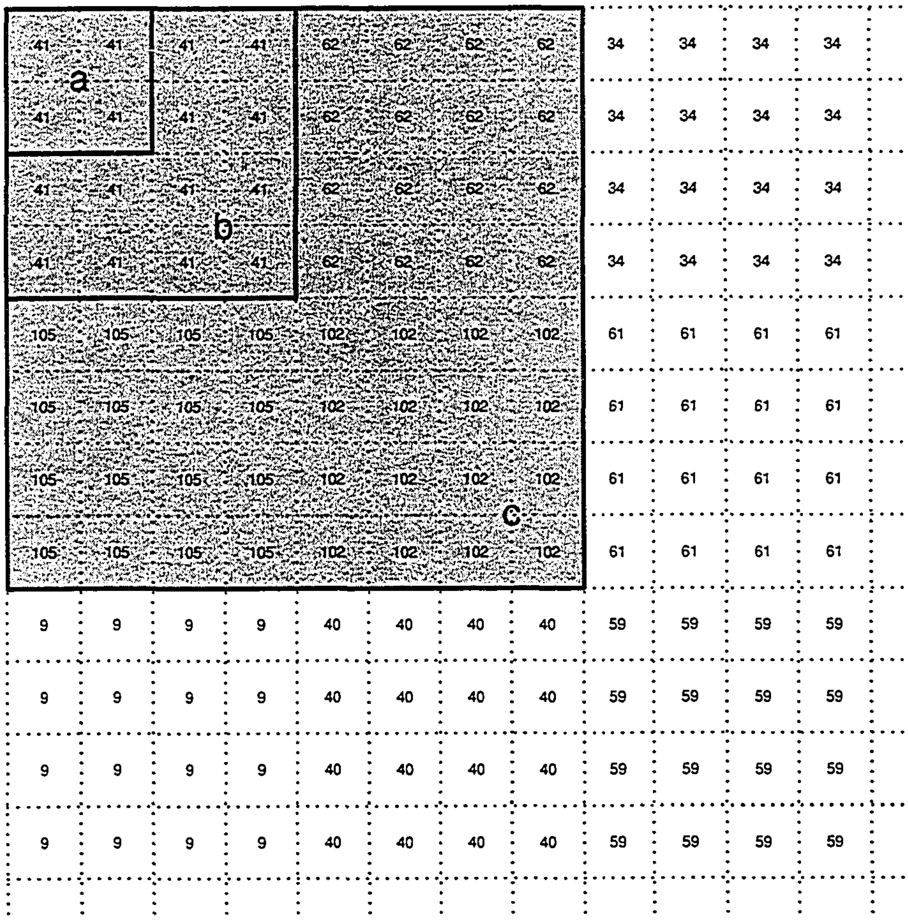
5.2.2 Multiple spatial scales in predator prey dynamics

Thus far, I have assumed that all species perceive environmental conditions at the same spatial scale. Switching has been driven by relative positions of b_1 and b_2 along a forest age gradient. To look at spatial aspects of niche differentiation, I also examine the effect of including *scale dominance* in predator behaviour. By *scale dominance*, I mean that predators can cover more ground relative to their prey and therefore judge resource gradients accordingly. If predators judge spatial gradients at a larger scale than their prey, they would *see* many smaller cells of prey as a single *pooled* prey source. That being the case, it should be more difficult for the fine scale spatial separation to take effect than if all species perceive their environments at the same scale.

To examine the effect that this has on population dynamics, I create a model where prey see the landscape at one spatial scale and predators select blocks of those cells. The predators see the total number of animals of both types, and the IFD is established on the basis of the density across the block of cells. There are therefore three characteristic spatial scales. The spatial scale at which prey see resources (S_N) is the base unit. Forests can have patches made up of several identically aged cells, making up the forest spatial scale (S_f). For example, S_f=4 implies that patches aggregate four cells of size S_N. The predator scale ($S_P \geq 1$) can aggregate several cells of size S_N. The predator then evaluates fitness based on the sum of all prey densities across the S_P cells.

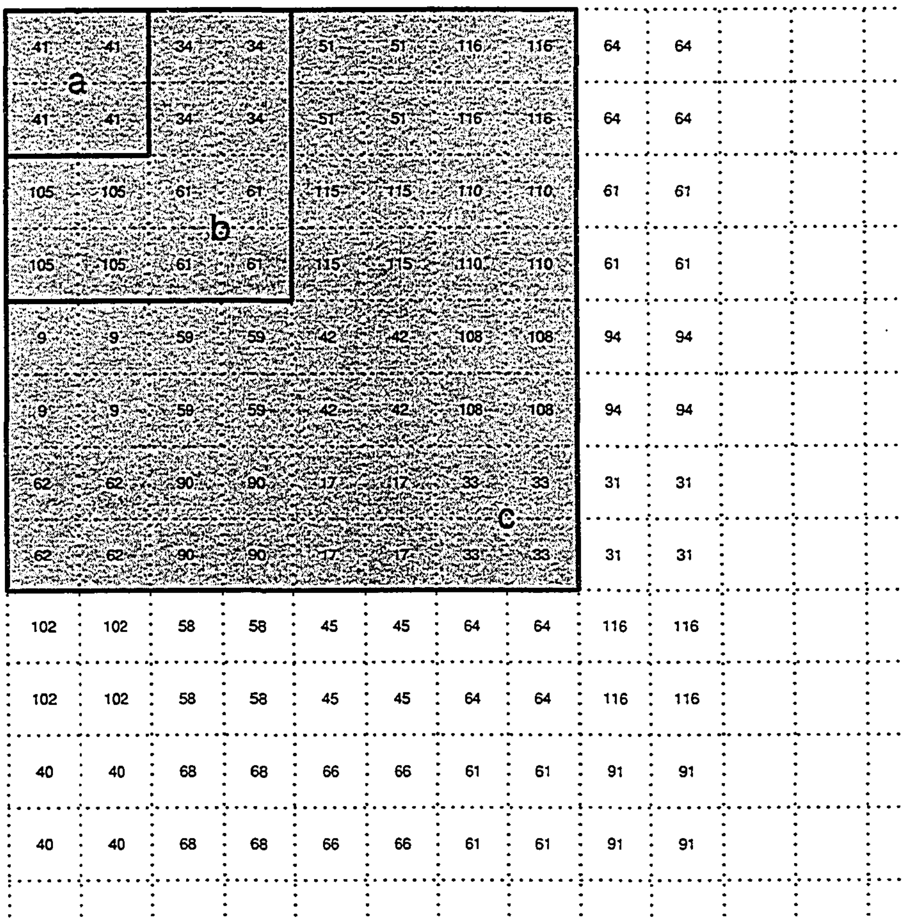
Figure 5.3 shows how varying the size of S_P might change the way predators allocate themselves spatially. This difference is visible when we consider the size of the clusters of forest ages. When the forest is clustered in 4×4 patches of common aged cells, prey will see resource and predation risk gradients at that scale. As long as the predators see resources at the scale of 4 or 16 prey spatial units ($S_P = 4$ or 16), the system will act as though the predators were seeing things at the same scale as the prey. This is only true because the forest scale (S_f) matches the predator scale. As soon as the scale of what predators see is greater than the forest spatial scale, the predators will judge fitness across several different ages of forest. When $S_P = 16$ it may be good habitat for Species 1, but additional risks accrue when $S_P = 64$, if adjacent cells are old enough to attract Species 2, and therefore predators. Figure 5.4 shows the same phenomena when forest patches occur at a smaller scale ($S_f = 4$). In this case, the disparity occurs due to a reduction in forest scale rather than an increase in predator scale. Either way, when the predator scale exceeds both the forest scale and the prey scale, we predict that prey would not be capable of exploiting spatial separations of forest types to their advantage. The larger S_P becomes in relation to S_f and S_N, the more that prey are forced to share predator-perceived habitat, despite how distinct their individual habitat selection curves might be.

We know that forest age has a direct bearing on the carrying capacities of the prey. Since we hypothesize that patch size mediates the foraging advantage that predators have over their prey, I simulate forests of varying age classes and patch size structures, to examine how spatial structure impacts the IFD's and the resulting functional responses of each prey species. Nine forests were simulated. In order to ensure a proper gradient across scenarios, I create random disturbances selected from a small set of random numbers through which I rotate. Patches are created by assuming an ignition rate and a fire size distribution. The choice of ignition rates is not intended to accurately simulate a true fire disturbance regime but rather to create forests across a gradient of age and patch size class distributions. I use ignition rates of 0.002, 0.004 and 0.01 and fire sizes drawn randomly from an exponential distribution with means of 4000, 8000 and 16000 hectares respectively. I repeatedly draw



41	41	41	41	62	62	62	62	34	34	34	34
41	41	41	41	62	62	62	62	34	34	34	34
41	41	41	41	62	62	62	62	34	34	34	34
41	41	41	41	62	62	62	62	34	34	34	34
105	105	105	105	102	102	102	102	61	61	61	61
105	105	105	105	102	102	102	102	61	61	61	61
105	105	105	105	102	102	102	102	61	61	61	61
105	105	105	105	102	102	102	102	61	61	61	61
9	9	9	9	40	40	40	40	59	59	59	59
9	9	9	9	40	40	40	40	59	59	59	59
9	9	9	9	40	40	40	40	59	59	59	59
9	9	9	9	40	40	40	40	59	59	59	59

Figure 5.3: Perceived distribution of resources by prey and predators when forest patches are at the scale of $S_f = 16$ prey spatial units. Dashed grids represent the scale at which prey see the land. Numbers indicate the age of forest in the cells and shaded areas represent the scale at which predators see the landscape. Areas (a), (b) and (c) represent scales of $S_P = 4$, 16, and 64 prey spatial units respectively.



41	41	34	34	51	51	116	116	64	64		
41	41	34	34	51	51	116	116	64	64		
105	105	61	61	115	115	110	110	61	61		
105	105	61	61	115	115	110	110	61	61		
9	9	59	59	42	42	108	108	94	94		
9	9	59	59	42	42	108	108	94	94		
62	62	90	90	17	17	33	33	31	31		
62	62	90	90	17	17	33	33	31	31		
102	102	58	58	45	45	64	64	116	116		
102	102	58	58	45	45	64	64	116	116		
40	40	68	68	66	66	61	61	91	91		
40	40	68	68	66	66	61	61	91	91		

Figure 5.4: Perceived distribution of resources by prey and predators when forest patches are at the scale of $S_f = 4$ prey spatial units. Dashed grids represent the scale at which ungulates see the land. Numbers indicate the age of forest in the cells and shaded areas represent the scale at which predators see the landscape. Areas (a), (b) and (c) represent scales of $S_P = 4$, 16, and 64 prey spatial units respectively.

from the same set of random numbers in order to make sure that differences between artificial landscapes are due to parameter choices and not random chance.

Figures 5.5 and 5.6 show the proportion of forest at a given age, and the proportion of the forest composed of patches of given sizes. As ignitions become more frequent, the age distribution becomes younger for a given mean patch size. Similarly, mean forest age declines when mean patch size increases at a given ignition rate.

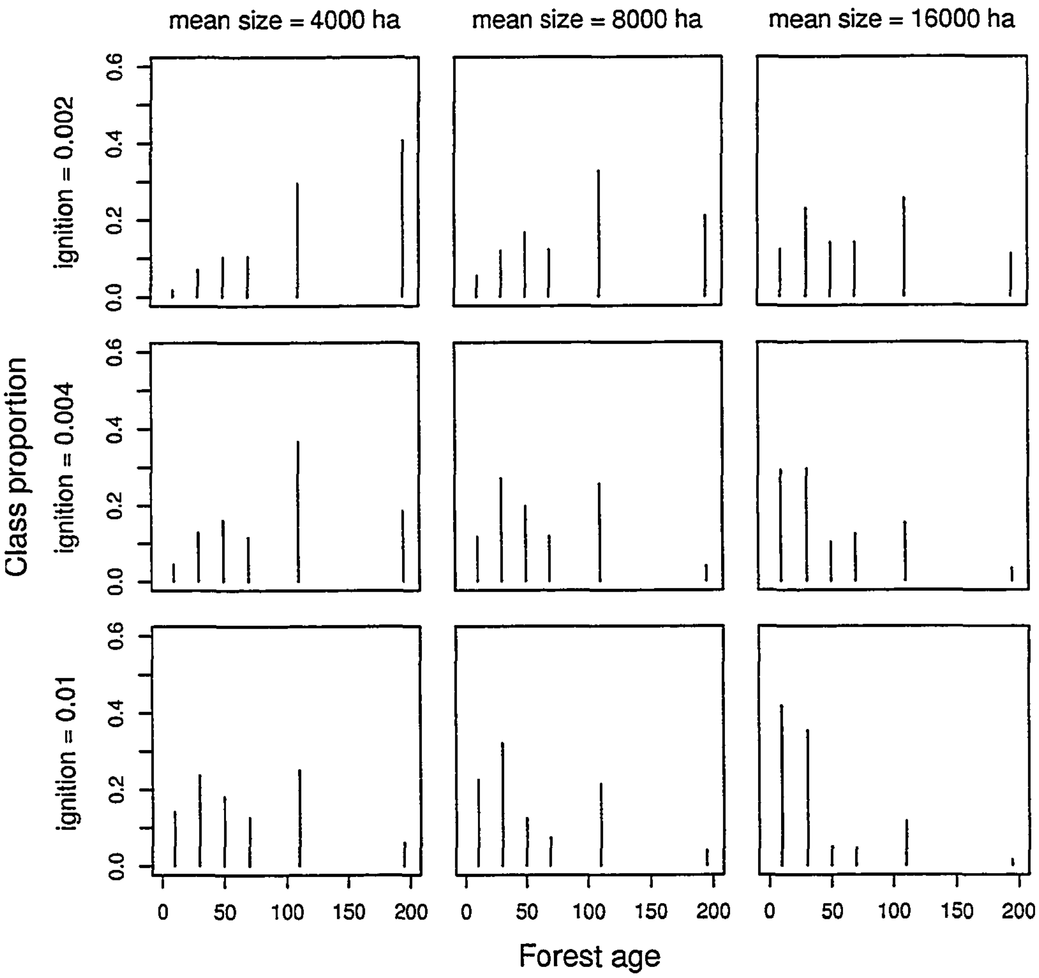


Figure 5.5: Proportion of forest covered by each age class. Each plot shows the proportion of each age class represented in the forest landscape for given combination of ignition rates (probability of fire starting in given cell) and mean patch size (number of 4 km^2 cells).

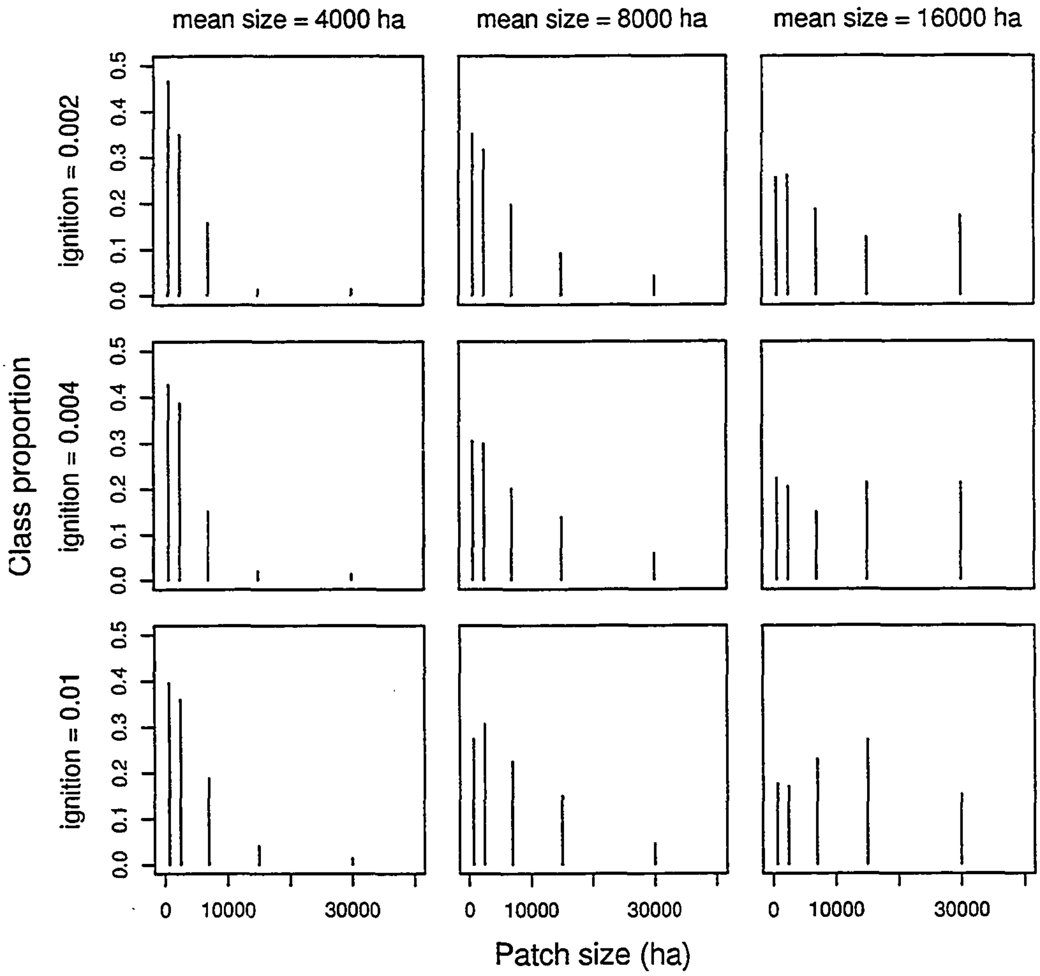


Figure 5.6: Plot of the relative proportion of each patch size class in the forest landscape for given combination of ignition rates (probability of fire starting in given cell) and mean patch size (number of 4 km^2 cells).

I simulate the IFD's of all animals and calculate the changes to the functional response as patch sizes are increased and decreased to emulate natural disturbances and forest harvest scenarios. A sensitivity analysis of the behaviour of the system across a range of natural and human altered conditions is presented in the next section.

5.3 Results

I first examine the sensitivity of switching in response to perceived changes across resource gradients. Figure 5.7 shows switching away from Species 1 as densities of that species decline. The result is repeated for each carrying capacity curve. Three different densities of Species 2 are simulated for each case. Figure 5.8 shows the same from the perspective of Species 2, with a curve for each of three densities of Species 1. All of the curves are plotted at the lower density range, where the concavity of the Type 3 curve is most important to the declining species. I exclude the upper range of the curve because plotting across the entire range makes it more difficult to see the shape on the left hand side. The algorithm used to calculate the IFD is incapable of producing a larger kill rate than would result from homogeneous mixing, so we know that the functional response will not exceed the maximum killing rate on the right hand side (i.e. they are assymptotic).

The strongest switching occurs when there is sufficient spatial separation from alternate prey and sufficient alternate prey for the predators to switch *to.* Habitat niches overlap the least in the upper right and lower left of Figures 5.7 and 5.8. This has different interpretations for Species 1 and for Species 2. Figure 5.5 shows that about 40% of the forest is older than 110 years. Unless $b_1 = 80$, there is very little habitat available for Species 1 to disperse to. Figure 5.8 shows more switching from Species 2 as b_1 approaches 80. This is because when $b_1 = 40$, Species 1 are occupying many of the same cells as

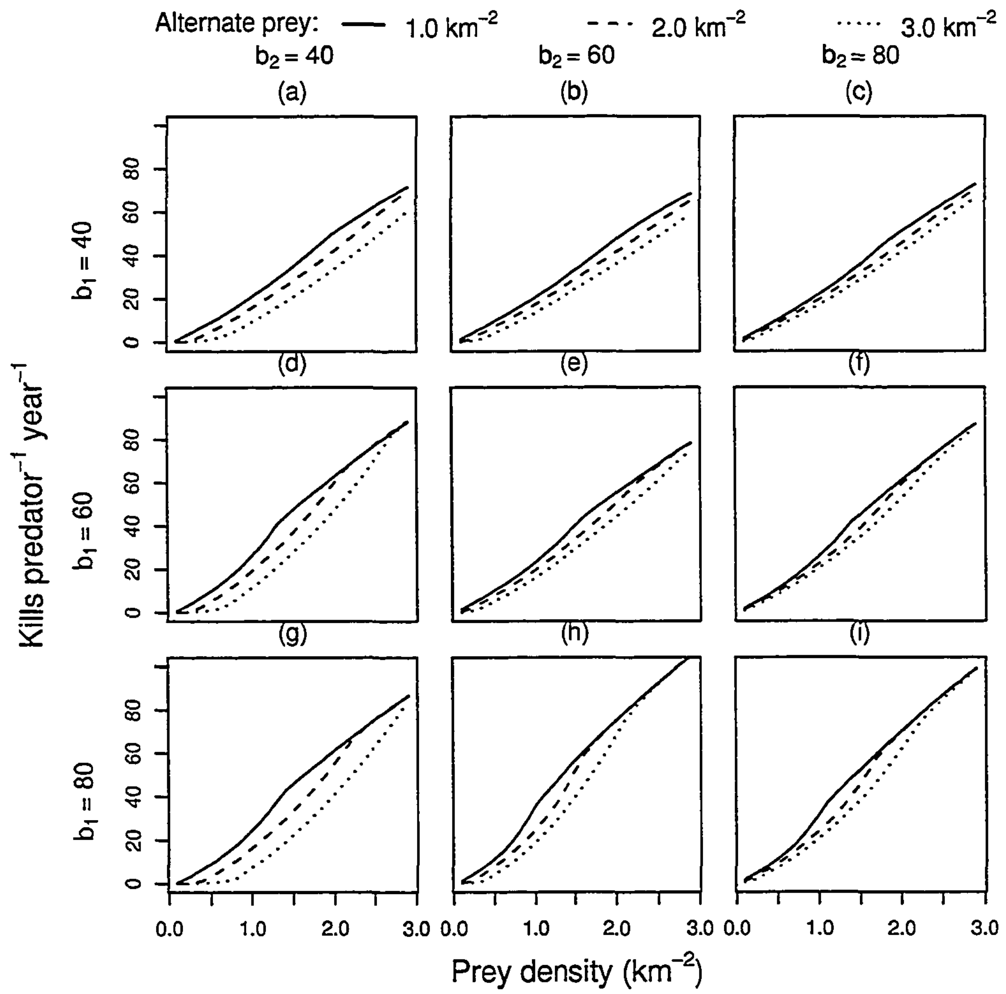


Figure 5.7: Plot of switching behaviour across a range of densities of species 1. X-axis is the density of Species 1. Y-axis is the number of kills per predator. Each plot shows the switching for a different combination of carrying capacities and half-maxima. The plot is truncated to display the concavity on the left side of the sigmoidal shape, but the right sides of curves are asymptotic.

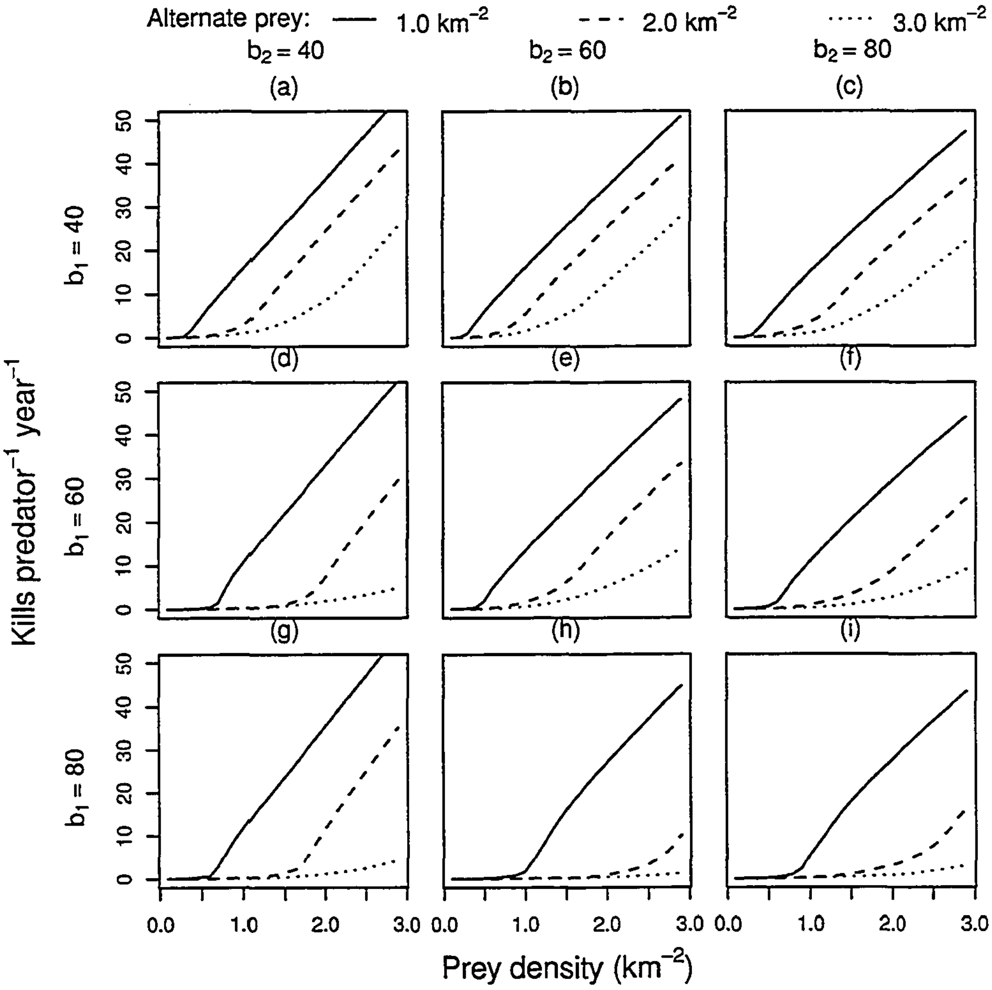


Figure 5.8: Plot of switching behaviour across a range of Species 2 densities. X-axis is the density of Species 2. Y-axis is the number of kills per predator. Each plot shows the switching for a different combination of carrying capacities and half-maxima. The plot is truncated to display the concavity on the left side of the sigmoidal shape, but the right sides of curves are asymptotic.

Species 2. Figure 5.7 shows more switching from Species 1 as b_1 approaches 80, but mainly when $b_2 = 40$, since that is the only case where Species 2 select sufficiently opposite habitat. The simulated conditions favour Species 2 because of the age class distributions. That is the main reason that the switching is more apparent on Species 2 than on Species 1. The main result shown in Figures 5.7 and 5.8 is that it takes low habitat niche overlap and sufficient quantities of habitat for switching to occur.

The simulated forest conditions until now have corresponded to the "middle" case of age distributions and patch size distributions. In the results that follow, fire frequency and fire sizes are varied to make ages span young to older distributions as well as to span a range of mean patch sizes. Figures 5.5 and 5.6 show the landscape characteristics of those cases. I also explore the effect of predator scale dominance over prey. Figures 5.9 - 5.12 show the effect of increasing the predator spatial scale to 4 prey cells. The switching behaviour depends on the availability of alternate prey, the forest conditions and the size of the predator behavioural window. Figures 5.9 and 5.10 show the effect that increasing the predator spatial scale has on the functional response of Species 1. When the predator window gets bigger, there is less switching and for the most part, Species 1 kill rates go up. Also as the forest gets younger -which occurs moving away from the upper left corner- more switching is seen in Species 2 and less in Species 1. This is because Species 1 is crowded into small patches. Large predator windows also have a less detrimental effect when patch sizes are large, which occurs in the rightmost columns. Species 2 kill rates decrease when the predator window is increased in large patches. This is because the simulated forests in the rightmost column also tend to be younger as larger disturbances result from each ignition. Species 2 is inhabiting the large patches and Species 1 is forced into contact with predators more frequently. This avails new prey resources that were not detected at a

Table 5.3: Effect of variation in the predator spatial scale on switching behaviour. Upward arrows indicate that increasing the spatial scale of predators increased switching behaviour. Downward arrows indicate a decrease in switching.

Size	Small patches	Large patches
Old	Species 1 ↓, Species 2 ↑	Species 1 ↓, Species 2 ↑
Young	Species 1 ↓, Species 2 ↑	Species 1 ↑, Species 2 ↑

smaller predation scale, translating to more consumption of Species 1 and a correspondingly higher handling time of that species.

The effect of changing predation scales is shown in Figure 5.13 for Species 1 and Figure 5.14 for Species 2. In each case, the functional response is shown for an alternate prey density of $3.0/\text{km}^2$. When the predator spatial scale is increased, it reduces the amount of switching in some cases, whereas it increases it in others. This illustrates how apparent competition is exacerbated in some cases, whereas in others the increased predator scale facilitates apparent mutualism. It appears to be determined by habitat supply of prey species and the spatial scale at which it is distributed. If large patches form with the same frequency as small ones, the formation of large patches will cause the forest to be younger in comparison. For that reason, the method used to generate the random landscapes created large patch mosaics that contained insufficient quantities of old forest. Figure 5.13 is such a case.

Table 5.3 summarizes the changes to the functional response and the switching behaviour when the predator spatial scale is increased. The results focus on the extreme cases of the four combinations of youngest, oldest, smallest and largest patches.

5.4 Discussion

I have shown that behavioural assumptions about habitat selection and predation can lead to spatial patterns that have a direct bearing on the functional

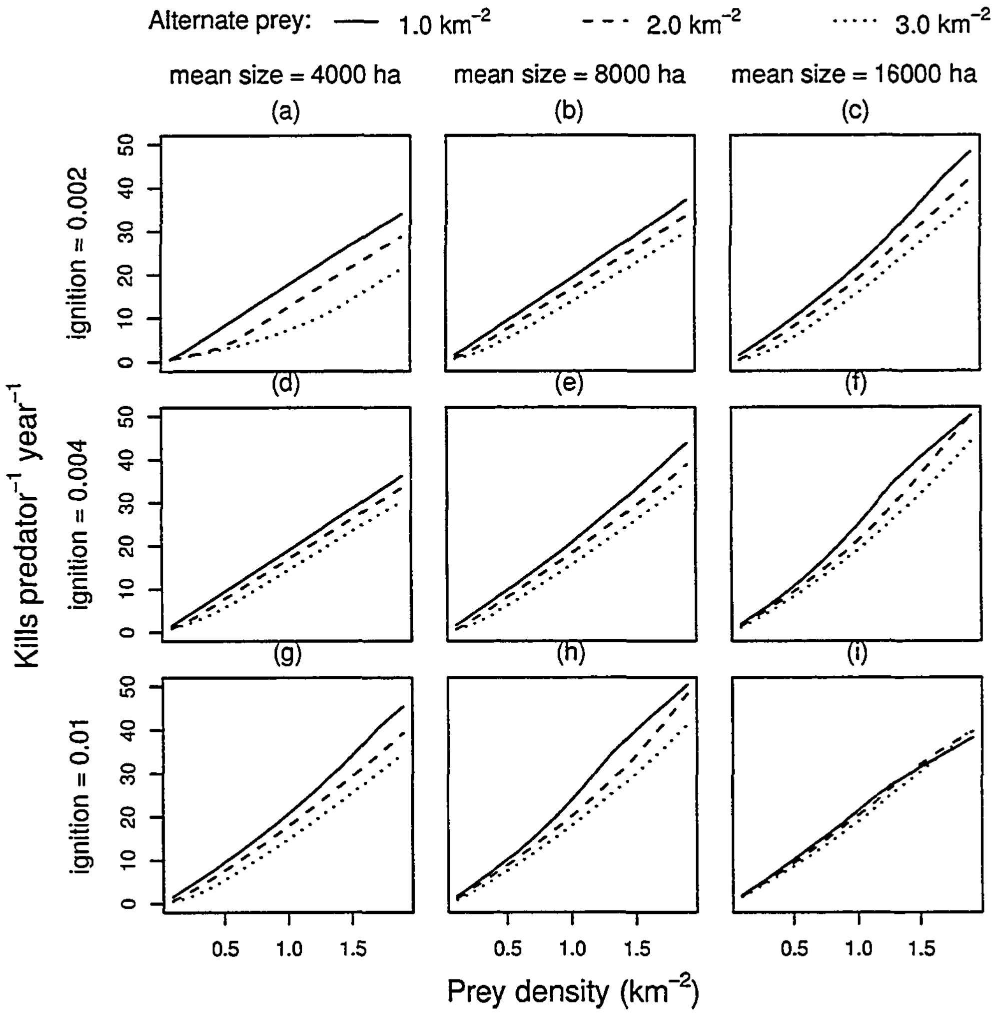


Figure 5.9: Changes in switching behaviour of predation on Species 1 with a predator scale of 1 prey unit. Patch sizes increase from leftmost column to rightmost column. Ignition frequencies increase from uppermost row to lowermost row. Oldest and smallest patches are found in the upper left hand corner. Largest and youngest patches found in lower right corner.

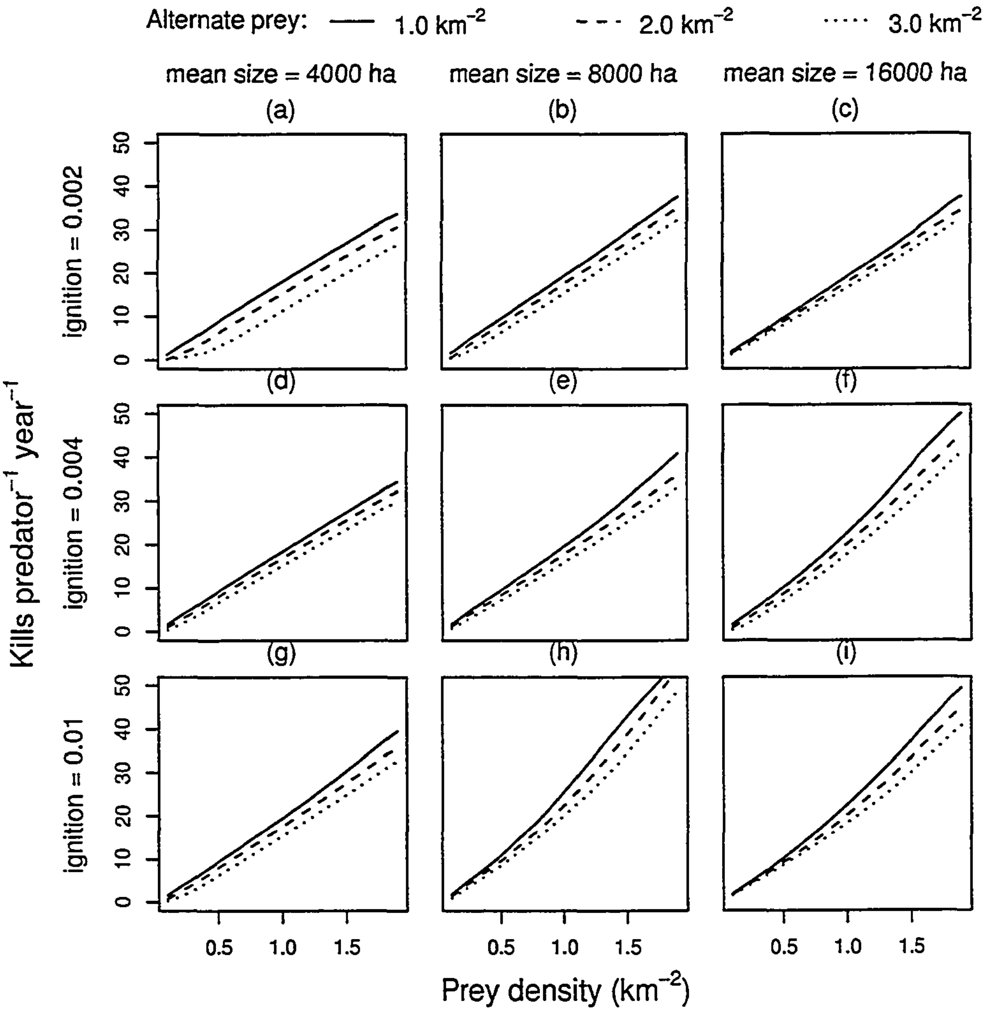


Figure 5.10: Changes in switching behaviour of predation on Species 1 with a predator scale of 4 prey units. Patch sizes increase from leftmost column to rightmost column. Ignition frequencies increase from uppermost row to lowermost row. Oldest and smallest patches are found in the upper left hand corner. Largest and youngest patches found in lower right corner.

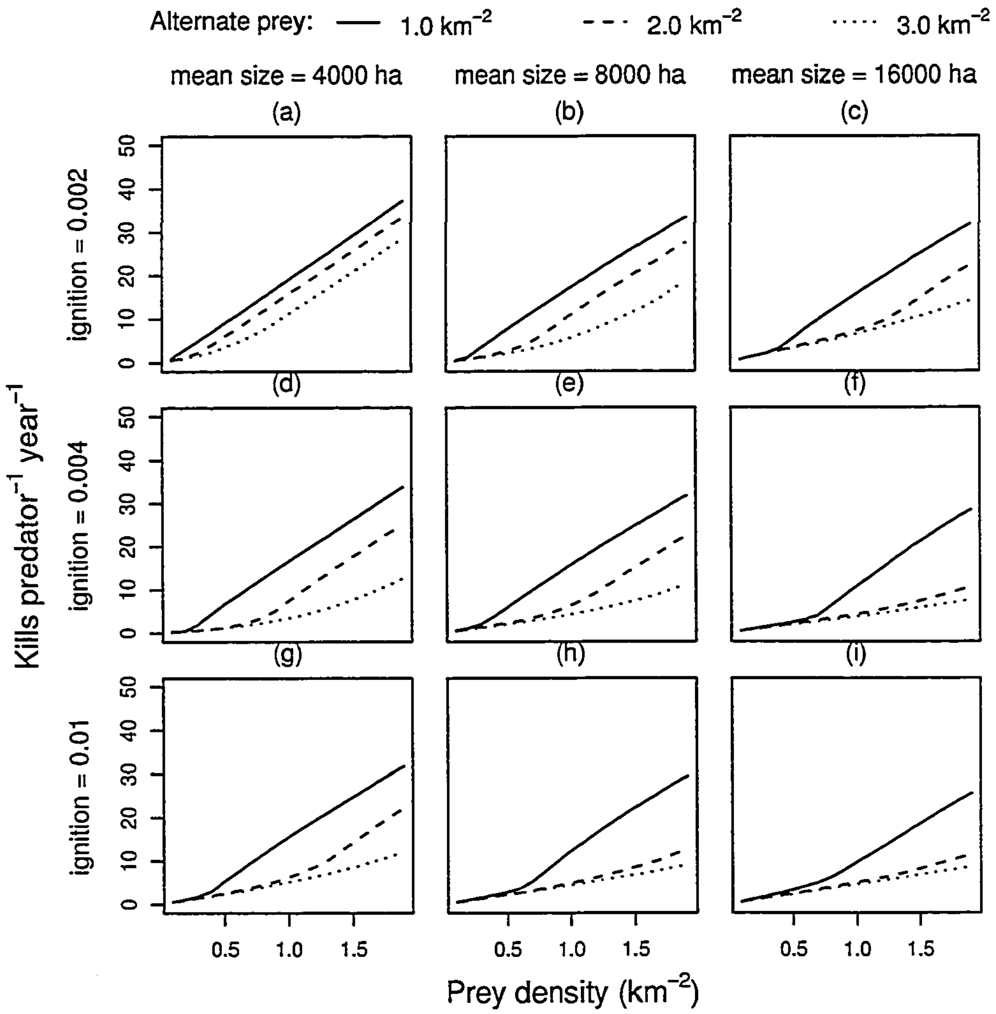


Figure 5.11: Changes in switching behaviour of predation on Species 2 with a predator scale of 1 prey unit. Patch sizes increase from leftmost column to rightmost column. Ignition frequencies increase from uppermost row to lowermost row. Oldest and smallest patches are found in the upper left hand corner. Largest and youngest patches found in lower right corner.

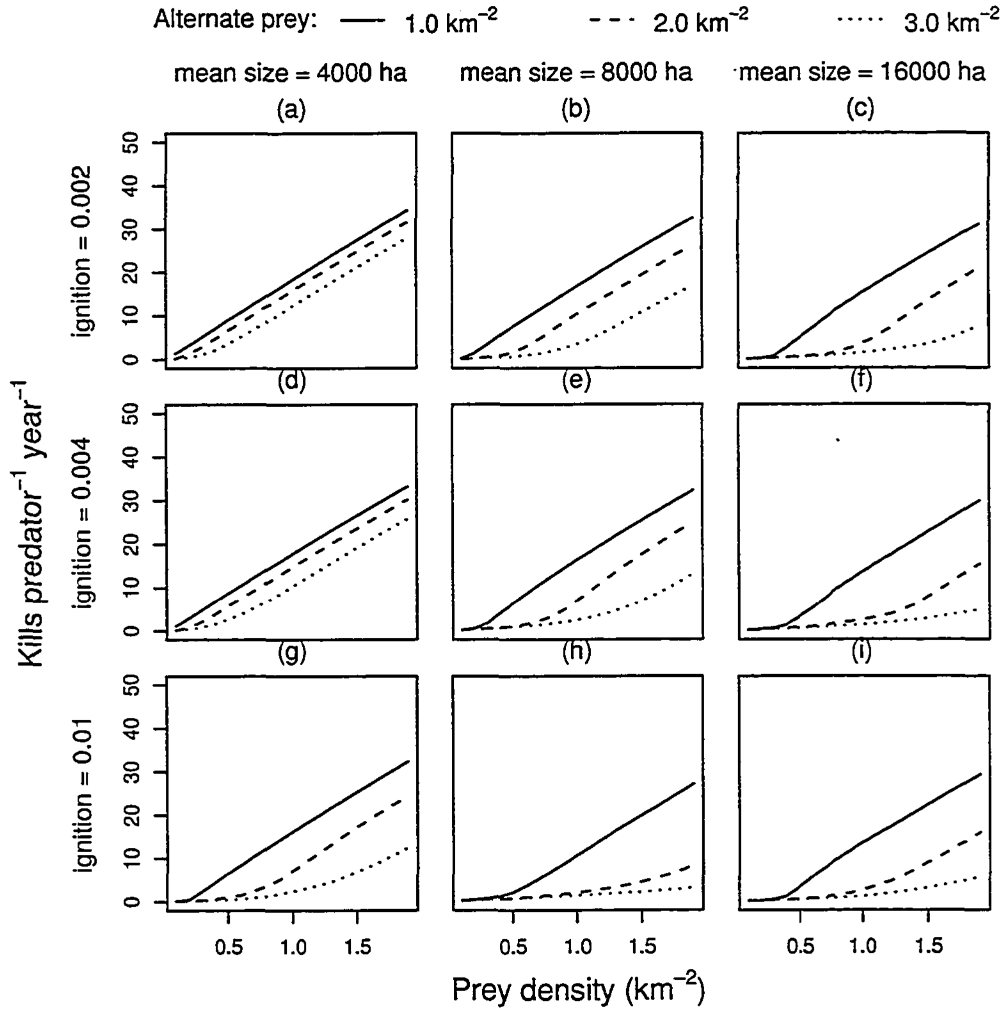


Figure 5.12: Changes in switching behaviour of predation on Species 2 with a predator scale of 4 prey units. Patch sizes increase from leftmost column to rightmost column. Ignition frequencies increase from uppermost row to lowermost row. Oldest and smallest patches are found in the upper left hand corner. Largest and youngest patches found in lower right corner.

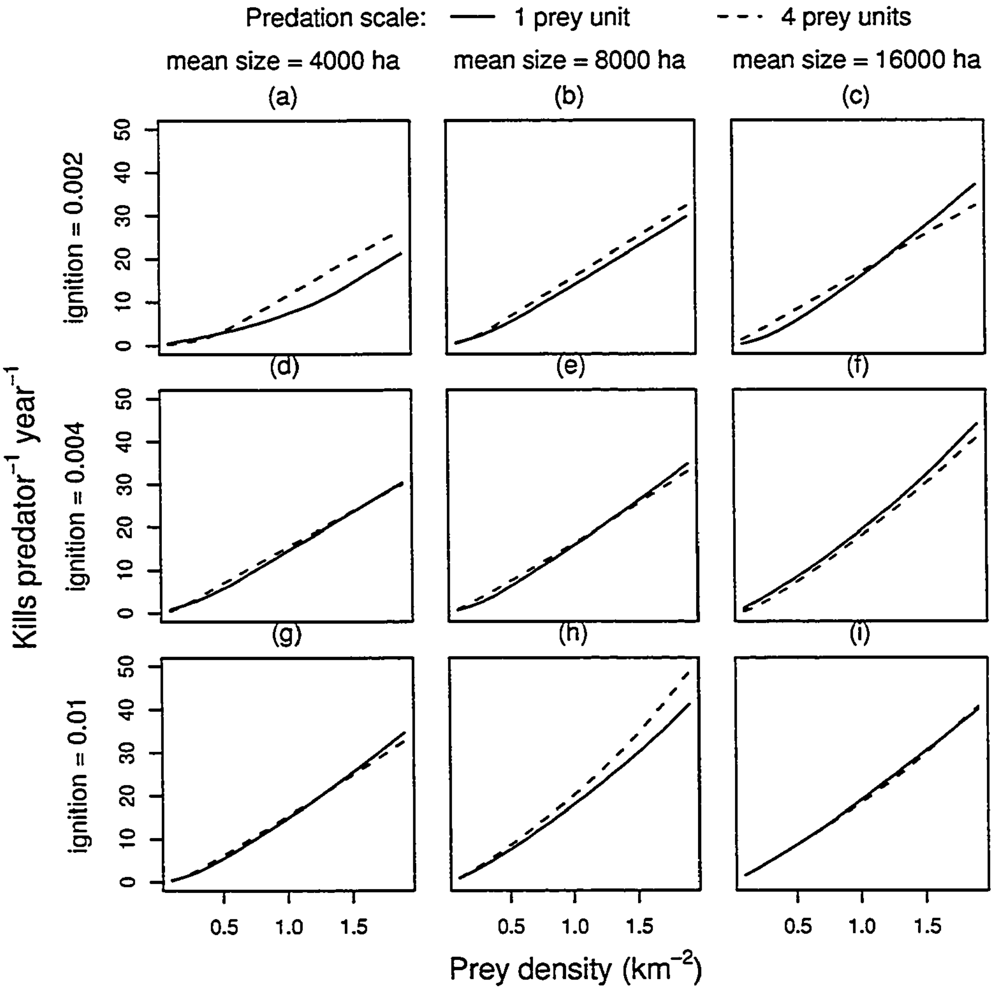


Figure 5.13: Changes in switching behaviour of predation on Species 1 across predator spatial scales. Patch sizes increase from leftmost column to rightmost column. Ignition frequencies increase from uppermost row to lowermost row. Oldest and smallest patches are found in the upper left hand corner. Largest and youngest patches found in lower right corner.

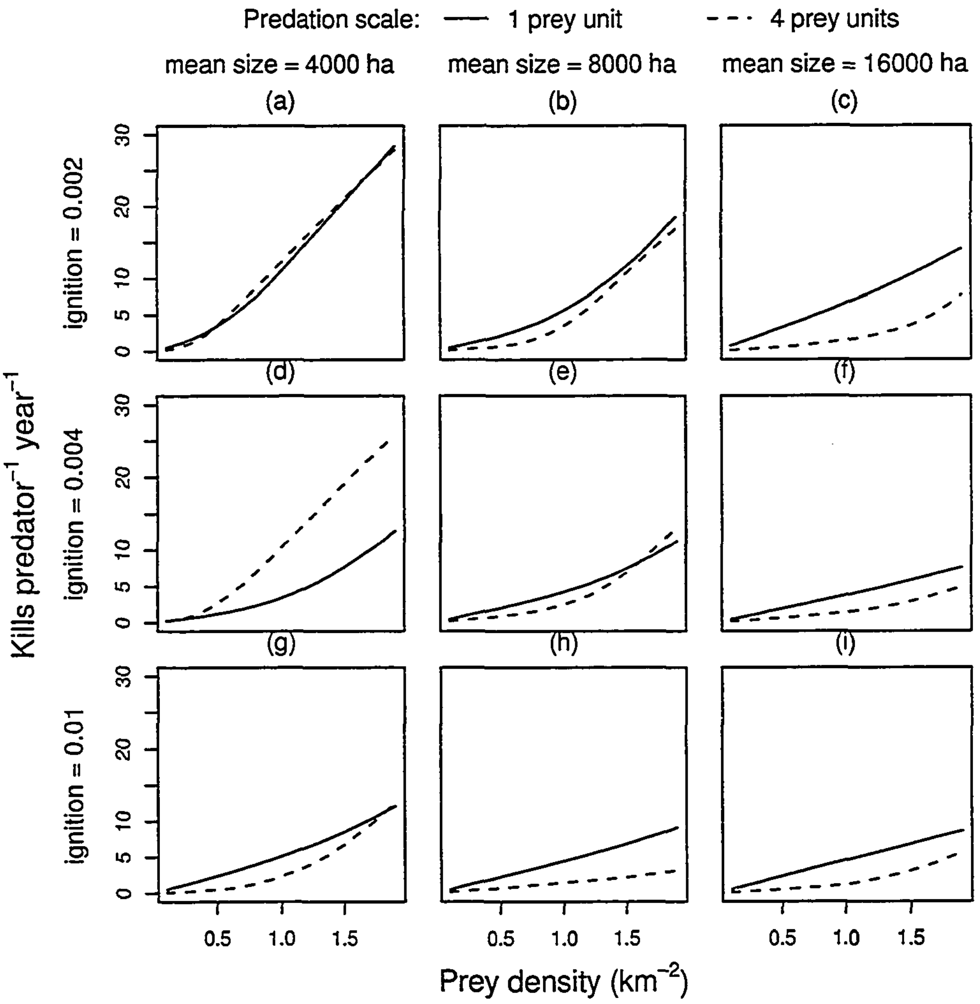


Figure 5.14: Changes in switching behaviour of predation on Species 2 across predator spatial scales. Patch sizes increase from leftmost column to rightmost column. Ignition frequencies increase from uppermost row to lowermost row. Oldest and smallest patches are found in the upper left hand corner. Largest and youngest patches found in lower right corner.

response. The densities of alternate prey and the spatial scale of predators can affect apparent competition, apparent mutualism, and prey switching. If prey switching emerges at low densities, a prey species can escape depensatory predation and extirpation. Switching can only occur if the following conditions are met:

Condition 1 Prey are habitat differentiated.

Condition 2 Habitats are in sufficient supply.

Condition 3 Habitat of each species is spatially separated from the other.

Condition 4 Alternate prey are in sufficient abundance to allow switching to occur.

Condition 5 Predator behavioural spatial scale does not effectively dominate the scale of the spatial separation of habitats.

The results of this chapter are general, but can be interpreted in the context of caribou conservation in a system involving moose and wolves. In the prey switching conditions listed above, Condition 1 is an inherent property of the caribou-wolf-moose system, corroborated by the life histories of caribou and moose. Conditions 2 and 3 are the most likely to be violated in altered systems. Industrial activities are known to change the amount and distribution of habitat. Condition 4 is probably met in declining caribou populations, but it is only a condition favouring caribou if Conditions 2, 3 and 5 are met, which is uncertain. In fact, high alternate prey populations and poor habitat supply and distribution are the most frequently cited causes of caribou declines (Edmonds 1988; Thomas 1995; Hervieux et al. 1996; Edmonds 1998; Wittmer 2004).

Theoretical implications

Spatial heterogeneity is believed to play a role in stabilizing predator prey systems and promoting population persistence. This occurs via clumped prey distributions (Hassel and May 1973; Hassel and May 1974), decreased apparent competition through habitat partitioning (Holt 1977; Holt 1984), apparent mutualism (Abrams et al. 1998) and prey switching (Murdoch 1969; Murdoch et al. 1975; Oaten and Murdoch 1975). In various ways, the foraging behaviour and the spatial distributions of resources result in what we ultimately measure as habitat selection (Rozenzweig 1991). In particular, the effect of habitat availability and behavioural spatial scales can play a role in shaping the relative functional responses across ranges of densities (Fryxell and Lundberg 1998).

The results of this chapter suggest that Type 3 functional responses can arise from spatial patterns predicted by fine-scale spatial behavioural. This provides a spatial mechanism and a basis for using Type 3 functional responses to predict the population dynamics of multiple prey systems. I have also shown that switching of this type can only occur if certain conditions apply. Without adequate habitat supply and appropriate spatial structure for the particular niches of the prey, spatial patterns may not predict a sigmoidal response. Spatial behaviour of predators and prey can provide the means for declining populations to escape predation at lower densities if predators can switch to an alternate prey. However, this can only happen if there are sufficient alternate prey for the predator to switch *to* and if habitat niches of prey are sufficiently dissimilar. A further caveat is that the spatial scale of the landscape, and the behaviour of prey and predators must not be such that predators are *scale dominant* over prey, or the advantages of niche differentiation are eroded. There are therefore management consequences pertaining to both the amount as well as the spatial distribution of resources.

In the context of wolf behaviour within ungulate ranges, the size of wolf territories relative to ungulate forage behaviour can play a major role. Bernstein et al. (1999) demonstrated that when predator migration rates were high, the mosaic of habitat patches effectively reduces to a single patch from the perspective of the predator. It follows that if wolf movement rates are fast relative to ungulates, they will be able to "out-maneuver" prey in the patch selection process, over-riding predator avoidance. It has also been shown that mortality on small scales can be inversely density dependent if predators are judging the availability of multiple prey resources at large spatial scales with fast movement rates (Bernstein et al. 1991). These results suggest that since wolves defend large territories, they exhibit behaviour that could lead to the type of scale dominance described in the analysis of this chapter.

Management implications

The importance of multiple spatial scales in population dynamics has been established in a general context (Blaine and DeAngelis 1997; Peterson et al. 1998; Roos et al. 1998; Donaldson and Nisbet 1999), and more specifically in the context of caribou habitat selection (Johnson et al. 2001; Szkorupa 2001; Johnson et al. 2002a; Johnson et al. 2002b). It is at the core of one of the most important problems facing caribou under current forest management policies: the loss of large old growth forest patches (Cichowski 1996; Hervieux et al. 1996; Brown 1998). To examine how spatial scales of forests, ungulates and wolves interact, I simulated population dynamics under a range of scenarios designed to identify how relative spatial scales influence system behaviour. In particular, I looked for scaling conditions that caused an *effective* loss of spatial separation through scale dominance in predation. Forest conditions and habitat selection predicted prey-switching across a spatial grid with equal spatial scaling among prey and predators. When predation operated at a larger spatial scale than the prey, however, switching was reduced in most cases.

My results demonstrate that spatial distribution arising from evolutionary fitness behaviour can produce spatial patterns that result in density dependent inter-species encounter rates. The results also demonstrate that those behavioural mechanisms lead to different patterns when species abundances and landscape conditions change. This behaviour ultimately leads to *apparent* prey-switching when viewed across gradients of prey densities. In theory, this means that two prey species can co-exist. However, the switching only occurs if certain conditions are met. The question is therefore not *if* switching is possible. Rather, we need to determine whether or not the conditions exist for switching to take place. The degree of switching is sensitive to quantities of habitat, niche overlap of prey species, densities of prey and predators and the scale at which species perceive their resources and risks.

The results are not evidence that a Type 3 functional response should be used to predict the dynamics of caribou-moose-wolf systems. If such systems currently shows depensatory predation rates at low densities, however, policies should consider habitat supply and forest spatial structure that could reverse this. This analysis provides a mechanistic rationale that supports the most commonly lauded policy: to put aside large patches of old growth forest (Edmonds 1998; Thomas 1995; Hervieux et al. 1996; Szkorupa 2001). The justification has been that caribou need lichen-rich older forests to forage, and that these need to be large enough for spatial separation from alternate prey and predators. Many populations in British Columbia and Alberta have been declining under fairly typical forest extraction policies (Edmonds 1988; Edmonds 1998; Wittmer 2004). In most of those populations, violation of Condition 2 (habitat supply) and Condition 3 (spatial separation) are likely the cause. Predator and alternate prey densities are believed in most cases to have had a strong bearing on the declines. Predator densities are high enough in some cases that concerns have been raised that alternate prey management may cause predators to switch to caribou. I have shown that there are reasons to expect that reductions in alternate prey may cause increases in predation but they are entirely dependent on the supply and distribution of habitat. Management policies therefore need to consider the effects of restructuring supply and distribution of different age classes of forests.

Forest research has produced many studies of natural disturbances. Usually, a natural disturbance regime is characterized by disturbance rates (Van Wagner 1978), resulting forest age structure (Johnson and Van Wagner 1985; Andison 1997) and patch size distributions (Andison 1997; Armstrong 1999). It is widely agreed that boreal forests are dominated by large infrequent fire events. Forest management policies on the other hand, have created smaller than "natural" patch mosaics (violation of patch size condition), and generally reduced the mean age of forests (violation of the niche condition), while agricultural encroachment has led to a net reduction in forested land (violation of the supply condition). The results presented in this chapter suggest that predation on caribou could increase as a result of either a reduction in habitat quantity as well how it is distributed spatially. The frequency of fires and harvest thus has a direct bearing the ability of a system to exhibit prey switching.

Future directions

The results presented here demonstrate the outcome of one possible system applied under IFD assumptions and with a particular set of parameters. To empirically evaluate whether the IFD applies to a caribou-moose-wolf system, we would need to have animal locations of the two prey and the predator, as well as spatially referenced kill data. If the densities of all species were available from GPS collars recording the coordinates once per hour say, the data could be sampled at random to compare the distribution of the animals to a distribution predicted by the IFD model. With that information it would be possible to use a spatial likelihood objective function to fit predicted spatial distributions under various parameter combinations until a set of *best-fit* parameters maximized the likelihood of observing the data. The maximum likelihood estimates could then be used to parameterize a population dynamics model that could simultaneously predict spatial patterns, the distribution of kill rates and population dynamic trends over time. If the solution to the spatial likelihood predicted an emergent sigmoidal functional response, we would then expect the time series predictions to predict coexistence of the three species.

Given that animal behaviour is so difficult to monitor, the practical solution is to focus on the most dominant factors of the switching behaviour: habitat availability and spatial separation. These can be interpreted in the context of some of the widely agreed upon facets of caribou conservation and applied to simple interim policies aimed at making predator avoidance possible. Szkorupa (2001) found significant avoidance of younger stands of forest by caribou. Wittmer (2004) found strong evidence that survival rates are higher in older stands. James et al. (2004) found that caribou avoided areas inhabited by moose and that predation rates by wolves were higher in stands associated with moose. The implicit assumption about forests being driven to a younger state is that portions of the old forest are being cleared, resulting in young stands being found adjacent to remaining old stands. The results presented here predict that limited switching will be possible in precisely this type of situation. The solution remains the same: policies need to be aimed at cutting less forest and structuring the spatial arrangement of cleared areas such that large old patches will remain. It is perhaps redundant to restate what has been suggested before, but the analysis herein at least provides the mechanistic basis to argue for reductions in forest harvest rates and conservation of large tracts of old growth forest. It also demonstrates that one of the most commonly lauded arguments against caribou extirpation predictions (i.e., "Don't worry, predation rates will decline when densities are very low") may not apply in the type of situations where caribou are declining at present. The remaining habitat may not be in sufficient supply, nor adequately distributed to predict the switching behaviour demonstrated here, and avoid local extirpation.

Chapter 6

General conclusions

Overview of thesis

This thesis explores the dynamics of broad-scale patterns observed in woodland caribou systems in Alberta and elsewhere. It focusses on the effect of moose populations expanding in caribou ranges and the implications to subsequent predation on caribou by wolves responding numerically to moose. Population dynamics models indicate that if the current environmental conditions in the Redrock Prairie Creek caribou winter range persist, caribou are at risk of extirpation. Models predict wolf populations within the range of densities observed in wolf packs throughout North America while also predicting that caribou populations will gradually decline from predation by wolves. An analysis of equilibrium population densities indicates that the long-term viability of caribou ultimately depends on maintaining lower moose densities so that encounter rates with wolves remain low. Simulations of the effects of environmental variation suggest that caribou extirpation risks are not improved by environmental fluctuations around conditions that prevailed during the period of observed trends. A sensitivity analysis suggests that as long as moose populations remain high, caribou can only avoid extirpation if encounter rates between caribou and wolves are low. Simulations consistently show that caribou populations decline due to predation when wolf densities exceed approximately 0.008/km^2, which is consistent with declining caribou populations elsewhere. When wolf predation on caribou is modelled with a Type 3 functional response, caribou escape predation, but simulations of fine scale spatial behaviour show that spatial structure may play a role in shaping the form of the functional response. Results show that the emergence of Type 3 functional responses may depend on: 1) the niche breadth of prey, 2) the availability of resources in those niches, and 3) the spatial scales of predators, prey and resource distribution.

6.1 Key findings

Caribou populations are declining under current conditions

Four models were statistically fit to empirical trends. The parameters that provide the best fit to the data also predict declining caribou populations or extirpation.

Caribou persistence depends on reducing moose populations

An analysis of the relative effects of key parameters on equilibrium densities indicates that reducing the encounter rate between caribou and wolves has the greatest benefit to caribou populations when moose birth rates are at their highest. Given the practical difficulties of managing encounter rates in the short term, a further analysis was performed to investigate the potential effect of reducing moose densities. Results show that if moose densities are reduced with intensive management, caribou will stabilize at higher densities. This strategy is predicated on the fact that wolf predation on caribou occurs because wolves respond numerically to elevated moose densities and habitat structure provides inadequate spatial refuge. Moose reductions are deemed to be a more expedient way to reverse caribou declines than habitat alteration. Interim wolf reductions may also be considered to prevent wolf predation on caribou when moose densities decrease.

Environmental variation exacerbates caribou declines

When parameters are assumed to vary in relation to habitat supply and distribution, caribou populations continue to decline, and in some cases, decline faster than without environmental variation. Caribou recruitment rates decrease sharply after disturbances, while moose recruitment rises sharply. Caribou habitat recovery post-disturbance is too slow to allow caribou populations to recover before predation from wolves causes extirpation. Additionally, depending on disturbance parameters, the change to forest structure with disturbances either brings about a decline in productivity, or an increase in the encounter rate with wolves, further increasing predation pressure on caribou. Only a model with a sigmoidal functional response predicts caribou persistence.

Caribou decline at wolf densities $> 0.008/\mathrm{km}^2$

Consistently, models predicted that caribou populations would enter a declining phase when wolf density exceeded $0.008/\mathrm{km}^2$. When mechanisms were in place to reduce the effective rate of search, caribou were capable of escaping extirpation, but these cases required extremely low rates of encounter. These low rates could only be explained by prey switching, but the data were inadequate to conclude if switching was occurring.

Prey switching can depend on the diet niche of prey and predators

A detailed simulation analysis of spatial behaviour of predators and prey in relation to the spatial distribution of resources shows that prey switching can be apparent in aggregated data if both predators and prey can detect resource gradients that allow prey to strategically forage while avoiding predation risks.

The spatial distribution of resources must be such that predators can maximize energetic gain without necessarily having access to both prey types.

Prey switching can depend on the behavioural scales of individual species

Simulation analysis shows that prey switching can only occur if the spatial scale of predator behaviour does not exceed the spatial scale of prey behaviour and the distribution of resources of the individual prey. If predators can forage across multiple spatial units of prey, switching cannot occur because the prey cannot escape the perspective of the predator. This result implies that coexistence requires some *characteristic* natural scale to be maintained in the spatial distribution of resources.

6.2 Management implications

Management recommendations pertain to the preservation of habitat, the restoration of habitat, the control of access, and the direct control of species abundances. Habitat disturbances include roads, seismic lines and harvest blocks, which have all been shown to have negative impacts on caribou survival. As such, management policies should attempt to coordinate the timing of disturbances such that they are focussed in the same areas rather than spread out over the landscape. The following summarizes some management perspectives drawn from the results of this thesis:

Forest harvest regulations on cut sizes and old growth retention

Forest management policies should aim to increase the amount of forest contained in large old forest patches (>1200 hectares and >140 years). Parameter estimates of predation search rates were predicated on the fact that large old-growth patches comprised ≈11% of the forest. When search rates were negatively correlated to the proportion of large old-growth patches, policies that increase the proportion of large old-growth patches predicted improvements in caribou survival if the proportion of large old-growth patches increased to between 15 and 20%. Using this as a guideline, habitat conservation could use 20% as the broad-scale target for the establishment of caribou reserves in the RPC winter range.

Historically, the two-pass system has been used for harvest scheduling in the study region. This has the unfortunate consequence of creating two pulses of young seral forest, which improves moose production with a commensurate pulse and can result in a numerical response in wolves. This is precisely the type of situation that should be avoided, but which may have occurred in the RPC winter range in the 1990's. Careful attention should be taken to ensure that the distribution of harvest blocks does not create these pulses of young forest browse favourable to moose production in the vicinity of caribou reserves. Forest harvest scheduling could incorporate a design that ensures there is an adequate supply (15-20%) of large old-growth patches separated from harvest blocks. Given the caveat that wolf spatial behaviour may dominate the scale at which patches are distributed, the separation between caribou reserve habitat and the location of harvest blocks should be evaluated at scales similar to the those at which wolves form territories. Territory sizes of approximately 600-1000 km^2 suggest that wolves can occupy areas that measure on the order of 30×30 km, implying that a 30 kilometer separation translates to an entire wolf territory of separation. While it is unlikely that wolves would be excluded from such areas, the intent is to create a situation where wolf search behaviour is less likely to result in incidental encounters with caribou.

Limits on seismic line density and the impact rating of seismic lines

Assuming wolves travel faster on seismic lines, an increase in the density of seismic lines implies that a greater proportion of the area will exhibit higher search rates and that animals will have fewer options to avoid associated high predation. Policies should aim to reduce the net effect of seismic lines on search rates by reducing seismic line density and/or reducing the impact rating of lines by minimizing width and accelerating forest regeneration on cut lines. Vegetation restoration techniques should be applied to minimize the amount of time that lines support high quality moose habitat.

Moose harvest and monitoring

A variety of modelled results demonstrated negative effects on caribou as a result of moose. In all cases, caribou population persistence was improved if moose populations were reduced, either by setting the fixed harvest rate 10% higher than the current estimate, or by setting a lower target moose density. Caribou persistence was improved if wolf control was implemented simultaneously. Moose density should be reduced incrementally by 20% per year until caribou show signs of recovery, with an ultimate target of returning to the estimated 1989 density of 0.2 moose/km^2. Once this target is reached, harvest quotas should be implemented to retain moose at that density.

Moose densities were not monitored in the RPC during the period of this study. Policies that include reducing moose densities should begin with a census of moose densities and recruitment and be followed by gradual reductions until caribou populations show signs of an increase. Monitoring should include GPS collaring to gather information on the location of animals for spatial predictions that govern the emergent Type 3 functional response.

Wolf control

The RPC caribou population is currently one of the few herds in Alberta not considered to be declining, despite the long-term predictions presented in this thesis. The most recent census estimated wolf densities at approximately

0.011 animals/km^2. While wolf control may ultimately be required if densities of wolves increase, it is not warranted at this time. In the event that caribou populations begin the predicted decline, wolves should be reduced to less than 0.008 animals/km^2 with simultaneous moose reductions. Since caribou have generally not been shown to decrease when wolf densities are below this density, it provides an initial target density for reduction. Once this density has been reached monitoring of caribou populations will indicate if the reduction has been successful in recovering caribou populations.

Historically, recovering ungulate populations from suppression by wolves has required reducing wolves to very low numbers over very large spatial extents. There are two options for reducing wolf densities across caribou ranges: 1) reduce individual packs to fixed numbers of animals such that the overall density meets the target, and 2) remove entire wolf packs. The advantage of the first option is that it maintains the territory structure already in place. On the other hand, the second option has the additional advantage that it reduces the total number of predation units on the landscape. This advantage will likely be transient, however, as wolf pack sizes increase and wolves split to establish new packs in the vacant territory.

Access control

Roads and seismic lines provide the means for unwanted human activity in critical caribou areas. Human travel on roads increases the likelihood that caribou will be involved in collisions, and therefore has a direct impact on caribou mortality. Human presence on seismic lines will have the additional effect of driving predators into caribou inhabited areas away from roads. Access does, however, provide a potential benefit to caribou: during the hunting season, it improves hunting effort on moose, and therefore facilitates the goal of reducing moose densities.

General

The management options listed above have been identified by this study and others as potentially important for caribou conservation. The targets provide strategic guidelines to shape policies for experimental implementation within an adaptive management framework. In order to evaluate the outcomes, monitoring is required. Because all of the options are predicated on the fact that changes can bring about reduced predation on caribou, collection of wolf kill rate data is essential. This should be collected during the winter, when caribou are in the RPC range, and should be spatially referenced so that kill rates can be attributed to occurrences in particular habitat types and in relation to distances to disturbances.

6.3 Future directions

The dynamics explored in this thesis were general relationships between forest structure and key parameters that govern trophic interactions between wolves and ungulates. The management actions that can be applied to these relationships are very simple. More sophisticated management actions can be considered if dynamic interactions can be demonstrated in more detail. James and Stuart-Smith (2000) showed that although caribou generally avoided seismic lines, mortality rates were higher in their vicinity than elsewhere. Similarly, Smith et al. (2000) showed that caribou avoided clearcuts, but we know that regenerating forests will attract moose. Management actions could also consider directly controlling moose and wolf densities in areas adjacent to preferred caribou habitat. If wolves are monitored to collect kill composition and kill rates spatially, a model could be developed to predict the effect of spatially targeted reductions. This would mean that reductions could be focussed on a smaller area and would be less costly. The IFD model developed in this thesis provides the basis for doing this. If spatial accounting is extended to include information about each cells surroundings, fitness calculations could be sensitive to the fact that a cell is part of a large old patch or near a seismic line. This would cause each species to select habitat not only because of its inherent food value but also its proximity to other risks. The model could then be used to evaluate the effectiveness of spatially targeted species control.

6.4 Limitations and disclaimers

Data were inadequate to conclude which model structure best predicts the behaviour of the system. All models fit empirical trends equally well. This is problematic because the models predict qualitatively different outcomes on longer time scales. The data limitations were as follows:

Moose data

Moose densities were not collected in the RPC range, but rather assumed from the densities that were estimated in surrounding areas. Harvest statistics for moose were also not available in the RPC winter range during the period over which the analysis was performed, despite normally being available approximately every five years. Since wolf conversion efficiency was derived from another study (Hayes and Harestad 2000a), an overestimation of moose abundance could overestimate the subsequent predation effect on caribou.

Kill rates

There was no kill rate data spanning the time of observed relative abundance trends. This means that predation rates had to be estimated from balancing assumed adult natural mortality with estimated birth rates of ungulates. Kill rate data would improve estimates of predation effects on caribou and moose. This would greatly improve the estimates of effective rates of search, and therefore predation mortality.

Spatial distribution of animals unavailable

GPS collar data were available for both caribou and wolves but were not concurrent with the time period of the relative abundance trends. There was no coverage for moose. The snowtrack data provided only a single sample of spatial distributions for each year and therefore could not be used to test the IFD model. GPS collar data from wolves could be used to calculate the location of kills on the basis of the reduction in daily distance travelled following a kill. Again, available wolf GPS data did not cover the time span of relative abundance data.

General

Only a model with a Type 3 functional response for wolves preying on caribou predicts caribou persistence without drastic reductions in predation search rates on caribou. Given the many caveats to applying Type 3 functional responses, a mechanistic basis was proposed and evaluated through simulations. However, the mechanism that was proposed could not be tested against empirical data. Spatial distribution of kill rates was not available to fit predicted to observed kill distributions.

An examination of environmental variation on the dynamics of the system was predicated on the fact that base parameter values can be taken from a statistical fit to empirical trends and varied with environmental changes from the end of the fitting period. There are two important biases that come from this: 1) the trends may reflect conditions that no longer persist beyond the sample period, 2) the length of the sample period may have been too brief to properly reflect all behavioural aspects of the system. If the empirical trends of a cyclic system are in a growth phase for instance, parameter estimates will bias recruitment and potentially underestimate prey capture rates. When environmental variation is added, biases on predation search rates can be compounded with environmental scaling factors.

6.5 Summary

This thesis is a broad investigation into the effects of model structures on the qualitative behaviour of predator prey models. It shows the limitation of model fitting procedures to distinguish between candidate models and the uncertainty associated with parameter estimation and population trend projections under environmental variation. Despite limitations in estimating parameters and projecting trends, simulation results consistently demonstrate that caribou populations are incapable of sustaining elevated moose and wolf densities. The results in this thesis clearly point to habitat management as the long term solution to recovering woodland caribou populations. Fine-scale behaviour necessary for prey switching may ultimately depend on restoring forests closer to natural states. Larger tracts of old-growth forest are needed to provide caribou with adequate food resources away from incidental predation by wolves preying on moose. Since habitat restoration is a slow process, interim policies should consider direct control of species abundances. In particular, moose populations could be experimentally reduced and wolf densities should be controlled below $\approx$0.008 animals/km^2 until caribou populations show an increase. This may be necessary to prevent further declines while habitat conditions are restored.

Bibliography

Abrams, P. A. 1994. The fallacies of "ratio-dependent" predation. Ecology, **75**:1842–1850.

Abrams, P. A. 1997. Anomalous predictions of ratio-dependent models of predation. Oikos, **80**:163–171.

Abrams, P. A., R. D. Holt, and J. D. Roth. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. Ecology, **79**:201–212.

Abrams, P. A and C. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. Ecology, **77**:1125–1133.

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management, **59**:584–594.

Akcakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. Ecological Monographs, **62**:119–142.

Andison, D. W. 1997. Landscape fire behaviour patterns in the foothills model forest. Internal report, Foothills Model Forest.

Anonymous. 1998. Alberta Sustainable Resource Development Department. Northern moose management program, [online] URL: http://www3.gov.ab.ca/srd/fw/hunting/northmoose/98nmoose.html.

Arditi, R. and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. Journal of Theoretical Biology, **139**:311–326.

Armstrong, G. W. 1999. A stochastic characterisation of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable fores management. Canadian Journal of Forest Research, **29**:424–433.

Ballard, W. B. and V. Van Ballenberghe. 1997. Predator-prey relationships. In A. W. Franzmann and C. C. Schwartz, editors, Ecology and management of the North American moose, pages 247–273. Smithsonian Institution Press, Washington, DC.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs, **98**:1–54.

Ballard, W. B., J. S. Whitman, and D. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs, **114**:49.

Bangs, E. E., T. N. Bailey, and M. F. Portner. 1989. Survival rates of adult female moose on the Kenai peninsula, Alaska. Journal of Wildlife Management, **53**:557–563.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations, and communities. Blackwell Scientific, Cambridge, MA, 2nd edition.

Bergerud, A. T. 1974. Decline of caribou in North America following settlement. Journal of Wildlife Management, **38**:757–771.

Bergerud, A. T. 1988. Caribou, wolves and man. Trends in Ecology and Evolution, **3**:68–72.

Bergerud, A. T. 1990. A review of the dynamics of ungulates and wolves in north-eastern British Columbia 1976-1990. Draft report, Bergerud and Associates.

Bergerud, A. T. 1992. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. In D. R. McCullough and R. H. Barrett, editors, Wildlife 2001: Populations, pages 1008–1021. Elsevier, Barking, Essex.

Bergerud, A. T. and W. B. Ballard. 1988. Wolf predation on caribou: The Nelchina herd case history, a different interpretation. Journal of Wildlife Management, **52**:344–357.

Bergerud, A. T. and W. B. Ballard. 1989. Wolf predation on the Nelchina caribou herd: A reply. Journal of Wildlife Management, **53**:251–259.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion into the mountains. Canadian Journal of Zoology, **62**:1566–1575.

Bergerud, A. T. and J. P. Elliott. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology, **76**:1551–1569.

Bergerud, A. T. and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology, **64**:1515–1529.

Bergerud, A. T. and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology, **65**:1597–1606.

Bergerud, A. T. and J. B. Snider. 1988. Predation in the dynamics of moose pupulations: a reply. Journal of Wildlife Management, **52**:559–564.

Bergerud, A. T., W. Wyett, and B. Snider. 1983. The role of wolf predation in limiting a moose population. Journal of Wildlife Management, **47**:977–988.

Bernstein, C., P. Auger, and C. Poggiale. 1999. Predator migration decisions, the ideal free distribution, and predator-prey dynamics. American Naturalist, **153**:267–281.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1991. Individual decisions and the distribution of predators in a patchy environment II: The influence of travel costs and structure of the environment. Journal of Animal Ecology, **60**:205–225.

Blaine, T. W. and D. L. DeAngelis. 1997. The interaction of spatial scale and predator-prey functional response. Ecological Modelling, **95**:319–328.

Boertje, R. D., W. C. Gasaway, D. B. Grangaard, and D. G. Kelleyhouse. 1988. Predation on moose and caribou by radio-collared grizzly bears in east-central Alaska. Canadian Journal of Zoology, **66**:2492–2499.

Bolker, B., M. Holyoak, V. Krivan, L. Rowe, and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. Ecology, **84**:1101–1114.

Boutin, S. 1992. Predation and moose population dynamics: A critique. Journal of Wildlife Management, **56**:116–127.

Boyce, M. S. 1992. Wolf recovery for Yellowstone National Park: A simulation model. In C. E. McCulloch and R. H. Barrett, editors, Wildlife 2001: Populations, pages 123–137. Barking, Essex. Use type 3 FR.

Boyce, M. S. and E. M. Anderson. 1999. Evaluating the role of carnivores in the greater Yellowstone ecosystem. In T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors, Carnivores in Ecosystems: The Yellowstone Experience, pages 265–283. Yale University Press, New Haven and London.

Briggs, C. J. and M. F. Hoopes. 2004. Stabilizing effects in spatial parasitoid-host and predator-prey models: a review. Theoretical Population Biology, **65**:299–315.

Brooks, S. P. 1998. Markov chain Monte Carlo method and it's application. The Statistician, **47**:69–100.

Brown, W. K. 1998. Integrating woodland caribou needs and forestry: perspectives of Alberta's forest industry. Rangifer Special Issue, pages 213–219.

Brown, W. K. and D. P. Hobson. 1998. Caribou in west-central Alberta: information review and synthesis. Prepared for the research sub-committee of the west-central alberta caribou standing committee., Terrestrial and Aquatic Managers Ltd.

Burden, R. L. and J. D. Faires. 1985. Numerical Analysis. Prindle, Weber and Schmidt, Boston, MS, 3rd edition.

Carpenter, S. R., K. L. Cottingham, and C. A. Stow. 1994. Fitting predator-prey models to time series with observation errors. Ecology, **75**:1254–1264.

Caughley, G. and A. R. E. Sinclair. 1994. Wildlife Ecology and Management. Blackwell Scientific Publications, Oxford.

Chib, S. and E. Greenberg. 1995. Understanding the Metropolis-Hastings algorithm. The American Statistician, **49**:327–335.

Cichowski, D. 1996. Managing woodland caribou in west-central British Columbia. Rangifer Special Issue, pages 119–126.

COSEWIC. 2000. Canadian species at risk. Technical report, Committee on the Status of Endangered Wildlife in Canada.

Crete, M. 1989. Approximation of K carrying capacity for moose in eastern Quebec. Canadian Journal of Zoology, **67**:373–380.

Crete, M., R. J. Taylor, and P. A. Jordan. 1981. Simulating conditions for the regulation of a moose population by wolves. Ecological Modelling, **12**:245–252.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology, **63**:644–652.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1995. Winter wolf predation in a multiple ungulate prey system, Gates of the arctic national park, Alaska. In L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors, Ecology and conservation of wolves in a changing world, pages 223–230. Canadian Circumpolar Institute, Occasional publication No. 35, Edmonton, AB.

Donaldson, D. D. and R. M. Nisbet. 1999. Population dynamics and spatial scale: effects of system size on population persistence. Ecology, **80**:2492–2507.

Dyer, S. J. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. M.Sc. Thesis, University of Alberta. M.Sc. Thesis

Dyer, S. J., J. P. O'Neill, S. M. Wassel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management, **65**:531–542.

Dzus, E. 2001. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta. Wildlife Status Report 30, Alberta Environment, Fisheries and Wildlife Management Devision, and Alberta Conservation Association.

Eberhardt, L. L. 2000. Reply: Predator-prey ratio dependence and regulation of moose populations. Canadian Journal of Zoology, **78**:511–513.

Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west-central Alberta. Canadian Journal of Zoology, **66**:817–826.

Edmonds, J. 1998. Status of woodland caribou in Alberta. Rangifer Special Issue, pages 111–115.

Fretwell, S. D. and H. L. Lucas. 1970. On territorial behaviours and other factors influencing habitat distribution in birds. Acta Biotheoretica, **19**:16–36.

Fryxell, J. M. and C. M. Doucet. 1993. Diet choice and the functional response. Ecology, **74**:1297–1306.

Fryxell, J. M. and P. A. Lundberg. 1998. Individual behaviour and community dynamics, volume 24 of *Population and community biology series*. Chapman Hall, New York.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs, **105**:1–41.

Fuller, T. K. and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. Journal of Wildlife Management, **44**:583–602.

Fuller, T. K. and L. B. Keith. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management, **45**:197–213.

Gasaway, W. C., R. D. Boertje, D. B. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs, **120**:1-59.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs, **84**:1–50.

Gelman, A. J., B. Carlin, H. S. Stern, and D. B. Rubin. 1995. Bayesian Data Analysis. Chapman and Hall, N.Y.

Gelman, A. J. and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science, **7**:457–472.

Gilpin, M. E. 1972. Enriched predator-prey systems: theoretical stability. Science, **177**:902–904.

Grand, T. 2002. Foraging-predation risk trade-offs, habitat selection, and the coexistence of competitors. American Naturalist, **159**:106–112.

Grand, T. and L. M. Dill. 1999. Predation risk, unequal competitors and the ideal free distribution. Evolutionary Ecology, **1**:389–409.

Gutierrez, A. P. 1992. Physiological basis of ratio-dependent predator-prey theory: the metabolic pool model as a paradigm. Ecology, **73**:1552–1563.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey on a subarctic ecosystem. Ph.D. Dissertation, University of British Columbia.

Haber, G. C. 1987. Exploitation of wolf-moose systems - Lessons from interior Alaska. Technical report, The Alaska Wildlife Alliance.

Hassel, M. P. and R. M. May. 1973. Stability in insect host-parasite models. Jounal of Animal Ecology, **42**:693–726.

Hassel, M. P. and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. Journal of Animal Ecology, **43**:567–594.

Hayes, R. D., A. M. Baer, and A. S. Harestad. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology, **78**:49–59.

Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Bear, C. L. Gardner, and M. O'Donohue. 2003. Experimental reduction of wolves in the Yukon: Ungulate response and management implications. Journal of Wildlife Management, **152**:1–35.

Hayes, R. D. and A. S. Harestad. 2000*a*. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology, **78**:36–48.

Hayes, R. D. and A. S. Harestad. 2000*b*. Wolf functional response and regulation of moose in the Yukon. Canadian Journal of Zoology, **78**:60–66.

Hervieux, D., J. Edmonds, R. Bonar, and J. McCammon. 1996. Successful and unsuccessful attemps to resolve caribou management and timber harvesting issues in west-central Alberta. Rangifer Special Issue, pages 185–190.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist, **91**:385–398.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada, **45**:60.

Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. Journal of Theoretical Biology, **12**:197–229.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist, **124**:377–406.

Houston, A. I. and A. Lang. 1998. The ideal free distribution with unequal competitors: the effects of modelling methods. Animal Behaviour, **56**:243–251.

James, A. R. C., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management, **68**:799–809.

James, A. R. C. 1999. Movement and distribution of woodland caribou (*Rangifer tarandus caribou*) in response to industrial development in northeastern Alberta. Ph.D. Dissertation, University of Alberta.

James, A. R. C. and A. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management, **64**:154–159.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002*a*. A multiscale behavioural approach to understanding the movements of woodland caribou. Ecological Applications, **12**:1840–1860.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002*b*. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology, **71**:225–235.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioural decisions made by woodland caribou at mutiple spatial scales. Oecologia, **127**:590–602.

Johnson, E. A. and C. E. Van Wagner. 1985. The theory and use of two fire history models. Canadian Journal of Forest Research, **15**:214–220.

Jost, C. and R. Arditi. 2001. From pattern to precess: identifying predator-prey models from time-series data. Population Ecology, **43**:229–243.

Kacelnik, A., J. R. Krebs, and C. Bernstein. 1992. The ideal free distibution and predator-prey populations. Trends in Ecology and Evolution, **7**:50–55.

Karns, P. D. 1997. Population, distribution, density and trends. In A. W. Franzmann and C. C. Schwartz, editors, Ecology and management of the North American moose, pages 125–140. Smithsonian Institution Press, Washington, DC.

Kendall, B. E., C. J. Briggs, W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet, and S. N. Wood. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. Ecology, **80**:1789–1805.

Krivan, V. and A. Sikder. 1999. Optimal foraging and predator-prey dynamics, II. Theoretical Population Biology, **55**:111–126.

Krivan, V. and I. Vrokoc. 2000. Patch choice under predation hazard. Theoretical Population Biology, **58**:329–340.

Kuzyk, G. W. 2002. Wolf distribution and movements on caribou ranges in west-central Alberta. M.Sc. Thesis, University of Alberta.

Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest yukon. Journal of Wildlife Management, **53**:548–557.

Loranger, A. J., T. N. Bailey, and W. W. Larned. 1991. Effects of forest succession after fire in moose wintering habitats on the Kenai Penninsula, Alaska. Alces, **27**:100–109.

Marshal, J. P. and S. Boutin. 1999. Power analysis of wolf-moose functional responses. Journal of Wildlife Management, **63**:396–402.

May, R. M. 1972. Limit cycles in predator-prey communities. Science, **177**:900–902.

McLoughlin, P. D., D. E., W. B., and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management, **67**:755–761.

McRoberts, R. E., L. D. Mech, and R. O. Peterson. 1995. The cummulative effect of consecutive winter's snow depth on moose and deer populations: a defense. Journal of Animal Ecology, **64**:131–135.

Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winter's snow. Journal of Animal Ecology, **56**:615–627.

Mech, L. D., T. J. Meir, J. W. Burch, and L. G. Adams. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. In L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors, Ecology and conservation of wolves in a changing world, pages 231–244. Canadian Circumpolar Institute, Occasional publication No. 35, Edmonton, AB.

Messier, F. 1984. Moose-wolf dynamics and the natural regulation of moose populations. Ph.D. Dissertation, University of British Columbia.

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. Canadian Journal of Zoology, **63**:1068–1077.

Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology, **60**:377–393.

Messier, F. 1994. Ungulate population models with predation: a case study with the North America moose. Ecology, **75**:478–488.

Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. In L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors, Ecology and conservation of wolves in a changing world, pages 187–197. Canadian circumpolar institute, Occasional publication No. 35.

Messier, F. and M. Crete. 1984*a*. Body condition and population regulation by food resources in moose. Oecologia, **65**:44–50.

Messier, F. and M. Crete. 1984*b*. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia, **65**:503–512.

Messier, F. and D. O. Joly. 2000. Comment: Regulation of moose populations by wolf predation. Canadian Journal of Zoology, **78**:506–510.

Miller, S. D. and W. B. Ballard. 1992. Analysis of an effort to increase moose calf survivorship by increased hunting of brown bears in south-central Alaska. Wildlife Society Bulletin, **20**:445–454.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs, **39**:335–354.

Murdoch, W. W., S. Avery, and M. E. B. Smyth. 1975. Switching in predatory fish. Ecology, **56**:1094–1105.

Oaten, A. and W. W. Murdoch. 1975. Switching, functional response, and stability in predator-prey systems. American Naturalist, **109**:299–318.

Oberg, P. R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. M.Sc. Thesis, University of Alberta.

Oberg, P., C. Rohner, and F. K. A. Schmiegelow. 2002. Responses of mountain caribou to linear features in a west-central Alberta landscape. In The Seventh International Symposium on Environmental Concerns in Rights-of-Way Management. Elsevier Science.

Orians, G. H., P. A. Cochran, J. W. Duffield, T. K. Fuller, R. J. Gutierrez, W. M. Hanemann, F. C. James, P. Kareiva, S. P. Kellert, D. Klein, B. N. McLellan, P. D. Olson, and G. Yaska. 1997. Wolves, bears, and their prey in Alaska: biological and social challenges in wildlife management. National Academy Press, Washington, DC.

Pascual, M. A., P. M. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology, **11**:966–976.

Peterson, G. D., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity and scale. Ecosystems, **1**:6–18.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series 11, National Park Service.

Peterson, R. O., R. E. Page, and K. M. Dodge. 1984*a*. Wolves, moose and the allometry of population cycles. Science, **224**:1350–1352.

Peterson, R. O. and R. E. Page. 1988. The rise and fall of Isle Royale wolves, 1975-1986. Journal of Mammalogy, **69**:89–99.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984*b*. Wolves of the Kenai penninsula, Alaska. Wildlife Monographs, **88**:1–52.

Renecker, L. A. and C. C. Schwartz. 1997. Food habits and feeding behavior. In A. W. Franzmann and C. C. Schwartz, editors, Ecology and management of the North American moose, pages 403–440. Smithsonian Institution Press, Washington, DC.

Rettie, W. J. and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology, **76**:251–259.

Rohner, C., W. K. Brown, and S. Shirkoff. 2000. Ten years of aerial snowtracking in the Redrock Prairie Creek caribou ranges: distribution, trend in abundance, and spatial overlap of large wildlife species. Internal report, Weyerhaeuser Company Ltd.

Roos, A. M. d., E. McCauley, and W. G. Wilson. 1998. Pattern formation and the spatial scale of interaction between predators and their prey. Theoretical Population Biology, **53**:108–130.

Rosenzweig, M. L. 1969. Why the prey curve has a hump. American Naturalist, **103**:81–87.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science, **171**:385–387.

Rozenzweig, M. L. 1991. Habitat selection and population interactions: The search for mechanisms. American Naturalist, **137**:S5–S28.

Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist, **97**:209–223.

Schneider, R. R., J. B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land uses in the Western Canadian Sedimentary Basin: a modeling approach. Conservation Ecology, **7**:[online] URL: http://www.consecol.org/vol7/iss1/art8.

Schwartz, C. C. 1997. Reproduction, natality and growth. In A. W. Franzmann and C. C. Schwartz, editors, Ecology and management of the North American moose, pages 141–172. Smithsonian Institution Press, Washington, DC.

Schwartz, C. C. and A. W. Franzmann. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces, **25**:1–10.

Seip, D. R. 1990. Ecology of woodland caribou in Wells Gray provincial park. Wildlife Bulletin B-68, BC Ministry of Environment.

Seip, D. R. 1991. Predation and caribou populations. Rangifer Special Issue, pages 46–52.

Seip, D. R. 1992*a*. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology, **70**:1494–1503.

Seip, D. R. 1992*b*. Wolf predation, wolf control, and the management of ungulate populations. In D. R. McCulloch and R. H. Barrett, editors, Wildlife 2001: Populations, pages 331–340. Elsevier, Barking, Essex.

Seip, D. R. 1998. Ecosystem management and the conservation of caribou habitat in British Columbia. Rangifer Special Issue, pages 203–211.

Servheen, G. and J. L. Lyon. 1989. Habitat use by woodland caribou in the Selkirk mountains. Journal of Wildlife Management, **53**:230–237.

Sinclair, A. R. E. 1989. Population regulation in animals. In J. M. Cherrett, editor, Ecological concepts: the contribution of ecology to an understanding of the natural world, pages 197–241. Blackwell Scientific, Oxford, U.K.

Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Philosophical Transactions of the Royal Society of London B, **358**:1729–1740.

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology, **54**:359–374.

Smith, K. G. 2004. Woodland caribou demography and persistence relative to landscape change in west-central Alberta. M.Sc. Thesis, University of Alberta.

Smith, K. G., E. J. Ficht, D. Hobson, and T. C. Sorensen. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. Canadian Journal of Zoology, **78**:1433–1440.

Stuart-Smith, A., C. Bradshaw, S. Boutin, D. Hebert, and A. Rippin. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. Journal of Wildlife Management, **61**:622–633.

Sutherland, W. J. 1983. Aggregation and the 'ideal free' distribution. Journal of Animal Ecology, **52**:821–828.

Szkorupa, T. D. 2001. Multi-scale habitat selection by mountain caribou in west-central Alberta. M.Sc. Thesis, University of Alberta.

Thomas, D. C. 1995. A review of wolf-caribou relationships and conservation implications in Canada. In L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors, Ecology and conservation of wolves in a changing world, pages 261–274. Canadian Circumpolar Institute, Occasional publication No. 35, Edmonton, AB.

Thompson, I. D. and R. O. Peterson. 1988. Does wolf predation alone limit the moose population in Pukaskwa park?: a comment. Journal of Wildlife Management, **52**:556–559.

Thurber, J. M. and R. O. Peterson. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. Journal of Mammalogy, **74**:879–889.

Turchin, P. 2002. Complex Population Dynamics: A Theoretical/Empirical Synthesis. Monographs in Population Biology, Princeton University Press, Princeton, NJ.

Van Baalen, M., V. Krivan, P. C. J. Van Rijn, and M. W. Sabelis. 2001. Alternative food, switching predators, and the persistence of predator-prey systems. American Naturalist, **157**:512–524.

Van Ballenberghe, V. 1985. Wolf predation on caribou: the Nelchina herd case history. Journal of Wildlife Management, **49**:711–720.

Van Ballenberghe, V. 1987. Effects of predation on moose numbers: a review of recent North American studies. Swedish Wildlife Research Suppl. 1, pages 431–460.

Van Ballenberghe, V. 1989. Wolf predation on the Nelchina caribou herd: a comment. Journal of Wildlife Management, **53**:243–250.

Van Ballenberghe, V. and W. B. Ballard. 1994. Limitation and regulation of moose populations: the role of predation. Canadian Journal of Zoology, **72**:2071–2077.

Van Ballenberghe, V. and W. B. Ballard. 1997. Population dynamics. In A. W. Franzmann and C. C. Schwartz, editors, Ecology and management of the North American moose, pages 223–246. Smithsonian Institution Press, Washington, DC.

Van der Meer, J. and B. J. Ens. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. Journal of Animal Ecology, **66**:846–858.

Van Wagner, C. E. 1978. Age class distribution and the forest fire cycle. Canadian Journal of Forest Research, **8**:220–227.

Walters, C. J. and D. Ludwig. 1994. Calculation of Bayes posterior distributions for key population parameters. Canadian Journal of Fisheries and Aquatic Sciences, **51**:713–722.

Walters, C. J. and S. J. D. Martell. 2004. Harvest management for aquatic systems. Princeton University Press, Princeton.

Walters, C. J., M. Stocker, and G. C. Haber. 1981. Simulation and optimization models for a wolf-ungulate system. In C. W. Fowler and T. D. Smith, editors, Dynamics of large mammal populations, pages 317–337. John Wiley and Sons, New York.

Walters, C., V. Christensen, and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7:139–172.

Wittmer, H. U. 2004. Mechanisms underlying the decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia. Ph.D. Dissertation, University of British Columbia.