FERTILITY CONTROL AND THE ECOLOGICAL CONSEQUENCES OF MANAGING NORTHERN WOLF POPULATIONS

by

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ABSTRACT

I hypothesized that sterilization would not alter basic wolf behaviour. I studied the behaviour of 17 surgically sterilized wolves from 7 small wolf packs. Sterilized wolves maintained existing pair bonds, defended their original territories, and exhibited denning behaviour. I constructed a simulation model to predict the long term ecological effects of sterilizing a wolf population. The model simulates lethal wolf control, wolf fertility control, human harvest of ungulates, and stochastic weather variation. Fertility control can augment rates of moose and caribou population increase, but lethal control is required to initiate the recovery of a critically small caribou herd. Dall sheep populations do not obviously benefit from wolf management. All prey populations are sensitive to weather variability and constant levels of harvest. The results of the short term behaviour study and the long term model simulations suggest that fertility control may be an effective way to manage wolf populations.

ACKNOWLEDGMENTS

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CHAPTER ONE: GENERAL INTRODUCTION

PART ONE: POPULATION CONTROL, FERTILITY CONTROL, AND WOLF MANAGEMENT

'Problem species' may require population management in many contexts. These can include situations where pest species inflict serious damage to habitat, where they cause the decline of endangered native species, where livestock populations or agricultural crops are threatened, and where human activities such as hunting and recreation are adversely affected (Bomford 1990). Pests include animals, birds, insects, weeds, mites, nematodes, fungi, insects, bacteria, and viruses and their vectors (Dent 1995). Pests can cause considerable damage to agricultural crops and to natural forest ecosystems which will affect commercial timber harvests. Terrestrial vertebrates, particularly exotic species, can threaten native flora and fauna due to overgrazing, predation, and competition (Rolls 1969). Solutions to these problems often involve controlling the population size of problem species.

Traditional population control

Animal population dynamics are determined by four processes: birth, death, immigration, and emigration or dispersal (Begon et al. 1990). Attempts to control population size have most often involved increasing death rates, herein called "lethal control". Various techniques have been used to control invertebrate pests, including chemical pesticides, host-plant resistance, biological control such as the introduction of

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predators and pathogens, cultural control, semio-chemicals, and sterile insect techniques

(Dent 1995). Terrestrial vertebrates have been targeted by poison baits, trapping,

shooting, and habitat manipulation or destruction. Other attempts of damage mitigation

have included exclosures, diversionary feeding, aversive conditioning, and the

introduction of competitors or predators (Bomford 1990, Cluff and Murray 1995). Canid

populations have proven to be particularly difficult to control due to their mobility, lack

of specialization for prey and habitat, and high reproductive rates (Harris and Saunders

1993).

Problems associated with lethal control

The advantages of conventional lethal control methods often include cost-

effectiveness, an immediate decline in population numbers, and damage mitigation

(Bomford 1990). Despite these desirable effects, there are many disadvantages associated

with conventional lethal control methods. These can include non species-specific agents

that can pose a potential threat to non-target species and to humans; inhumane treatment

of animals; large expense; short-lived population density suppression in species with

high recruitment; logistical problems of treatments applied on a large scale; and last,

reduced efficacy due to compensatory increases in breeding, survival, immigration and

decreased emigration (Bomford 1990). Depending upon the species under control,

culling can be controversial. In North America, the reduction of wolf populations to

bring about increases in wild ungulate numbers has been one of the most controversial

issues in wildlife management (Mech 1995)

Wolves: A history of controversy

Grey wolves (Canis lupus) have inhabited much of the Northern Hemisphere

where large native ungulate populations were found (Mech 1970). With the introduction

of domesticated ungulates, wolf-human conflicts led to the persecution of wolves and

their subsequent demise or disappearance from much of North America, Europe, and Asia

(Mech 1995). The current recovery of wolf populations is due in large part to a change in

public opinion which Mech (1995) calls the "environmental revolution". With the

creation of the U.S. Endangered Species Act in 1966, favourable publicity, and increased

scientific and public awareness about wolves, the grey wolf has been allowed to

recolonize many areas in the United States (Mech 1995). The rapid recovery of wolf

populations and their expansion into non-wilderness areas has recently led to an increase

in the number of conflicts with human interests, especially livestock raising and hunting.

In Canada, wolf numbers are estimated between 52,000 and 60,000, and

populations are considered to be stable, particularly in northern regions where human

population density is low. In the Yukon, where my study was conducted, there are an

estimated 4500 wolves. Wolf hunting is permitted with a big game license (Hayes and

Gunson 1995).

It is widely believed that wolf predation can strongly limit ungulate populations,

and in some cases may regulate them to low prey densities (Fuller and Keith 1980,

Messier and Crête 1985, Hayes et al. 1991, Seip 1992, Messier 1994, Messier 1995,

Hayes 1995) (See Chapter One Part Two and Chapter Three). Large scale government

wolf control programs have been in place as recently as 1997 in the Yukon, and have

been implemented in northern environments as a way to increase ungulate populations used for subsistence. Wolf reduction programs have been carried out in Alaska, Yukon, British Columbia, Alberta, Ontario, Quebec and the Northwest Territories because of declines in moose (Alces alces), caribou (Rangifer tarandus tarandus), and deer (Odocoileus virginianus, O. hemionus columbianus) populations (Banville 1983, Gunson, Harbo and Dean 1983, Kolenosky 1983, Tompa 1983, Bergerud and Elliot 1986, Ballard et al. 1987, Potvin et al. 1992, Seip 1992, Hatter and Janz 1994, Hayes 1995, Hayes and Gunson 1995, Boertje et al. 1996).

Problems with lethal wolf control

The advantages of lethal wolf control can include an immediate and large increase in ungulate calf survival and expected high rates of increase of ungulate populations (Hayes 1995, Boertje et al. 1996). There are also disadvantages. Some methods such as trapping and poisoning are not specific to wolves, posing a potential threat to other mammals. For example, a Yukon wolf poisoning program in the 1950's caused a large number of wolverine (Gulo gulo) and raven (Corvis corax) mortalities (R.D. Hayes, pers. commun.). Most lethal control methods are also generally considered to be inhumane (Cluff and Murray 1995). Aerial shooting programs, have been highly effective but can be expensive.

Regardless of the methods used, culling provides only short term decreases in wolf numbers. Once a wolf pack is removed from a territory, it is quickly replaced by another pair, which usually reproduces within a year. In 2 areas of the Yukon, reduced

wolf populations recovered to pre-control densities within 3-4 years (Hayes et al. 1991,

Hayes 1995). Initially, low wolf densities enhance the survival, reproduction and hunting

success of the re-colonizing wolves, suppress dispersal, and increase the survival rates of

immigrating animals. Lastly, any form of lethal wolf control is considered by some

people to be ethically, politically, and ecologically unacceptable (Mech et al.1996a,

Haber 1996). In Alaska, public protest and litigation have effectively eliminated the use

of lethal control in intensive wolf management programs (C. Gardner, pers. commun.).

Wolf control in Aishihik, Yukon

In Aishihik, Southwest Yukon, many people rely upon wild ungulate populations

for subsistence. The 1993 Champagne-Aishihik First Nation Land Claims settlement

reflects the importance of woodland caribou and moose in the diet of the local First

Nations. An important clause in the agreement guarantees plentiful game for subsistence

harvest. In the late 1980's, declines of Aishihik moose, caribou, and Dall sheep

populations were observed and local communities requested wolf population reduction to

help increase game populations (Yukon Fish and Wildlife Branch 1994, Ward and Larsen

1995). A citizen group designed a consensus-based, Yukon-wide wolf management plan,

which included conditions for conducting lethal aerial control (Yukon Wolf Management

Planning Team 1992). The planning team also recommended experimenting with non-

lethal control methods, such as fertility control. As a main part of the plan to aid in the

recovery of ungulate populations in Aishihik, Yukon Territorial Government (YTG)

biologists conducted a program of experimental fertility control and aerial shooting and

ground snaring of wolves from 1993 to 1997, which reduced the Aishihik wolf population to 30% of its pre-control population size (Hayes 1992, YTG unpubl. data).

Intensive large scale mortality control of wolves may no longer be a viable management option in the Yukon, due largely to a shift in public opinion and increased understanding about the regulatory effects of wolf predation (Gasaway et al. 1992, Messier 1994, Hayes 1995). Viewed by many as more ethical (Bomford 1990, Cluff and Murray 1995), fertility control has become popular idea.

Fertility control of wildlife populations: the theory

In an effort to overcome some of the problems associated with traditional methods of population control, researchers have been investigating the possibility of controlling wildlife populations by reducing birth rates, herein called "fertility control". Knipling's (1959) theoretical paper is credited with the idea of applying fertility control to vertebrate populations. More recent theoretical models suggest that fertility control may suppress population densities without some of the negative consequences associated with conventional methods (Garrott 1991, Garrott and Siniff 1992, Garrott et al. 1992, Hone 1992, Caughley et al. 1992, Seagle and Close 1996, Barlow 1994, 1997; Barlow et al. 1997; Sinclair 1997).

Fertility control of wild populations may be an effective alternative to lethal control for several reasons. First, decreased birth rates may have a prolonged effect of limiting population density. Using a theoretical rat population, Bomford and O'Brien (1990) showed that killing 90% of the rats maintained the population density at below

pre-control levels for 4 years, whereas the sterilizing 90% of the population (both sexes) suppressed population size for more than 6 years. This longer term effect can stem from density-dependent factors which reduce the rate of exponential population growth. If sterilization does not affect social behaviour, then treated animals may decrease the reproductive success of fertile individuals in the population by competing for food, mates and habitat. Territorial behaviour also may restrict immigration. In addition, fertility control may allow for flexible management, because some chemical and immunological agents are species-specific and can be active for varying periods. Finally, because animals are not killed, fertility control can be perceived to be more ethically and socially acceptable (Bomford 1990, Cluff and Murray 1995).

However, fertility control alone may not be a useful technique when immediate damage mitigation is required, because sterile individuals remain in the population and can be assumed to modify their habitat in the same way that fertile animals do. Compensatory responses such as reduced juvenile and adult mortality, decreased dispersal rates and increased immigration may occur. In cases where reproduction is density-dependent, fertility control may only serve to determine which animals, and not how many, will reproduce. If behaviour is altered, increased survival, food consumption and absolute numbers may be observed (Bomford, 1990). Ultimately, fertility control may be inappropriate in certain situations where species-specific and cost-effective methods are not available. In summary, fertility control appears to have potential as a useful management technique where conditions are suitable, but there is still little field evidence that it can be effective for managing wild populations.

Fertility control of wildlife populations: the application

The appeal of the possible benefits of fertility control of certain wildlife populations has led to a large scale investigation of sterilization agents over the last four decades. Chemical sterilants, surgical sterilization, biological agents and immunocontraception have been assessed as alternatives to conventional methods for their potential to control animal reproduction (Bomford 1990; Kirkpatrick et al. 1990 a,b; Tyndale-Biscoe 1994; Asa 1992, in press; MacIvor and Schmidt 1996, Howse et al. 1998).

Much of this research has focused on lab animals under lab conditions. Many other studies have investigated sterilants using a small sample of captive animal populations (Table 1.1). Bomford (1990) and, more recently, MacIvor and Schmidt (1996) provided a good overview of the research into fertility control and wildlife contraception.

Increasingly, success is reported for fertility control of free-ranging mammals, using several different techniques including synthetic hormones and immunocontraception. Insect pest populations have been controlled using sex pheremones to disrupt mating (e.g. Critchley et al. 1985, Cassagrande 1993, de Vlieger and Klijnstra 1993), and sterile insect techniques have been used to reduce cattle screw worm populations (Davidson 1974, Drummond et al. 1988). Notably, white-tailed deer (Bell and Peterle 1975, Plotka and Seal 1989, Turner et al. 1996), black-tailed deer (Jacobsen et al. 1995), grey seals (Halichoerus grypus: Brown et al. 1996), Etosha lions

(Pantera leo: Orford et al. 1988), red foxes (Vulpes vulpes: Bubela 1995) and feral horses (Equus caballus: Kirkpatrick et al. in press) have been successfully sterilized. Table 1.2 provides an overview of successful fertility control field studies. Several unsuccessful studies involving fertility control have also been reported (Botti 1985, Munson 1993, Frank and Sajdak 1995), but these studies are generally not often reported and are difficult to find.

There have been very few studies which have examined fertility control for wild canids. Lord (1956) sterilized female grey foxes (Urocyon cineroargenteus) in Florida in order to estimate the size of the population, using the age-ratio reduction method. Both captive (Newsome, 1995) and wild (Bubela, 1995) red fox vixens were tubally ligated in Australia to determine the effects of sterilization upon their social behaviour. A similar study was carried out on captive coyotes (Canis latrans: F. Knowlton, pers. commun.). Most relevant of the recent studies was the surgical sterilization of 5 wild male wolves from 4 different wolf packs in Minnesota (Mech et al. 1996a).

Table 1.1 An overview of published studies of research in to wildlife fertility control, summarized from MacIvor and Schmidt (1995). Studies are classified according to the nature of the study, the fertility control technique investigated, and the taxon of the study species. The model category is specific to the fertility control technique, but not to animal taxon. "Review" indicates a publication which provides an overview of results from other studies, but does not present original data.

Fertility Control Method	Taxa	Nature of Study or Publication			
		Field	Lab	Review	Model
Hormonal	Small mammal	2	10	4	1
	Large mammal	7	13		
	Bird				
Chemical	Small mammal	13	48	25	1
	Large mammal	7	22		
	Bird	10	20		
Surgical	Small mammal	2			
	Large mammal	3			
	Bird	2			
Immunological	Small mammal		28	48	7
	Large mammal	9	22		
	Bird				
Mechanical	Small mammal				
	Large mammal	1			
	Bird				
Total		56	163	77	9

Table 1.2 Selected summary of published studies of successful field experiments with wildlife fertility control. Studies are classified by species, location of the study, method of fertility control used, outcome, and reference.

Species	Location	Method	Result	Reference
Etosha lion (Pantera leo)	Etosha National Park, Africa	mibolerone (hormone)	contraception, behavioural change	Orford et al. 1988
Feral horses (Equus caballus)	Nevada, Oregon	vasectomy	marginal success	Eagle et al. 1993 Kirkpatrick et al. In press
Red fox (Vulpes vulpes)	Australia	tubal ligation	contraception, no behavioural change	Bubela 1995, Newsome 1995
Grey seals (Halichoerus grypus)	Sable Island, Canada	SIZP immunocontraception	contraception	Brown et al. 1996
White-tailed deer (Odocoileus virginianus)	Various, U.S.	PZP immunocontraception	contraception	Bell and Peterle 1975, Plotka and Seal 1989, Turner et al. 1996
Black-tailed deer (O. hemionus columbianus)	California	synthetic progesterone, remote delivery	contraception	Jacobsen et al. 1995
Pectinophora gossypiella, Chilo suppressalis,codling moth and fruit tree leafrollers	Various	sex pheromones	successful mating disruption	Critchley et al. 1985, Cassagrande 1993, de Vlieger and Klijnstra 1993
Cochliomyia hominivorax	United States	sterile insect techniques	widespread success	Davidson 1974, Drummond et al. 1988
Grey wolf (Canis lupus)	Minnesota	vasectomy	probable success	Mech et al. 1996a
Grey fox (Urocyon cineroargenteus)	Florida	tubal ligation	no behavioural change	Lord 1956
Feral burro (Equus asinus)	US Virgin Islands	PZP immunocontraception	success	Turner et al. 1996
Norway rat (Rattus norvegicus), Red-winged blackbird (Agelaius phoeniceus), Beaver (Castor canadensis), Canada goose (Branta canadensis)	New York State	surgical sterilization	success	Converse and Kennelly 1994, Kennelly and Converse in press

Fertility control methods

All of the canid studies above have involved surgical sterilization by tubal ligation or vasectomy, with the assumption that if gonads are left intact, hormonal cycling and associated social and sexual behaviours will not be altered. The authors all reported no observable change in dominance hierarchy or social behaviour. Indeed, Kennelly and Converse (in press) advocate surgical sterilization for experiments with fertility control, because the merits of fertility control for a particular species can be tested without confounding side effects which are often associated with chemical and hormonal sterilants. Wolves, in particular, with their highly organized social hierarchy, are only suited to a technique such as surgical sterilization or, possibly, immunocontraception, where the gonads are intact and functioning (Asa 1995).

Wolves and fertility control

If sterilization of wolves can be achieved without altering fundamental social and territorial wolf behaviour (Mech et al. 1996a), their social biology may make wolves well suited to population suppression by fertility control.

Wolves are social animals that live in packs, usually comprised of the mating pair and their offspring, which live together in a well established social hierarchy. Packs maintain and defend territories from other wolves (Mech 1970). It is this territorial behaviour that makes wolves well suited to fertility control. If sterilized pairs of wolves remain in territories and defend them from potential immigrants, reduced wolf densities could be maintained for the lifetime of the treated animals. For management purposes,

pairs to be treated with fertility control can be chosen strategically to defend territories around important ungulate habitat, such as caribou calving grounds. Thus, fertility control could be used in a smaller portion of the wolf population than with lethal control, for which overall wolf densities commonly need to be reduced by up to 80% in order to rapidly benefit prey populations (Hayes et al. 1991). Fertility control could be more cost effective than lethal control over the long term, because territories with treated wolves do not have to be "treated" every year.

Wolf behaviour in summer may also be affected by fertility control. Denning wolf packs often separate in the summer and, individually, kill a large proportion of vulnerable calves (Doyle et al. unpubl. data). With no pups to raise, infertile wolves could reduce their energetic demand, thereby decreasing predation upon large ungulates, especially neonatal calves.

PART TWO: MODELLING WOLF-UNGULATE DYNAMICS

Wolves and their ungulate prey are large bodied, long-lived species that range over large areas. It is logistically difficult and often very expensive to study these animals and their interactions. Thus, various models can be useful to represent wolf-ungulate relationships, wolf behaviour, and the effects of management strategies, including fertility control.

Predator-prey interactions

Essentially, the basis of predator control programs is that predation is responsible for causing or maintaining low ungulate populations. Prey populations may be at low levels because they are limited by predation, and they may also be regulated to low densities by predators. Predation limits a prey population whenever predation is an additive source of prey mortality (Dale et al. 1994). A regulating factor is a density-dependent process that tends to stabilize population density over time (Sinclair 1989, Skogland 1991, Dale et al. 1994). Regulating factors can be examined with the concepts of numerical and functional responses. With regard to predator- prey interactions, a change in predator numbers in response to a change in prey numbers is a numerical response. An example of predator functional response is a change in per capita kill rate in response to a change in prey density. The shapes of numerical and functional response curves can be either linear (Type I), hyperbolic (Type II), or sigmoidal (Type III), (Holling 1959).

Predator-prey population models

Predator-prey models have been used to explore the functional and numerical

responses of wolves to changes in ungulate density. Understanding predator-prey

response is crucial to wolf management. Specifically, wolf control will be effective in

helping ungulate populations to increase over the long term only if wolf predation is an

important regulating factor of ungulate population size (Walters et al. 1981, Theberge and

Gauthier 1985).

Messier (1994,1995) presented several models of possible prey population

regulation mechanisms (Figure 1.1). He hypothesized that ungulate populations may be

regulated by either food (Food Model), predation (Predation Model), or a combination of

both factors (One- and Two- State Predation-Food Models). Where wolf predation is

absent or not density-dependent, moose are predicted to be regulated at high density by

food availability. In the One-State Predation-Food Model, predation is never sufficient to

regulate prey to low densities, whereas prey never escape predator regulation in the

Predation Model. In the Two-State Predation-Food Model, two stable equilibrium prey

densities are possible. At low population densities, herbivores are regulated by predators

(K_4), whereas resource exploitation regulates prey at high densities (K_3). Thus at high

densities, prey populations can escape a 'predator pit'. Both equilibrium densities are

associated with strong predation density-dependence (Sinclair 1989, Messier 1995). To

demonstrate a two-state equilibrium system, it must be shown that predation is density-

dependent, that predator removal results in an increase in prey populations, and that prey

populations do not return to their original low density when predator populations are restored to previous levels (Sinclair 1989). So far, there is no evidence for a two-stable state equilibrium for wolf-prey relations (Messier 1994, Hayes 1995)

Wolf-ungulate models and wolf management

Lethal wolf control can be an effective way to help increase ungulate survival. Theberge and Gauthier (1985) used qualitative models to describe 6 possible predator-prey relationships, and showed that wolf control should only be carried out when ungulate population density is well below the nutrient-climate ceiling (carrying capacity), mortality is the major factor limiting the ungulate population, and wolf predation is a major cause of ungulate mortality. Quantitative wolf-prey models by Walters et al. (1981) showed that with multiple prey, there can be two stable equilibria, one with high moose densities, and the other with low wolf densities and no moose. They do not, however, advocate wolf control unless there are few wolves and the cost in terms of public opinion is low.

Figure 1.1 Four conceptual models of ungulate (in this example moose) population regulation. The density relationship of wolf predation (solid line) and the growth rate of the prey without predation (broken line) are illustrated (from Messier 1995). K_1 to K_4 are stable equilibria, and K_U is dynamically unstable. The shaded areas represent the net population growth rate. Predators regulate the size of the prey population when the rate of predation mortality is greater than the rate of prey population recruitment. See text for a complete explanation.

FOOD MODEL

PREDATION-FOOD (1-STATE) MODEL

PREDATION-FOOD (2-STATE) MODEL

PREDATION MODEL

MOOSE DENSITY

% GROWTH WITHOUT PREDATION ········; % PREDATION ———
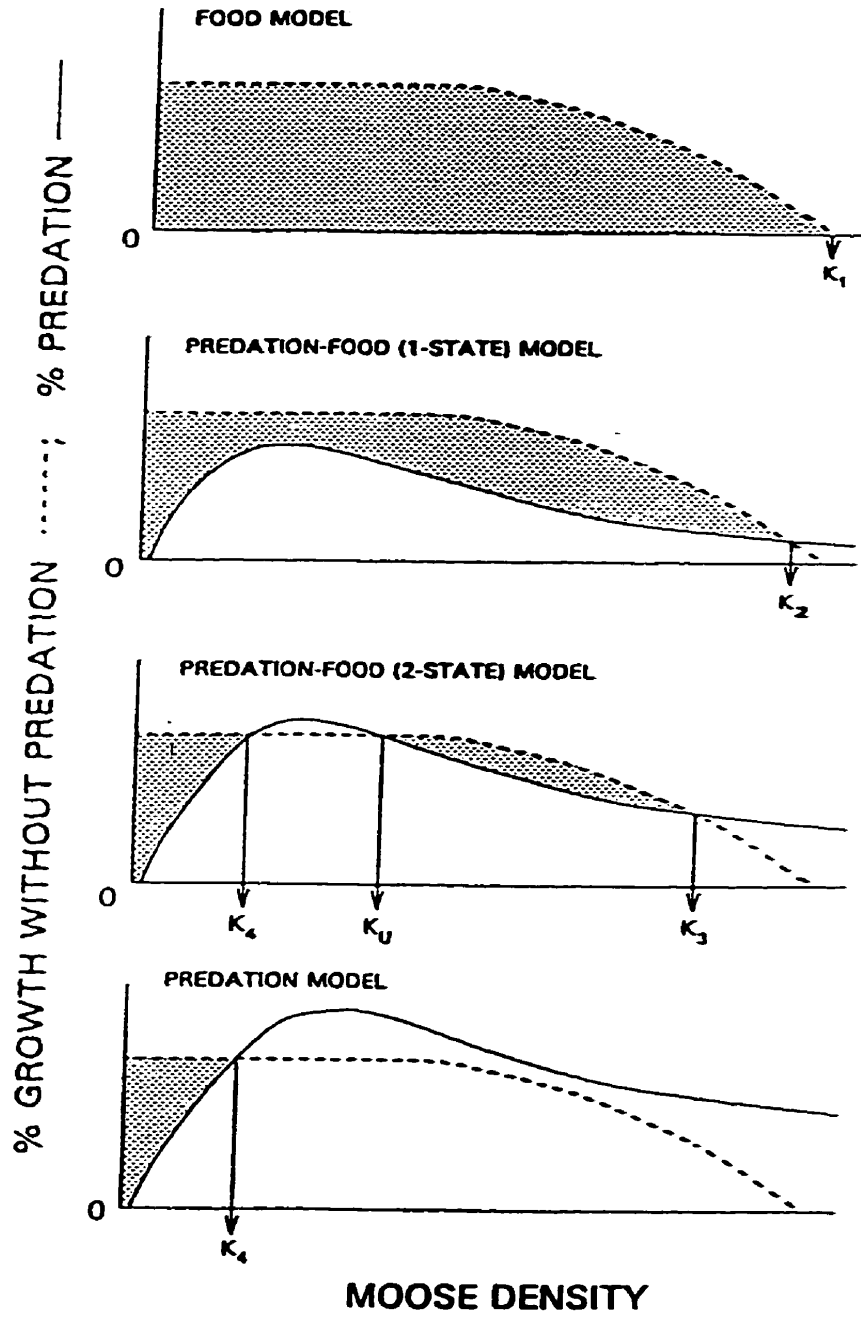
Empirical evidence of predator limitation and regulation of ungulates

A substantial body of literature suggests that ungulate populations can be limited by predation. The effects of wolf predation, bear predation, or a combination of the two can limit moose calf survival and population growth (Bergerud et al. 1983, Messier and Crête 1985, Van Ballenberghe 1987, Bergerud and Ballard 1988, Gasaway et al. 1992, Van Ballenberghe and Ballard 1994, Hayes 1995, Boertje et al. 1996, Crête and Manseau 1996, Eberhardt 1997). There is also evidence that predation limits caribou population growth (Bergerud and Elliot 1986, Seip 1992, Dale et al. 1994), and deer populations (Potvin et al. 1992, Hatter and Janz 1994). The case for predator regulation is not as strong, and there has been controversy over the role of predators in large declines of several ungulate populations (Thompson and Peterson 1988, Boutin 1992, Eberhardt and Pitcher 1992). Declines of caribou, moose, and deer populations may be a result of a combination of several factors including overharvest by humans, deep snow and adverse weather conditions, deterioration in range condition, as well as predation by wolves, and by brown and black bears (Bergerud et al. 1983, Ballard et al. 1987, Ballard and Larsen 1987, Eberhardt and Pitcher 1992, Van Ballenberghe and Ballard 1994).

Despite the strong case for predator limitation of ungulate population growth, there is little evidence that wolves regulate their prey in a manner that is consistent with any of Holling's (1959) functional response models. Messier (1994, 1995) found a density-dependent relationship between wolf per capita kill rate and moose densities ranging from 0.0 to 2.5 moose/km^2, and Dale et al. (1994) fit wolf predation on caribou to a Type II curve. However, a study by Hayes (1995) showed that wolf predation rates

between moose densities from 0.25 to 0.42 moose/km^2 were independent of moose

density, and that this data, when added to Messier's (1994,1995) results, fails to conform

to a density-dependent functional response curve across densities of 0.25 to 2.5

moose/km^2. Mech (in prep.) observed that the density dependence shown by Dale et al.

(1994) occurs at caribou densities ranging from 0.0 to 0.5 caribou/km^2, and that the

relationship is probably due to a numerical response by wolves, and not a functional

response. This argument is supported by evidence that kill rates cannot be predicted by

prey:wolf ratios (Peterson and Page 1987), but are correlated with pack size (Peterson and

Page 1987, Thurber and Peterson 1993, Dale et al. 1995, Hayes 1995).

Indeed, Mech (in prep.) argues that there is no biological or behavioural basis for

wolves to increase per capita kill rate with increasing prey density. He maintains that the

critical determinant of wolf kill rates is prey vulnerability, which in turn, may be

determined by density-dependent factors such as disease and the proportion of old

animals in ungulate populations. Any evidence of density-dependence may be explained

by wolf numerical responses to changes in prey density, through pup production, pup

survival, and dispersal (Hayes 1995, Mech in prep.).

Though the debate about evidence for wolf regulation of their ungulate prey is

unresolved, several wolf reduction programs have led to increases in ungulate calf

survival and ungulate population growth (Ballard et al. 1987, Bergerud and Ballard 1988,

Hatter and Janz 1994, Hayes 1995, Boertje et al. 1996, YTG unpubl. data). The

continued demand for management measures to increase game populations, combined

with public concern over lethal control methods, has led to an investigation of wolf fertility control.

Models have been used to represent wolf habitat, population dynamics and territoriality, and the effects of wolves upon ungulate populations (Crête et al. 1981, Hastings 1983, Ballard and Larsen 1987, Lewis and Murray 1993, Hatter and Janz 1994, Boyce 1995, Vales and Peek 1995, White et al. 1996, Mladenoff and Sickley 1998). Models have been particularly useful for examining the implications of wolf management strategies. Biologists have modelled the potential impacts of wolf reintroduction into the Greater Yellowstone Ecosystem (Boyce 1995) and the Northwest Montana Wolf Recovery Area (Vales and Peek 1995). Both models incorporate various management strategies by varying ungulate harvest rates, and Boyce (1995) factors wolf-human conflicts and wolf culls into wolf mortality. Ballard and Larsen (1987) used a simulation model to determine the role of wolf predation and the effects of wolf control in the decline and recovery of a south central Alaskan moose population. Similarly, Eberhardt and Pitcher (1992) used a model to conclude that decreased recruitment and range quality deterioration contributed to the effects of human harvest and wolf predation on the Nelchina caribou herd in Alaska.

Fertility control models

Although recent models have attempted to incorporate wolf management by lethal control, none have examined the potential effects of wolf fertility control. Some models have explored the population effects of sterilizing mammals (Garrott 1991, Garrott and

Siniff 1992, Garrott et al. 1992, Hone 1992, Caughley et al. 1992, Seagle and Close 1996, Barlow 1994, 1997; Barlow et al. 1997; Sinclair 1997). In general, the social biology and evolutionary strategies of the target species will determine the effectiveness of any fertility control regime (Caughley et al. 1992, Sinclair 1997). Barlow et al. (1997) modelled the effects of fertility control on animals with various mating systems, and determined that the greatest effect was observed when both sexes of a monogamous species were targeted.

For red foxes (social canids), Pech et al. (1997) used models to demonstrate that environmental variability influences the effectiveness of fertility control, and high levels of fertility control using permanent sterility were required. Similarly, Bubela et al. (unpubl. data) determined that 90% sterilization of both sexes was required to reduce red fox populations, and that immigration would nullify its effects.

A model to evaluate fertility control of wolves

There are empirical studies of the effects of fertility control upon individuals of target species, and theoretical models which simulate the population level effects of sterilization, but there is a paucity of studies which combine empirical fertility control results with modelling. Now that fertility control has been applied to wild wolves (Mech et al. 1996a, this study), behavioural and demographic data can be incorporated into a model which simulates the effects of fertility control upon a wolf population, as well as upon their ungulate prey populations. I used field data from local Yukon animal populations to parameterize wolf and prey submodels to validate the projections of the

system model. This can be instrumental to management agencies when considering various wolf and ungulate management strategies.

Potential for the use of fertility control to manage wolves in the southwest Yukon

This study has two components, which are equally important in assessing the potential role of fertility control in managing wolf and prey populations. In Chapter Two, I report the effects of surgical sterilization upon wolf social and territorial behaviour. This is crucial, because fertility control will not be effective for managing wolf populations if wolf social behaviour is fundamentally altered by sterilization. In Chapter Three, I incorporate the results from the behavioural study, as well as long term weather and moose, caribou, wolf and sheep population data into a simulation model, in order to predict long term ungulate populations' responses to fertility control of wolf populations. Finally, in Chapter Four, I present general conclusions about the potential of fertility control as a management tool and discuss opportunities for future research.

CHAPTER TWO : THE EFFECT OF SURGICAL STERILIZATION UPON THE SOCIAL AND TERRITORIAL BEHAVIOURS OF MALE AND FEMALE WOLVES

INTRODUCTION

Grey wolves (Canis lupus) were once the most widely distributed land mammals in the world (Carbyn 1983, Harris and Saunders 1993). Wolves ranged throughout the northern hemisphere wherever large ungulates were found: throughout North America, Europe, and Asia, from 20°N to the North Pole (Boitani 1995, Mech 1995). With the advance of human settlement and agriculture, including the domestication of animals for livestock, conflicts between wolves and humans led to a negative public opinion of wolves, and a systematic effort to eliminate them from much of their former range (Boitani 1995, Hayes and Gunson 1995, Mech 1995, Mech et al. 1996a). Until the latter part of this century, wolves survived only in wilderness areas, largely because they were not exterminated from sparsely populated areas (Mech 1995).

Since the mid 1970's, grey wolves have been recolonizing many areas from which they had been extirpated (Mech 1995). The current recovery of wolf populations is due in large part to a change in public opinion which Mech (1995) calls the "environmental revolution". In the United States, wolf recovery has been aided by their protection under the U.S. Endangered Species Act in 1966, favourable publicity, and increased scientific and public awareness about wolves (Mech 1995). Large wolf populations are now found

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in several eastern European countries, and wolves are now living in Italy, the Iberian

Peninsula, Norway, Sweden, and Greece. The rapid recovery of wolf populations and

their expansion into non-wilderness areas has led to an increase in the number of conflicts

with human activities such as livestock raising and hunting.

Wolf Control in Aishihik, Yukon

Between 1981 and 1991 in the Aishihik region of the Southwest Yukon, moose

and caribou populations declined substantially. These declines may have been

precipitated by human over-harvesting. The Aishihik caribou herd declined by 36-47%

to about 700 animals, while moose densities in the area were among the lowest of those

reported for the Yukon (Ward and Larsen 1995). The caribou bull/cow ratio reached a

low of 28 males/100 females in 1990 (Hayes 1992). Caribou calf survival was low at 7

calves/100 females in 1992. Moose recruitment was also low, as calves comprised only

8% of the population. A moratorium was placed on hunting, and local residents, hunters,

and First Nations called for wolf control to aid in the recovery of these declining

populations.

In 1992, the Yukon Renewable Resources Department of Fish and Wildlife

(YTG) designed an experiment to test the hypothesis that wolf predation is the most

probable cause of recent population declines of caribou herds in the Kluane and Aishihik

regions (Hayes, 1992). They predicted that wolf predation was limiting the caribou herd,

and that reducing the Aishihik wolf population would lead to significantly greater caribou

adult and calf survival in the Aishihik herd than that of herds in non-treated, experimental

control areas. The alternate hypothesis was that the removal of wolves would not cause ungulate population size and calf survival to increase. Rather, the ungulate populations were limited by density-independent or stochastic factors such as weather and forage, or by predation by animals other than wolves.

Late winter wolf numbers were reduced by aerial shooting and ground snaring to 30% of pre-control density in the Aishihik caribou herd range from 1993 to 1997. An evaluation after two years of wolf reduction showed that the observed results were consistent with the predictions of the wolf predation hypothesis (YTG, 1994). Moose and caribou surveys to 1997 showed continued increase in population numbers and calf survival indices. The Aishihik herd was estimated at 1150 animals in March, 1997, with calf survival at 45 calves/100 females. Moose calves comprised 24% of the Aishihik moose population in March, 1997, compared with average of 13% in control populations (YTG unpubl. data).

Problems with lethal wolf control

Lethal wolf control may lead to immediate and large increases in ungulate calf survival and high rates of ungulate population increase in the short term (Hayes 1995; Boertje et al. 1996, YTG unpubl. data). It is not, however, a panacea for ungulate management due to several important disadvantages. For example, some methods such as trapping and poisoning are not specific to wolves, posing a potential threat to other mammals. These methods are also generally considered to be inhumane (Bomford 1990, Cluff and Murray 1995). By contrast, aerial shooting programs, while perhaps more

humane and effective, are expensive. Regardless of the methods used, culling provides

only temporary decreases in wolf numbers. Once a wolf pack is removed from a

territory, it is quickly replaced by another pair, which usually reproduces within a year.

In the Yukon, reduced wolf populations naturally recover to pre-control densities within 3

to 5 years (Hayes et al. 1991, Hayes 1995). Initially, low wolf densities enhance the

survival, reproduction and hunting success of the re-colonizing wolves, as well as

increase the success of immigrating animals and suppress dispersal. Finally, lethal wolf

control is considered by some to be ethically, politically, and ecologically unacceptable

(Cluff and Murray 1995, Haber 1996, Mech et al. 1996a).

Wolves and fertility control

The many problems associated with lethal control of wild populations have led to

an exploration of fertility control, defined as the artificial reduction in a population's birth

rate by temporarily or permanently sterilizing individuals (Bomford 1990).

Recent studies have reported the successful contraception of free-ranging mammals

including red foxes (Vulpes vulpes: Bubela 1995), feral equids (Equus caballus:

Kirkpatrick et al. 1992, in press), white-tailed deer (Odocoileus virginianus: Turner et al.

1996, in press), black-tailed deer (O. hemionus columbianus: Jacobsen et al. 1995), grey

seals (Halichoerus grypus: Brown et al. 1996), male wolves (Mech et al. 1996a), and

Etosha lions (Pantera leo: Orford et al. 1988).

If wolves can be sterilized without altering fundamental social and territorial wolf

behaviour, their social biology may make wolves well suited to population suppression

by fertility control.

Wolves are social animals that live in packs, comprising the mating pair and their offspring, which live together in a well established social hierarchy. Packs maintain and defend territories from other wolves (Mech 1970). It is this territorial behaviour that makes wolves well suited to fertility control. If sterilized pairs of wolves remain in territories and defend them from potential immigrants, reduced wolf densities could be maintained for the lifetime of the treated animals. For management purposes, pairs to be treated with fertility control can be chosen strategically to defend territories around important ungulate habitat, such as caribou calving grounds. Thus, fertility control could be applied to a small portion of the wolf population depending on the objectives for ungulate population responses. For lethal wolf control, overall wolf densities commonly need to be reduced by up to 80% in order to rapidly increase prey populations (Hayes et al. 1991, Hayes 1995, Boertje 1996). Fertility control can be more cost effective than lethal control over the long term, because territories with sterilized wolves do not have to be handled every year.

Wolf behaviour in summer may be most affected by fertility control. Wolf packs often separate in the summer into various smaller groups and territorial behaviour declines during denning. Thus, wolves increase their ability to access vulnerable calves, increasing the predation rate (Doyle et al. unpubl. data). With no pups to raise, infertile wolf pairs are not restricted in their movements to the area around a den-site and so may continue to hunt large prey as a pair throughout their territory. Raising a litter can represent a four-fold increase in food demand for a pair (Mech et al. 1996a). Sterile pairs,

therefore, should have a lesser demand for food and an associated reduced predation rate upon large ungulates, especially neonatal calves. Accordingly, we chose to sterilize pairs which hold territories on or near sensitive caribou calving grounds. For all of these reasons, it is crucial to the success of the fertility control program that wolf social and sexual behaviour is not altered by the sterilization treatment.

Aishihik Fertility Control Study

In this study, we tested whether surgical sterilization of both sexes of wolves alters wolf social and territorial behaviours. We hypothesized that sterilizaton would not cause observable changes in basic wolf behaviour other than reproductive success. We tested for qualitative differences in wolf behaviour, for which "all or none responses" were expected. Specifically, we predicted that sterilized wolves would:

1. maintain established pair bonds,

2. if not already mated, form a new bond,

3. as a pack or pair, maintain and defend average-sized territories, and

4. prepare dens in the spring.

STUDY AREA

The study area includes a 20,000 km^2 wolf reduction area (Aishihik Experimental Area), called the "experimental treatment area" and portions of Kluane National Park and the Kluane Wildlife Sanctuary (22,000 km^2), called the "experimental control area" (Figure 2.1). The experimental control area is located in the north-eastern portion of the

St. Elias mountain range, characterized by metamorphic and volcanic peaks and icefields. Many peaks exceed 1,500 m and numerous others exceed 2,500 m. About 4400 km^2 of the protected area are vegetated. The experimental treatment area encompasses part of the rugged Ruby Range mountains, which are composed of volcanic rocks. These are mostly lava and basalt, with intrusions of gradodiorite and quartz dionite (Oswald and Senyk 1977).

Major rivers include the Nisling, the Duke, the Donjek, the Aishihik, and the Alsek. Southern drainages flow to Alsek, which drains into the Pacific Ocean. Northern drainages flow into the Yukon River system. Major lakes in the study area are Kluane Lake, Aishihik Lake, and Sekulmun Lake. The study area is characterized by poor drainage in valley bottoms, and is part of the discontinuous, scattered permafrost zone. The high peaks in the control zone exhibit continuous permafrost.

Treeline occurs at about 1,200 m. The vegetation in well-drained soils is dominated by white spruce (Picea glauca); black spruce (Picea mariana) is commonly found in most lowland areas. Lowland areas also support aspen (Populus tremuloides) and balsam poplar (Populus balsamifera). Lodgepole pine (Pinus contorta) is only found along the eastern edge of the experimental area. Willow (Salix sp.), dwarf birch (Betula glandulosa), alder (Alnus crispa), soapberry (Sheperdia canadensis) and ericaceous species comprise the understory shrubs.

Most of the area lies in the rain shadow of the St. Elias Mountains. Low elevations receive 190-285 mm of precipitation annually. Average annual temperature is -4°C. In January, the average temperature in Haines Junction is -20°C, and in Burwash

Landing it is -31°C (Environ. Can. unpubl. data).

Major prey species in the study area are woodland caribou (<u>Rangifer tarandus tarandus</u>), moose (<u>Alces alces</u>), and Dall sheep (<u>Ovis dalli</u>). A small herd of elk (<u>Cervus elaphus</u>) were introduced to the area, and a small number of mule deer are also present (<u>Odocoileus hemionus</u>). Some horses (<u>Equus equus</u>) and fewer than 50 mountain goats (<u>Oreamnos americanus</u>) also inhabit the region (YTG unpubl. data).

Historic hunting pressure from several sources was high on caribou, moose, and Dall sheep. The study area encompasses part of three First Nations traditional hunting areas, and four rural communities: Haines Junction, Canyon, Burwash Landing, and Destruction Bay. Several big-game outfitters also bring trophy hunters to the region.

Figure 2.1. Map of the study area in the southwest Yukon. Wolf packs treated as part of

the fertility control experiments were located within the area identified as Aishihik

Experimental Area. This was also the area of the 1992-1997 wolf mortality control

experiment, and the area where caribou, moose and sheep populations have been

censused. Untreated (experimental control) wolf packs were located to the south and

west of the Aishihik Experimental Area, in and around Kluane National Park.

Aishihik Experimental Area

Study Area

Alaska

Yukon

N.W.T.

Kluahe National Park

Kluane Wildlife Sanctuary

Beaver Creek

Wellesley Lake

Burwash Landing

Destruction Bay

Kluane Lake

Kluane Widlife Sanctuary

Haines Junction

Kathleen L.

Dezadeash Lake

Kloo Lake

Alaska Highway

Haines Highway

Nordenskiold Wetland Habitat Protection Area

Carmacks

Sekulmun Lake

Robert

Drury Lake

Little Salmon L.

Campbell Highway

South Klondike Highway

WHITEHORSE

Marsh Lake

1 cm = 14.5 km

MATERIALS AND METHODS

This study began in February 1996, and continued until May 1998. We tracked, radio-collared and sterilized wolves during annual late winter censuses from January until March. Tracking and capturing wolves involved at least one technician or biologist to dart the animals, and fixed-wing and helicopter pilots, all of whom have years of experience. The surgical sterilizations were performed by qualified veterinarians.

Wolf tracking and census

Wolves were located from the air by snow tracking methods (Hayes 1995). Two fixed-wing aircraft (PA-18 Supercub and Maule M7) searched simultaneously, using methods described by Hayes (1995) and Ballard et al. (1982). We flew along riparian areas and water courses and carefully searched open forests, lake shores and meadows, where we were most likely to find wolf tracks. We followed wolf tracks until wolves were found or until the number of wolves could be estimated from separate trails.

Wolf capture and handling

Once we located a pack in the study area, we used a Bell 206B helicopter to capture wolves to be collared and treated. We darted wolves from a low flying helicopter using 2 cc Capchur darts (Palmer Chemical and Equip. Co., Douglasville, Georgia). Wolves received an average dose of 12.5 ± 5.9 SD mg/kg of equal weights tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Laboratories Inc., Fort Dodge, Iowa) during the capture procedure. Once wolves were immobilized, we fitted

them with Telonics MOD 500 radio collars (Telonics, Meza, Az.), which are equipped

with mortality sensors and weighed 900 g.

We estimated the age of captured wolves by examining tooth coloration and wear,

and the length and eruption patterns of canines (Van Ballenberghe et al. 1975). Blood

samples were taken for later analysis of genetic relatedness and incidence of disease.

Sterilization

Wolves ranging in the wolf reduction area (experimental treatment area) were

surgically sterilized and fitted with radio collars. None of the wolves captured in the

experimental control area were sterilized, but they were collared and monitored

concurrently to obtain experimental control information for the fertility control study.

Vasectomies and tubal ligations were performed, so that hormone production and cycling

were not affected. Detailed sterilization procedures are described in Spence et al. (199N).

Both sexes were sterilized to prevent fertilization from occurring if an alpha wolf were to

die and be succeeded prior to breeding season. Where possible, wolf pairs were selected

for treatment. One pack of 7 was reduced by shooting to a pack of 3, and 2 lone wolves

were sterilized.

In 1994, we vasectomized a male wolf in a heated tent in the field. One

vasectomy and a tubal ligation in 1996, and all of the surgeries in 1997 were performed

inside a heated building. The two other tubal ligation procedures in 1996 were performed

in a heated tent at the capture sites. Three wolves were brought to a veterinary clinic for

the procedures in 1998. Wolves were transported from the field by helicopter and held in

a "squeeze box" (1.8 m x 0.6 m x 2.0 m) until surgeries were performed, approximately

4 to 5 hours following initial capture. All wolves were awake and alert when they were

prepped for surgery. Following surgery, wolves were isolated in "capture boxes" (0.6 m

x 0.6 m x 2.0 m) and held overnight without food before being released at the original

capture site. Wolves were alert and mobile upon release.

Monitoring by aerial radio telemetry

    We observed the survival, movements and behaviour of radio-collared wolves

from when they were first captured until the conclusion of the study in May 1998. In

total, we followed wolves for 474 wolf-months, averaging 14.8 months per wolf (range:

3-27 months). All radio-collared wolves were relocated and, when possible, observed

from fixed-wing aircraft as described by Mech (1974). We obtained location and

behaviour data approximately every 2-3 weeks throughout the winter and spring, and

once a month during the summer and fall months. In particular, we observed the social

organization and associations of both sterilized and intact radio-collared wolves.

Den-site observations

    Yukon wolves typically dig dens and remain there for the birth of pups in early

May (Rausch 1967). For about the first 8 weeks after parturition, the mother will remain

at the den-site with her pups. The male will hunt and return to the den regularly to

provide food (Mech 1970). If a pack is denning, collared alpha wolves (breeding pair)

will be found at the den site, at least in early May. To determine whether a wolf pack was denning, we monitored collared wolves intensively during the denning period each year. Reproductive behaviour was assessed from 5 to 10 May 1996, 28 April to 1 May 1997, and 11 to 14 May 1998. We obtained aerial relocations of each wolf pack at least once a day, at different times during the day, until a den was located or we could be certain that the alpha female was not attending a den. We assumed that no litter was produced if the alpha female was travelling long distances and not returning to the same location each day, as pups would not survive without her continual attendance and care.

Once wolf packs had abandoned their initial den-sites, we visited some of the dens. We looked for evidence that the den had been re-excavated and visited, and for signs that pups had been raised. In particular, recent digging, fresh prey remains and pup scats were judged to be evidence that a pack had produced a litter.

Home range estimation

It was not possible to obtain enough relocations to adequately describe wolf home ranges, since typically 30 to 60 locations are required to reach an asymptote for an observation area-curve (Messier 1985, Fuller and Snow 1988, Ballard et al. 1987). However, pooled data over the years of the study were sufficient to obtain approximate home range estimates using the 95% Minimum Convex Polygon Method. We used the Calhome home range estimation program (Kie et al. 1994) to generate home range estimates.

Wolf survival estimates

Annual survival probabilities were estimated using the Kaplan-Meier procedure, modified for staggered entry of radio-collared individuals (Pollock et al. 1989). The method assumes that newly tagged animals have the same survival probability as previously tagged animals. We assumed that censored wolves had dispersed or that their collars had stopped functioning, which provides an upper bound for annual survival. Because of the social nature of wolves, our data violates the assumption that the survival rates of indivuduals are independent. This will cause variances to appear smaller than they actually are (Pollock et al. 1989).

RESULTS

Effect of sterilization

Females were estimated to weigh 37 to 45 kg and males 36 to 50 kg. Captured wolves ranged in age from just under one year to older than 6 years. Nine tubal ligations and 8 vasectomies were performed during late winter from February 1994 to February 1998. Tables 2.1 and 2.3 provide a summary of the treatment history and behaviour of sterilized wolf packs.

The female from the Dogpack Lake pair, treated in 1996, apparently did not recover from the initial capture and surgery. Ten days after the procedure, she was found dead less than 2 km from the site where she had been left to recover. When the carcass was retrieved, it was too heavily scavenged for necropsy. The wolf appeared healthy

throughout the surgery and her body temperature was normal and stable when she was left to recover. The cause of death remains unknown. All other treated wolves rejoined their mates and resumed travelling and hunting within days of being released.

A second female wolf, treated in early 1997, died approximately 3 months following surgery. Upon necropsy, the Talbot Creek female had a severe infection of one of the ligated uterine segments. The pathology report indicated that the infection was not related to the surgery. Her mate has since formed a new pair bond. This new alpha female was sterilized in January, 1998.

None of the sterilized pairs have produced litters, except for the pair from Lister Creek. The female apparently produced one male pup, which was first observed in July, 1996. The alpha male had not been sterilized the previous winter. Subsequently, the male was shot by a hunter. The male pup remained with its mother, and was vasectomized in December, 1996. The mother and her pup were joined by a new alpha male and one other wolf by January 1998. The vasectomized pup subsequently dispersed. The new alpha male was sterilized in January, 1998.

All sterilized wolf pairs have maintained their pair bonds, and remained in their original territories. The two lone, treated wolves eventually met and formed a pair bond in May 1997, about 3 months following treatment. The female was subsequently shot by hunters in September 1997. The remaining male was joined by an adult female and two sub-adult males. The female was treated in February, 1998.

The Hopkins female died (natural mortality) in April, 1998. The male formed a new pair bond prior to mid-May.

The Kloo Lake female spent time at a den in late April and early May of 1996 and 1997. At the den-site, there was evidence of fresh digging, but there were no fresh prey remains. The Lister Creek female also visited an old den-site in 1997 and 1998, although no pups were produced.

Pup production in experimental control packs

Pup production by experimental control packs varied by year. In 1996, at least 50-60% of control wolf packs attended dens in May and successfully reared pups. In 1997, all 7 control packs had active dens in May, and all but one of those packs were seen with pups in late winter. Only 2 of 8 control wolves may have had active dens in May, 1998. These results are summarized in Table 2.2

Home range estimates

The mean size of territory used by sterilized wolf packs was 1007 +/- 188 (SE) km^2 (n=6). The mean pack territory size for experimental control packs was 1545 +/- 525 (SE) km^2 (n=4), which is not significantly different than that of treated wolf packs (t-test for independent samples p=0.29). The sterilized wolf pack territory size also did not differ significantly from a sample of wolf pack territory estimates from Kluane National Park from 1994-1997 (Barichello and Spence in prep., p=0.56). The territory size estimates are shown in Table 2.3.

Wolf mortality

The mean annual survival rate of sterilized wolves from 1994 to 1998 was 0.95 (n=16).

For radio-collared wolves in the experimental control area, mean annual survival was

0.82 (n=33). Survival estimates are summarized in Tables 2.5 and 2.6.

Table 2.1 Summary of the history of sterilized wolf packs in the Aishihik experimental

treatment area. Capture, treatment, behaviour, and survival information data are

summarized by year. Handling occurred in late winter, and reproductive success is

reported from observations in May. The number of wolves present in each pack ( ) is

reported for late winter.

Wolf Pack	1994	1995	Year 1996	1997	1998
Kloo Lake	(2) Feb.-Male vasectomy in field	(2) May - no reproduction	(2) Feb. - Female tubal ligation May- no reproduction, dug den	(3) May - no reproduction	(2) May - no reproduction
Lister Creek			(2) Feb. - Female tubal ligation May - 1 male pup produced Aug. - alpha male shot by hunter Dec. - pup vasectomy	(2) May - no reproduction, attended den	(4) Winter - joined by 2 males May - no reproduction, attended den
Dogpack Lake			(2) Feb. - Female tubal ligation, died at capture site (drug problem?) July - Male mortality (natural)		
Onion Creek				(3)- Feb. - Female tubal ligation, 2 vasectomies May - no reproduction	(2) Winter - young male dispersed May - no reproduction
Hopkins Lake				(2) Feb. -1 tubal ligation, 1 vasectomy May - no reproduction	(2) Apr.- Female died (natural mortality) May -new alpha female, no reproduction
Talbot Creek				(2) Feb. -1 tubal ligation, 1 vasectomy May - no reproduction June - female died of spontaneous infection	(2) Feb. - 1 tubal ligation (new female) May - no reproduction
Coon Creek lone female			(1) Collared in Kluane National Park	(1) Feb. - recollared in study area, tubal ligation Mar. - disperses, joins MacIntosh male May - no reproduction Sept. - shot by hunter	
MacIntosh lone male				(1) Feb.- vasectomy Mar. - joined by Coon Creek female May - no reproduction	(4) Feb. - 1 tubal ligation (new female) May - no reproduction

Table 2.2 Summary of radio-collared, untreated wolf packs from the experimental

control area. Survival and reproductive data are summarized by wolf pack and by year.

Reproductive behaviour was assessed in May, and reproductive success was confirmed

by pup production estimates in October.

Wolf Pack	Year				
	1994	1995	1996	1997	1998
Maple Creek			May-pups	May -5 pups	Winter- 7 wolves trapped May- no reproduction
Cottonwood Creek		May-pups	May- unknown reproduction	May-pups	May- possible reproduction?
Donjek River			May - no reproduction	May-pups	May- possible reproduction?
Alsek River			Winter- alpha male dies in avalanche	May-3 pups	May- no reproduction
Dusty River			Winter- alpha male dies in avalanche	Winter- new male joins female	Winter- female killed by moose
			May- no reproduction	May - active den Summer -pups die	May - no reproduction
Tatshenshini			May-pups		
Dalton Post	May-pups			May-pups	
Steele Creek				May-pups	
Gladstone Creek					May - no reproduction
Tincup Lake					May - no reproduction
Reproductive Success (proportion of packs)	1/1	1/1	1/2 or 3/5	6/7	1/4

Table 2.3 Summary of behavioural observations from sterilized wolves from 1994 to 1998. "Y" = behaviour was observed. "N/A" = not applicable. For example, the Coon Creek wolf initially travelled alone, and did not defend a territory until she joined the MacIntosh Creek male. New pair bonds were formed upon the death of an alpha wolf. The Kloo Lake and Lister Creek females attended dens. No other females were observed at dens, but they may have attended dens during the denning period and were not observed ("?").

Wolf pack	Months observed	Defend territory	Maintain Pair bond	Form new pair bond	Dig den
Kloo Lake	27	Y	Y	N/A	Y
Lister Creek	27	Y	Y	Y	Y
Onion Creek	15	Y	Y	N/A	?
Hopkins Lake	15	Y	Y	Y	?
Talbot Creek	15	Y	Y	Y	?
Coon Creek	18	N/A	Y	Y	?
MacIntosh Creek	15	Y	Y	Y	?

Table 2.4 A comparison of 95% Minimum Convex Polygon wolf territory estimates

between the sterilized wolf packs in the Aishihik experimental treatment area and the

untreated wolf packs in the experimental control area. The number of relocations used to

generate each estimate (n) is indicated. No significant difference was detected between

the sterilized and untreated wolf pack territories (independent sample t-test, p=0.29).

Sterilized Pairs	n	km 2	Control Packs	n	km 2
Kloo Lake	40	514	Cottonwood Lakes	27	519
Lister Creek	45	850	Donjek River	45	2770
Hopkins Lake	19	817	Kaskawulsh River	30	1842
Onion Creek	13	1116	Maple Creek	37	974
Talbot Creek	11	1010			
MacIntosh Lake	10	947			
Mean (+/-) 1 SE		1007 +/- 188			1545 +/- 525

Table 2.5 Kaplan-Meier annual survival estimates (Pollock et al. 1989) for radio-collared control animals in Kluane National Park from 1993-1998. Annual period began on 1 January.

Year	Number of wolves at risk	Number of deaths	Survival	Number of wolves censored	Number of wolves added	Variance	Lower 95% confidence bound	Upper 95% confidence bound
1993-1994	7	1	0.86	0	0	0.01	0.62	1.10
1994-1995	6	2	0.67	0	0	0.02	0.36	0.97
1995-1996	10	1	0.90	2	6	0.01	0.72	1.08
1996-1997	18	3	0.83	3	11	0.01	0.68	0.99
1997-1998	14	2	0.86	1	2	0.01	0.69	1.03
1998-	12	2	0.83	0	1	0.01	0.64	1.03
MEAN			0.82			0.01	0.62	1.02

Table 2.6 Kaplan-Meier annual survival estimates (Pollock et al. 1989) for sterilized

wolves in the Aishihik experimental treatment area from 1994-1998. Annual period

began on 1 January. The mean annual survival of sterilized wolves was significantly

higher than that of control wolves (Kaplan-Meier log-rank, χ^2, P<0.001, df=1)

Year	Number of wolves at risk	Number of deaths	Survival	Number of wolves censored	Number of wolves added	Variance	Lower 95% confidence bound	Upper 95% confidence bound
1994-1995	1	0	1.00	0	0	0.00	1.00	1.00
1995-1996	1	0	1.00	0	0	0.00	1.00	1.00
1996-1997	5	0	1.00	0	4	0.00	1.00	1.00
1997-1998	13	2	0.85	0	8	0.01	0.67	1.03
1998-	14	1	0.93	1	3	0.00	0.80	1.06
MEAN			0.95			0.00	0.89	1.02

DISCUSSION

We did not find any evidence to suggest that the basic behaviour of surgically sterilized wolves was different from that of non-sterilized wolves. We should have been able to detect changes in behaviour because the effects would have been easy to observe. First, if sterilized wolves did not maintain pair bonds, the alpha male and female wolves would have separated, or else one of the pair would have been killed or forced to disperse when the other found a new mate. Second, if hormone cycling had been disrupted by the sterilization, it is unlikely that wolves whose mates died would have been attractive to other wolves and been able to form new pair bonds. Third, if the sterilized packs were not able to defend their territories, they would be killed or forced to disperse, and new wolf packs would establish in those territories. Lastly, none of the sterilized females would display denning behaviour if their hormonal cycling had been altered.

Home range estimates

We pooled location data over 2 years to compare territory use between the experimental treatment and control packs, and for comparison with other Yukon wolf studies (Hayes et al. 1991, Hayes 1995) and estimates of wolf territory size from Kluane National Park (Barichello and Spence in prep.).

We did not expect there to be a treatment effect of sterilization on the size of area used by wolf packs. Several studies showed that territory size is not related to pack size (Ballard et al. 1987, Hayes 1995), and the sterilization procedure should not interfere with territorial defense. Any difference between territory use by the treatment and control

groups may be attributed to the lower prey base and significant geographical barriers such as high mountain peaks in the experimental control area.

Among North American wolf populations, wolf territory sizes vary greatly. Potvin (1987) reported average territory sizes of 199 km^2, ranging from 85 to 325 km^2 in the Papineau-Labelle reserve, Quebec. Mech (1994) reported values ranging from 26-420 km^2 for wolves in north-eastern Minnesota. By contrast, Ballard et al. (1987) reported Alaskan wolf home ranges which were as large as 3,077 km^2, averaging over 1,000 km^2. Reported home range areas for Yukon wolf packs ranged from 630-1753 km^2 (Hayes et al. 1991) and from 722 km^2 to 3,800 km^2 (Hayes 1995). The latter 3 studies involved recovering wolf populations following lethal control programs. Recolonizing populations were characterized by low pack density, small average pack size and few territorial overlaps during the first few years following wolf control (Ballard et al. 1987, Hayes et al. 1991, Hayes 1995). Large territory sizes in exploited and recovering wolf populations are expected due to limited interaction with other wolf packs and empty territories available for colonization (Hayes et al. 1991, Peterson et al. 1984). Similar to these wolf populations, the current recovering Aishihik wolf population is characterized by low wolf density (1.7 wolves/1000 km^2), low pack density (0.47 packs/ 1000 km^2), and small mean pack size (2.8 wolves/pack) (YTG unpubl. data). We expect that Aishihik wolf territory sizes will initially be large relative to those from other stable, high density wolf populations, or ones that are restricted by available habitat.

Wolf mortality

We found no evidence to suggest that surgical sterilization increases wolf

mortality. The estimated mean annual survival rate of sterilized wolves (0.95) is higher

than that of collared wolves in the experimental control area (0.82) , and higher than the

mean annual survival rate (0.82) of wolves in the recovering Finlayson wolf population

(Hayes 1995). The survival probabilities of sterilized wolves may be biased high due to

the very small sample size, which also causes the confidence limits to be wide. However,

there were no censored animals in from the treatment group, which improved precision.

Pollock et al. (1989) recommended that at least 20 animals should be tagged at all times,

and that 40 to 50 animals are required for good precision. Clearly, our data does not meet

these requirements.

Surgical sterilization

The Lister Creek litter may be the result of an incomplete ligation, or the female may

have already ovulated and bred before her uterine ligation was performed on 15 February

1996. The litter of a single pup suggests that she did not reproduce normally. Rausch

(1967) estimated that Alaskan wolves breed between 15 February and 15 March, but

evidence suggests that parturition times may vary by as much as a five weeks, for wolves

in a given area in the same season (Fuller 1989, Ballard et al. 1991, pers. obs.), over the

span of years (Harrington et al. 1983), or among breeding seasons for the same female

(Boyd et al. 1993). Fuller (1989) cited various studies to demonstrate that breeding

season and parturition date vary with latitude. Given the variability of breeding times, we could not know when wolves were breeding and be sure that we did not sterilize females after they had bred.

Another line of evidence suggesting that surgical sterilization does not alter hormonal cycling is the denning behaviour of the Lister Creek and Kloo Lake females. Denning behaviour of non-gravid wolves has been reported for wolves in the Northwest Territories and in Yellowstone National Park (Mech et al. 1996b). These authors suggest that denning behaviour may be initiated by prolactin, an anterior pituitary hormone which can induce parental behaviour. Kreeger et al. (1991) reported that prolactin has a strong circannual rhythm in both intact and neutered wolves of both sexes, and peaks prior to the summer solstice, when wolves typically whelp (Mech et al. 1996b). Another possible explanation is that sterilized, non-gravid wolves dig dens because they continue to experience ovarian hormonal changes in the luteal phase of the reproductive cycle, called pseudopregnancy (Kreeger et al. 1991, Asa and Valdespino 1998). Reproductive hormones are almost certainly involved, but females may attend dens simply out of habit as well. Non-breeding pack wolves are often found at den-sites and may be involved in helping to rear young (Mech 1970, Harrington et al. 1983, Fuller 1989, Ballard et al. 1991, Asa 1995). Sterilized, nulliparous wolves may attend den-sites in April and May simply because they were at den-sites during that time while living in their natal packs. Similarly, sterilized wolves with a previous breeding history may attend den-sites in the spring out of habit from rearing their young in the past. But if reproductive hormones are at least partly responsible for den-site behaviour, the denning behaviour of the Lister

Creek and Kloo Lake females provides evidence that tubal ligations do not interfere with hormonal production and/or cycling.

Further evidence that wolf sexual and social behaviours were not altered by fertility control is the formation of new pair bonds by four sterilized alpha wolves whose mates died during the study. Two of these wolves, the Lister Creek female and the MacIntosh male, formed new pack associations and retained their original territories and their alpha dominance status.

Fundamentally, it is important to ask whether not raising pups is very unusual for wolves, and whether the resulting social effects will have long term negative effects on the population (Asa 1995, Haber 1996, Mech et al. 1996a). Mech et al. (1996) noted that some infertile wolf pairs do not stay together and disperse.

Results from this study and others suggest that pup production may be highly variable. Only 59 % of packs out of a sample from Kluane National Park and other untreated wolves in the study area successfully raised pups from 1994 to 1998 (Barichello and Spence in prep.). In the recovering wolf population in Finlayson, Yukon, Hayes (1995) reported that 16.1% of wolf packs did not reproduce during the study. Ten percent of packs bred after 2 years without a litter, and another 10% only produced a litter after 4 years. Harrington et al. (1983) suggested that heterogeneous prey densities may cause wide annual variation in wolf pup production, and Boertje and Stephenson (1992) reported that fewer adult females reproduce at low prey densities. Variable pup and adult survival rates due to weather, food availability and social factors may greatly influence annual litter raising success. Especially in fragmented wolf populations, high adult

mortality leads to numerical and social instability in packs (Haber 1996). In this study, 6

wolves from 5 different packs died and either failed to find a new mate or to reproduce in

time for the next breeding season. Therefore, it may not be very unusual for wolf pairs in

exploited wolf populations not to raise a litter.

The key to whether or not fertility control can be an effective wolf management

tool depends upon whether sterilized pairs remain in their territories and maintain pair

bonds. Results from several studies indicate that infertile pairs can hold their territories.

Mech et al. (1996) reported that 5 vasectomized wolves from 4 packs remained in their

territories for up to 7 years until they died or their transmitters failed, and that during that

time pack size did not increase. Also, Hayes (1995) reported two naturally infertile pairs

in the recovering Finlayson, Yukon wolf population. One pair stayed together and

maintained their territory for 3 years before successfully raising a litter. The other pair

did not reproduce, but remained together and defended their territory for 4 years until

they were killed by an adjacent pack.

Other fertility control studies

To our knowledge, the sterilization of free-ranging female wolves has not

previously been reported. However, the few studies which have examined fertility control

for wild canids provided evidence that fertility control of wolves might be a viable

management tool. Lord (1956) sterilized female grey foxes in Florida in order to estimate

the size of the population, using the age-ratio reduction method. Both captive (Newsome,

1995) and wild (Bubela 1995) red fox vixens were tubally ligated in Australia to

determine the effects of sterilization upon social behaviour. A similar study was carried out on captive coyotes (F. Knowlton, pers. commun.). Most relevant of the recent studies is the surgical sterilization of 5 wild male wolves from 4 different wolf packs (Mech et al. 1996a).

All of these studies used surgical sterilization by tubal ligation or vasectomy, with the assumption that if gonads are left intact, hormonal cycling and associated social and sexual behaviours will not be altered. The authors all reported no observable change in dominance hierarchy or social behaviour. Indeed, Kennelly and Converse (in press) advocated surgical sterilization for experiments with fertility control, because the merits of fertility control for a particular species can be tested without confounding side effects which are often associated with chemical and hormonal sterilants. For wolves in particular, hormone induced contraception may interfere with sexual and social behaviours (Gardner et al. 1985). Asa (1996) suggested that suppression of normal cycling in wolves could result in decreased aggression in males, a lack of male interest in females, reduced territorial scent marking. She hypothesized that those effects could lead to the prevention of pair bonding or pack dissolution.

Management Implications

To our knowledge, this is the first report of uterine ligations of free-ranging female wolves, and is one of the first controlled field experiments which tests the viability of fertility control of wild populations. There are several important limitations that should be noted. First, the size of the sample of treated wolves and the relatively

short period over which some of them have been monitored limits statistical power and thus the conclusions about the long term effects of the treatment upon individuals. The size and topography of the study area and the expense of using aircraft in all aspects of the field work amounted to considerable logistical difficulties associated with capturing, sterilizing, and returning wild wolves to their territories. These factors necessarily limited the number of wolf pairs that we were able to sterilize and monitor. Second, the quality of the behavioural data is limited to what can be observed by aerial telemetry methods. The sterilization may have caused more subtle changes in wolf behaviour than the basic changes we tested for, but we were not able to detect these given our experimental design.

This fertility control experiment will contribute to the study of the long-term effects of predator control and provide empirical testing of predator-prey regulation models. The reduced Aishihik wolf population is ideal to test the merits of reproductive control. Surgical methods to impose permanent sterility upon both sexes of the remaining pairs in the control area are logistically and economically feasible on this scale. As our results suggest, sterilized wolves maintain their territories and can exclude fertile immigrants to a target area. Following lethal control, fertility control may provide a time lag in which ungulate populations have a better chance to increase, effectively slowing the predator population growth rate. This may ultimately reduce the frequency of, and eventually the need for, culling. The hypothesis that fertility control can reduce the rate of population increase can be tested by comparing the recovery rate of the sterilized Aishihik wolf population with naturally recovering populations in the southern Yukon.

Wolf managers need immediate alternatives to culling. Mech (1995) and Mech et al. (1996a) asserted the necessity of some form wolf control and/or wolf management where wolves live and in areas they are recolonizing. Conflicts with human interests, it seems, are inevitable, and yet lethal wolf control programs are all but obsolete. Public outcry has ended recent lethal wolf control programs in the Yukon and Alaska, where managers still aim to increase ungulate populations through predator reduction (Hayes 1992, Ward and Larsen 1995, Boertje et al. 1996). Wolf control, despite several successes with increased ungulate calf survival (Hayes 1995, Boertje et al. 1996, YTG unpubl. data), has long been a controversial subject in the literature, as well. Questions about whether wolf predation limits ungulate population growth are at the root of an academic controversy about predator-prey dynamics in general, and specifically about the validity of the assumptions which lead to wolf control (Walters et al. 1981, Theberge and Gauthier 1985, Ballard et al. 1987, Bergerud and Ballard 1988, Thompson and Peterson 1988, Skogland 1991, Boutin 1992, Eberhardt and Pitcher 1992, Gasaway et al. 1992, Potvin et al. 1992, Hatter and Janz 1994, Dale et al. 1994, Messier 1994, 1995; Seip 1991, Crête and Manseau 1996). In addition, Haber (1996) raises questions about the social impact of culling upon wolves. But the ethical, moral, and economic issues are perhaps the crux of what Mech (1995) calls "the dilemma of wolf management", pitting mostly urban "wolf protectionism" against rural anti-wolf sentiment.

The dilemma continues, and managers are faced with searching for alternatives to lethal control to meet their mandates of managing big game populations. Translocation of live wolves, compensation for livestock losses due to wolf predation, zoning, public

education, and public hunting and trapping are some alternatives (Mech et al. 1996a).

Based on the results of our study, fertility control represents yet another option.

Particularly in recovering, low density wolf populations, fertility control represents a way

to slow the increase of wolf population recovery, and to maintain low wolf densities in

key management areas. Used in conjunction with translocation or public harvest by

hunting or trapping, fertility control may be particularly effective. It is currently being

applied in conjunction with live translocation of subordinate wolves and public trapping

efforts to manage the FortyMile caribou herd in Alaska (C. Gardner, pers. commun.).

This technique has potential for application to other wolf-ungulate systems, as well.

New applications

The results from our study suggest that surgical sterilization can be used

effectively to prevent wolf reproduction without altering basic wolf behaviours.

However, surgery is expensive and invasive. Anaesthesia and surgery are associated with

a certain degree of risk of complications and infection. Currently, the scale on which

wolf fertility control can be applied is limited by the logistics of capturing, handling, and

performing surgery on wild wolves.

The development of new contraceptive techniques, such as immunocontraception,

may facilitate large scale wolf management by fertility control. In particular, porcine

zona pellucida (PZP) has been used to produce antibodies which can prevent fertilization

by blocking sperm binding sites on ova (Dunbar and Schwoebel 1988). Kirkpatrick et

al. (in press) have successfully induced contraception in feral horses (Equus caballus),

Przewalski horses (E. przewalski), and onagers (E. hemionus) for up to 6 years with annual booster shots, and have used remote delivery systems. White-tailed deer (Turner et al. 1996) and grey seals (Brown et al. 1996) have also been sterilized with PZP.

If proven to have no behavioural side effects, a PZP vaccine could be delivered to wolves via darts, eliminating the need for expensive, invasive, and risky handling of wolves for surgery.

Wolf fertility control can be used for conservation efforts, as well. In our study, the exploited Aishihik wolf population borders the wolf population in Kluane National Park, where the protection and conservation of wolves and other animals is a primary concern. Due to large territory sizes and long distance dispersal movements, wolves are not necessarily protected by park boundaries. Once outside the park, they are vulnerable to trapping and other control measures. A recent study demonstrated that parks may not be large enough to provide sufficient protection for wolves, particularly those whose territories range outside park boundaries. Forbes and Theberge (1996) found that 56% of Algonquin Park wolf mortalities were human caused, and that 68% of those mortalities occurred outside the park boundaries. Half of these were due to regular seasonal movements of wolves following white-tailed deer.

This study design used the fertility controlled territories as a buffer zone between protected wolves from Kluane National Park, and low wolf density areas on the adjacent caribou calving grounds. The concept of wolf buffer zones is addressed most recently by Mech (1994), who documented high intraspecific mortality of wolves (91%) within 3.2 km of the estimated edge of wolf pack territories. He suggested that wolves avoid

territorial boundaries due to the high risk of mortality associated with encountering neighbouring wolf packs. Sterilized wolf packs may be used to establish a buffer zone between protected wolf populations and areas where wolves are vulnerable to human caused mortality.

Conclusion

The results from this study demonstrate that the behavioural characteristics of wolves are not altered by surgical sterilization, and that these characteristics allow fertility control to have a desirable effect upon wolf population dynamics. Research should now focus on the long term ecological effects of sterilizing wolf populations. The recovery of the Aishihik wolf population will continue to be monitored, as will the response of the Aishihik moose and caribou populations to the effects of wolf reduction and wolf fertility control. In the interim, it is possible to use the behaviour data from the sterilized wolves to parameterize a model designed to explore the population level effects of wolf fertility control on ungulate prey populations (Chapter Three).

Significantly, fertility control represents a new philosophical approach to wolf management. This approach is aimed at wolf-human coexistence, and acknowledges the role of the wolf as a predator in ecosystems. Wildlife managers now have the option of managing ungulate populations by wolf management, without having to resort to controversial culling.

CHAPTER THREE : A WOLF-PREY SIMULATION MODEL TO DETERMINE THE LONG TERM EFFECTS OF WOLF FERTILITY CONTROL AND OTHER MANAGEMENT STRATEGIES.

INTRODUCTION

Wildlife managers in Canada and Alaska have used predator control programs to manage moose, caribou, deer, and mountain sheep populations for harvest (Banville 1983, Gunson 1983, Harbo and Dean 1983, Kolenosky 1983, Tompa 1983, Bergerud and Elliot 1986, Ballard et al. 1987, Potvin et al. 1992, Seip 1992, Hatter and Janz 1994, Hayes 1995, Hayes and Gunson 1995, Boertje et al. 1996). Wolf control programs can lead to increases in ungulate calf survival and population growth (Ballard et al. 1987, Bergerud and Ballard 1988, Hatter and Janz 1994, Hayes 1995, Boertje et al. 1996). In Aishihik, Yukon, a government sponsored wolf control program was in place from 1992 to 1997, when 80% of the wolf population was annually removed over 5 years by aerial shooting and ground snaring.

Wolf-ungulate models

The theoretical rational for wolf control is that wolves can limit ungulate population growth, and may regulate prey populations at low densities (Fuller and Keith 1980, Messier and Crête 1985, Hayes et al. 1991, Seip 1992, Messier 1994,1995, Hayes 1995). Regulation theories are difficult to test in the field. Wolves and their ungulate prey are large, long-lived species that frequently live in cryptic habitats within large geographical areas. Understanding the functional relationships between them requires

detailed knowledge about the population dynamics of all of the species involved, as well as wolf predation rates under varying conditions (Sinclair 1989). The volume and detail of data required to examine predator-prey relationships is beyond the scope of most studies. Models can help to investigate functional relationships without the expense and logistical problems that would be required for experimental field studies.

The effects of predation upon ungulate populations has been investigated using conceptual and mathematical models. Theberge and Gauthier (1985) used qualitative models to describe 6 possible predator-prey relationships, and showed that wolf control should only be applied when ungulate population density is well below environmental carrying capacity, when mortality is the major factor limiting the growth of the ungulate population, and when wolf predation is a major cause of ungulate mortality. Messier (1994, 1995) presented 4 conceptual models to represent the mechanisms by which prey can be maintained at stable equilibrium densities. He predicted that ungulate density can be regulated by food, predation, or a combination of the two (Fig. 1.1).

Wolf-prey and wolf management simulation models

Quantitative models have also been used to simulate wolf-prey relationships and wolf habitat, population dynamics, and territoriality (Crête et al. 1981, Walters et al. 1981, Hastings 1983, Ballard and Larsen 1987, Lewis and Murray 1993, Hatter and Janz 1994, Boyce 1995, Vales and Peek 1995, White et al. 1996, Mladenoff and Sickley 1998). Models have been particularly useful for examining the implications of wolf management strategies. Boyce (1995) and Vales and Peek (1995) modelled the potential

impacts of wolf reintroduction into the Greater Yellowstone Ecosystem and the Northwest Montana Wolf Recovery Area, respectively. Both models incorporated various management strategies by varying ungulate harvest rates, and Boyce (1995) accounted for wolf-human conflicts and wolf culls as sources of wolf mortality. Boyce's model predicted a general decline in prey populations with the reintroduciton of wolves, but the model results did not suggest a 'predator pit', due to high prey densities and productivity (Boyce 1995). Vales and Peek (1995) predicted the number of wolves that could be supported by elk and mule deer populations according to varying ungulate harvest strategies. Ballard and Larsen (1987) used a simulation model to determine the role of wolf predation and the effects of wolf control in the decline and recovery of a south central Alaskan moose population. Similarly, Eberhardt and Pitcher (1992) used a model to conclude that decreased recruitment and range quality deterioration contributed to the effects of human harvest and wolf predation upon the Nelchina caribou herd in Alaska.

Alternatives to lethal wolf control

Despite practical and theoretical evidence that wolf control can help increase ungulate populations, public opposition to large scale government wolf culls has prompted wildlife managers to investigate alternative, non-lethal methods of controlling predator populations. These may include fences, guard dogs, or other repellents to restrict predator access to livestock, or techniques such as diversionary feeding, aversive conditioning, relocation of problem animals, and fertility control. Cluff and Murray

(1995) reported that all of these non-lethal alternatives were more publicly acceptable than lethal control methods which include, in decreasing order of public acceptability: shooting from the ground, fast acting poisons, bounties, aerial shooting, killing pups at dens, steel leghold traps, and slow acting poisons, such as cyanide.

Fertility Control

The Yukon Territorial Government (YTG) responded to public opposition to the Aishihik lethal wolf control program by sponsoring a wolf fertility control experiment. Nine female and 8 male wolves from 7 wild wolf packs were surgically sterilized during the 4th and 5th years of the wolf reduction program and the 1st year of wolf population recovery. These sterilized packs were monitored for 3 years to determine the effects of surgical sterilization upon wolf social and territorial behaviour. Spence et al. (1998, Chapter Two) concluded that wolf behaviour was not obviously affected by sterilization.

Fertility control of wild canids has also been tested on red foxes (Vulpes vulpes) in Australia (Bubela 1995), and on wolves in Minnesota, where five wild wolves from 4 packs were vasectomized by Mech et al. (1996a). In both studies, no behavioural changes were observed. These field studies have examined the effects on sterilized individuals. However, the efficacy of fertility control as a management tool will depend upon the long term population level effects of fertility control upon predators and their prey. At present, simulation models can be used to investigate these effects.

Fertility control models

Recent models have attempted to incorporate wolf management by lethal control, but none have examined the potential effects of wolf fertility control. Several models have explored the general population effects of sterilizing mammals (Garrott 1991, Garrott and Siniff 1992, Garrott et al. 1992, Hone 1992, Caughley et al. 1992, Seagle and Close 1996, Barlow 1994, 1997; Barlow et al. 1997; Sinclair 1997). In general, the social biology and evolutionary strategies of the target species will determine the effectiveness of any fertility control regime (Caughley et al. 1992, Sinclair 1997). Barlow et al. (1997) modelled the effects of fertility control on animals with various mating systems, and determined that the greatest effect was observed when both sexes of a monogamous species were targeted.

For red foxes, Pech et al. (1997) used models to demonstrate that environmental variability influences the effectiveness of fertility control, and that high population levels of permanent sterility were required. Similarly, Bubela et al. (unpubl. data) determined that 90% sterilization of both sexes was required to reduce red fox populations, but that high levels of immigration could nullify its effects.

A model to evaluate population level effects of fertility control of wolves

Empirical studies have demonstrated the effects of fertility control upon individuals, and theoretical models have been used to simulate the population level effects of sterilization. However, there is a paucity of studies which combine the results of fertility control experiments with modelling. In this study, I combined the results from

the Aishihik wolf fertility control study with long term local caribou, moose, and Dall

sheep population data to construct, parameterize, and validate a simulation model. I used

the model to predict the effects of various management strategies, including fertility

control and mortality control, upon a wolf population and its ungulate prey. Hunting and

stochastic weather variability are also incorporated into the model.

STUDY SITE

The Aishihik study area is a 20,000 km^2 area in Southwest Yukon. (Map: Figure

2.1). This area was the site of the 5-year Aishihik wolf reduction program, in which the

wolf population was reduced to 20% of its pre-control size. Fertility control was applied

to 7 wolf pairs in the wolf control area, beginning in the 4th year of the wolf reduction

program (Spence et al. 1998, 199N, Chapter Two).

The region is located at the north-eastern edge of the St. Elias mountain range,

which is characterized by metamorphic and volcanic peaks and icefields. The wolf

control area encompasses part of the rugged Ruby Range mountains, which are composed

of volcanic rocks (lava and basalt), with intrusions of gradodiorite and quartz dionite

(Oswald and Senyk 1977).

Major rivers include the Nisling, and the Aishihik. Southern drainages flow to the

Alsek River, which drains into the Pacific Ocean. Northern drainages flow into the

Yukon River system. Major lakes in the study area are Kluane Lake, Aishihik Lake, and

Sekulmun Lake. The study area is characterized by poor drainage in valley bottoms, and

is part of the discontinuous, scattered permafrost zone.

Treeline occurs at approximately 1,200 m. The vegetation in well-drained soils is dominated by white spruce (Picea glauca). Black spruce (Picea mariana) is commonly found in most lowland areas. Lowland areas support aspen (Populus tremuloides), and balsam poplar (Populus balsamifera). Lodgepole pine is (Pinus contorta) is only found along the eastern edge of the experimental area. Willow (Salix sp.), dwarf birch (Betula glandulosa), alder (Alnus crispa), soapberry (Sheperdia canadensis) and ericaceous species are the dominant understory shrubs.

Most of the area lies in the rain shadow of the St. Elias Mountains. Low elevations receive 190-285 mm of precipitation annually. Average annual temperature is -4°C. In January, the average temperature in Haines Junction is -20°C, and in Burwash Landing it is -31°C (Environment Canada unpubl. data).

The major mammalian prey species in the study area are woodland caribou (Rangifer tarandus tarandus), moose (Alces alces), and Dall sheep (Ovis dalli). The Aishihik caribou herd ranges entirely within the control area. The ranges of the Kluane and Klaza herds include only portions of the study area. Some horses (Equus equus) and fewer than 25 mountain goats (Oreamnos americanus) also inhabit the region (J. Carey, pers. commun.). A diverse small mammal community is dominated by the snowshoe hare (Lepus americanus) (Boutin et al. 1995). The study area encompasses part of three First Nations traditional areas. Four rural communities, Haines Junction, Canyon, Burwash Landing, and Destruction Bay, border the study area. Several big-game outfitters operate in the region.

MATERIALS AND METHODS

I used Microsoft Excel 5.0 to construct a population simulation model which includes wolves, moose, caribou, and Dall sheep. The model is projected for 25 years, which is realistic and suitable for management planning. For the prey populations, only reproduction, natural mortality, wolf predation and other predation on summer calves are considered explicitly. Stochastic weather variability is incorporated into the model as randomly occurring severe winter conditions prior to calving season, which reduce moose and caribou calf production. Range quality, disease, and other factors were not considered explicitly. Harvest is annually removed from the winter moose, caribou and sheep populations. Moose and caribou harvest levels are determined as a percentage of the population. Where lethal wolf control is applied, harvest begins the winter following the last wolf pack removal. For simplicity, age classes for all of the species sub-models are restricted to subadult (wolf pups, caribou calves, moose calves and yearlings, and sheep yearlings) and adult classifications. Sex ratio and classification are not specified.

All of the sub-models are evaluated with 2 seasonal time steps per year, except for the sheep which are evaluated annually. The year is divided into "summer" (May-August), and "winter" (September-April). Appendix 3.1 contains the complete list of all of the parameters and equations used in the wolf and prey sub-models. Reference to these equations is explicit in the description of each sub-model, below. Sources of parameter values are listed in Table 3.1. Schematic representations of the wolf, caribou and moose, and sheep population sub-models are shown in Figures 3.1, 3.2, and 3.3, respectively.

Wolf sub-model

The wolf population is modelled on the basis of the number of packs in the 20,000

km^2 Aishihik wolf control area prior to wolf control. Wolf packs are classified as either

small (2-3 wolves), medium (4-9 wolves), or large ($\geq$10 wolves), as in Hayes (1995).

Wolf predation upon their ungulate prey is accounted as a fixed number of prey per pack,

according to pack size and season. I chose to use wolf pack number and size as predation

units as opposed to wolf number, because recent studies have shown that pack size is

strongly related to the number of prey killed by wolves (Hayes et al. 1991, Thurber and

Peterson 1993, Dale et al. 1995, Hayes 1995).

Table 3.1 List of data sources for parameter values in the wolf-prey system model.

Data Sources for Model Parameters

Species Submodel	Parameter Value	Source
Moose	Fecundity	1992 Aishihik composition data, unpubl.,YTG
		Alaskan moose natality rates, Gasaway et al. 1992
	Mortality	1992 composition data, unpubl.,YTG, estimate
	Other sources of calf mortality	estimate
	Number killed by wolves	Winter: Hayes, 1995, numbers reduced by 30%
		Summer: Doyle et al., unpubl.data
Caribou	Fecundity	Pregnancy data, unpubl.,YTG
	Mortality	Aishihik herd census and compositon data, unpubl.,YTG
	Other sources of calf mortality	40Mile herd calf loss to predation, Aishihik herd rut counts (unpubl.)
	Number killed by wolves	Summer: Doyle et al., unpubl.data
		Summer: 40Mile herd calf loss to predation, Aishihik herd rut counts
		Winter: Estimate based on census data, same ratio by pack size as for moose
Dall Sheep	Fecundity	Talbot Arm composition data, unpubl.,YTG
	Mortality	Talbot Arm sheep census data, unpubl.,YTG
	Number killed by wolves	estimate based on Sumanik, 1987 and Talbot Arm census data
Wolves	Pup production,	Finlayson wolf population data, Hayes, 1995
	Dispersal	Finlayson wolf population data, Hayes, 1996
	Mortality	Finlayson wolf population data, Hayes, 1997
	Population recovery	Aishihik wolf censuses, unpubl., YTG; Finlayson wolf population: Hayes 1995
Other values	Harvest estimates	Quock, unpubl.,1992 YTG Harvest data, unpubl.
	Long term weather data	Environment Canada summaries, unpubl.

Figure 3.1 A simplified diagram of key state variables for the wolf sub-models, and their

input into the system model through predation on moose, caribou, and Dall sheep.

(---------→ = wolf predation)

Wolf sub-models
(Small, Medium, Large Packs)

Caribou-hunting wolves
(End winter)

Moose-hunting wolves
(End winter)

(-) lethal
control,
dispersal,
natural
mortality

(+) reproduction
(with/without fertility
control), immigration

(-) lethal
control,
dispersal,
natural
mortality

Caribou-hunting wolves
(End summer)

Moose-hunting wolves
(End summer)

Lone wolf

Caribou
sub-model
(links to Fig. 3.2)

Dall Sheep
sub-model
(links to Fig. 3.3)

Moose
sub-model
(links to Fig. 3.2)

Figure 3.2 A simplified diagram of the key state variables for the caribou and moose

population sub-models. The summer populations link into the main model as depicted in

Figure 3.1.

```
                    ┌─────────────────────────────────┐
                    │                                 │
                    │   Caribou/Moose Population       │
                    │      (End Winter)                │
                    │                                 │
                    └─────────────────────────────────┘
```

(+)
reproduction
(+/-weather),
(-) wolf
summer
predation,
other calf
mortality

(-) wolf winter
predation,
natural adult
mortality,
adult harvest

```
                    ┌─────────────────────────────────┐
                    │                                 │
                    │   Caribou/Moose Population       │
                    │      (End Summer)                │
                    │                                 │
                    └─────────────────────────────────┘
```
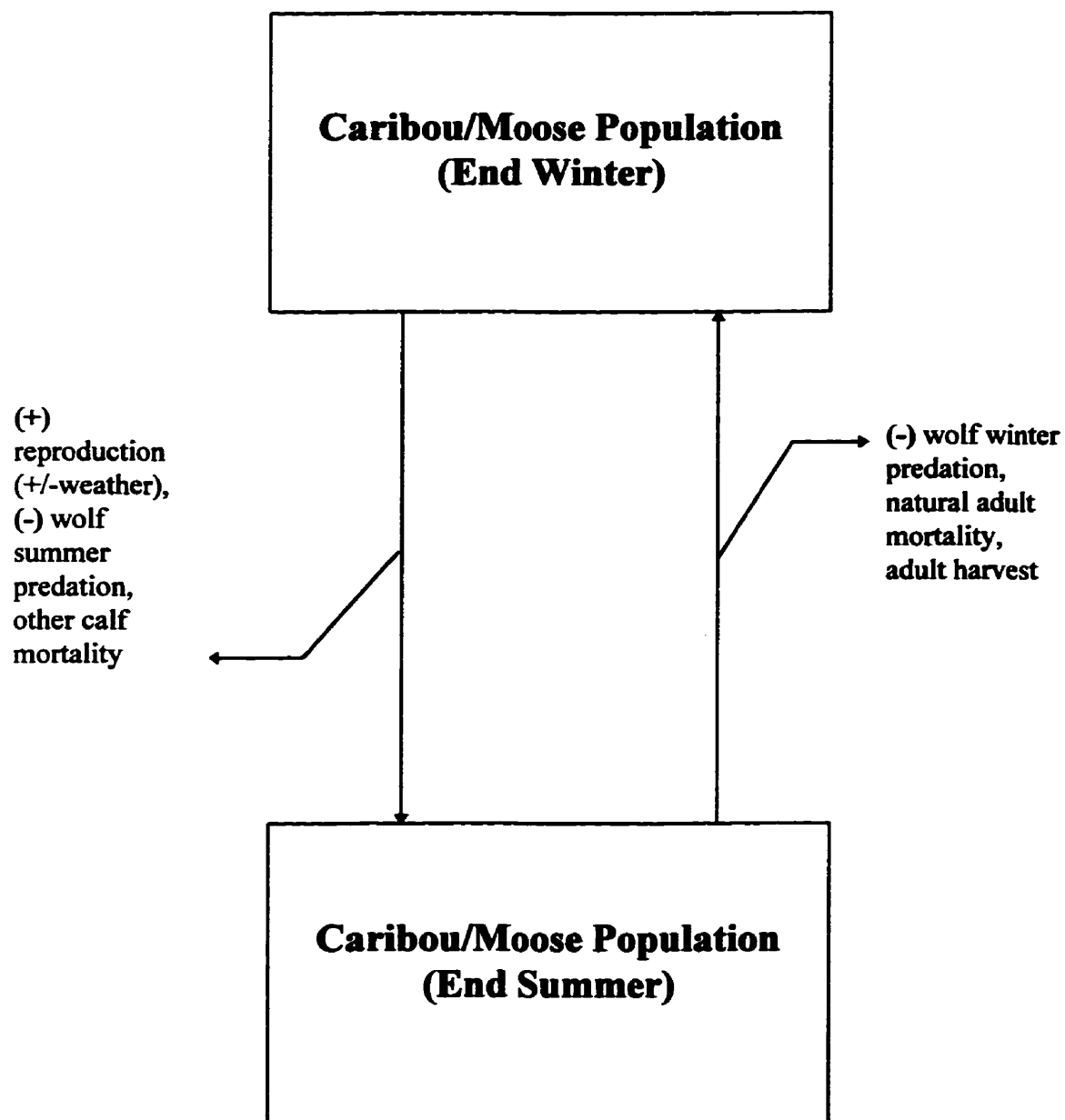
Figure 3.3 A simplified diagram of the key state variables for the Dall sheep population

sub-model. The population is linked to the system as depicted in Figure 3.1

Yearlings
(variable annual recruitment)

Adults
(fixed annual survival)

Total Dall Sheep

Wolf predation
(Lone wolf, small-,
medium-sized packs)

Harvest
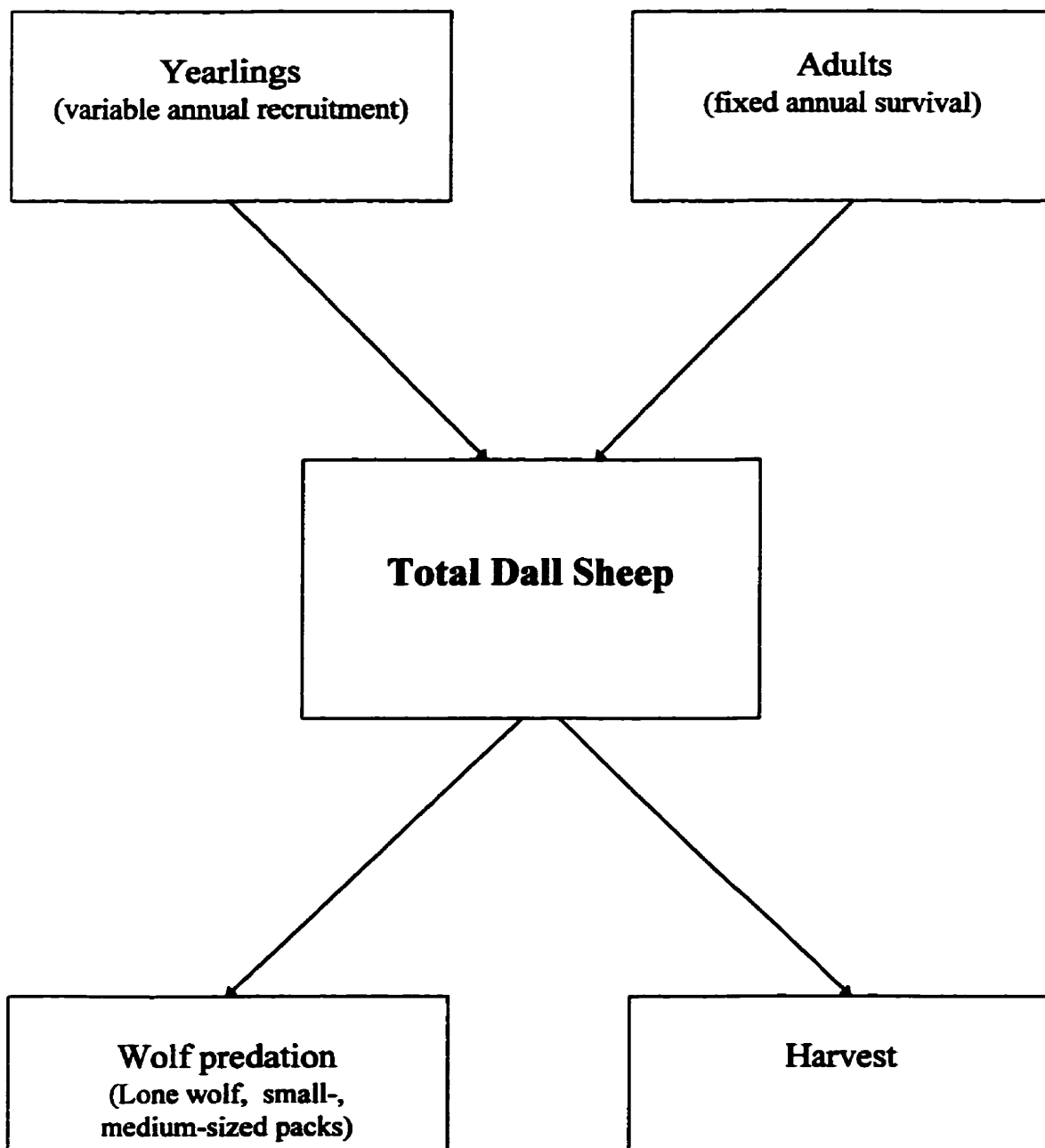
Wolf pack size increases annually from small to medium to large, according to reproductive success rates, and moderated by dispersal rates and splitting of large packs (eqs. 6-10). Lone wolves are not part of the wolf sub-model, but are included in wolf predation upon Dall sheep.

The wolf sub-model is subdivided into 2 parts which are independent sub-populations: one sub-population occupies territories on the Aishihik caribou summer calving grounds and only hunts caribou throughout the year, and the other occupies territories distributed throughout the rest of the wolf control area and hunts only moose. In the Aishihik wolf control area, wolves occupying territories outside of the caribou summer calving grounds may have winter access to caribou, but I assumed for simplicity that wolf packs either hunt caribou or moose all year long, but not both. Wolf packs that hunt sheep are calculated as a percentage of the total number of packs in both sub-populations. Having two wolf sub-populations allows for flexibility of management of wolves. Mortality and/or fertility control can be applied only on the caribou calving grounds, or throughout the entire study area, at different levels of intensity. Both sub-populations are open to the pool of immigrants (see below).

The wolf model is not explicitly territorial, but it does keep track of the number of wolf territories within the study area. Fertility control, lethal control, natural mortality and dispersal occur over winter, creating territorial vacancies (eq.1). Reproduction and immigration into vacant territories are calculated over summer. Vacancies are filled by small and medium packs annually at a fixed rate (eqs. 2,3), derived from the observed wolf recolonization following wolf control in Aishihik [Yukon Territorial Government

Department of Renewable Resources (YTG), unpubl. data]. I assumed that no large

packs colonize the area due to the low prey base because this has not been observed in

Aishihik. However, the structure of the model does allow for large pack immigration if

required. When filling vacancies, the model does not distinguish between immigrants

from outside the study area, which I assumed to come from an infinite pool, and

dispersers from within the study area. Large packs split and fill vacancies as medium

packs before immigrants and dispersers are added as new packs.

The number of wolf packs is evaluated seasonally. The number and size

distribution of wolf packs in the summer acts on the prey models for both the summer

and winter seasons, because the number of occupied territories is stable and generally

constant from summer to summer, regardless of the shifts in occupancy and pack size

distribution that occur over winter. This assumes that territorial vacancies created in

early winter will most likely be filled by the end of summer due to immigration from

outside the study area, and by dispersal and pack splitting from local packs (R.D. Hayes,

pers. commun.).

The number of wolf territories is a function of the winter moose population for

both sub-populations of wolves. This assumes that the moose population can support

caribou-hunting wolf packs as alternate prey. I also assumed that wolf numerical

response to declining prey populations will be an adjustment of pack size and pack

number (Dale et al. 1994, Hayes 1995). A maximum number of large packs in each sub-

population is determined according to the caribou and moose population size at the end of

winter. When the number of large packs in winter exceeds the maximum number of large packs for the prey base, large packs split and become medium packs (eqs. 4,6,7).

The model allows for simulations of mortality control, fertility control, and immigration from outside the study area. Mortality control of wolves is simulated by removing numbers of small-, medium-, and large-sized wolf packs from the two sub-populations in winter. The total number of packs removed over 5 years (39) in the simulations is equal to the removal or reduction of packs during the lethal wolf control program carried out in Aishihik from 1992-1997 (YTG unpubl. data). I assumed that wolf reduction is motivated primarily by a decline in caribou, thus all winter wolf packs on the caribou summer calving grounds are removed. The remainder of the total number are removed from the moose-hunting sub-population.

To simulate wolf population recovery following mortality control through immigration and dispersal, vacancies are filled at a reduced "immigration efficiency" (eq. 2). Only 25% of territorial vacancies are filled over the summer following each year of wolf pack removal. Following wolf control, filling of vacant territories is moderated over 4 years by an immigration efficiency factor, thus simulating the gradual recovery of exploited wolf populations to pre-control levels (Hayes et al. 1991, Hayes 1995, Boertje et al. 1996, YTG unpubl. data). The immigration efficiency increases in yearly increments (0.5, 0.75, 0.9, 1) following wolf control. Otherwise, vacant territories which arise from death or dispersals are filled within the year when the wolf population is naturally regulated (no lethal wolf control).

Fertility control is "applied" to a percentage of small packs which do not breed, regardless of the reproductive rate of small packs, for the period that fertility control is applied (eq. 5a). However, sterilized pairs have the same death and dispersal rates as non-sterilized pairs. In the Aishihik wolf reduction simulations, fertility control is applied to small pairs during the 4th year of wolf removal (Year 5), to mimic the Aishihik wolf control program.

Moose sub-model

Where possible, and unless otherwise indicated, all initial moose population parameters are based upon observed population indices from the Aishihik South moose population in 1992 (Ward and Larsen 1995). The moose population is divided into calves, yearlings, and adults. The population number is calculated biannually, at the end of summer and at the end of winter (eqs. 40,41). The reproductive rate (mRp) is calculated as the number of calves, including twins, per adult female (from Gasaway et al. 1992), multiplied by the percentage of adult females in the moose population (eq. 24). Calf production is calculated using the logistic equation for population growth (eq. 36).

In the model, wolf predation in the summer favours calves, then yearlings (eqs. 26, 27). Adults are less susceptible to wolf predation in the summer (eq. 28). The number of moose killed by wolves is extrapolated from Doyle et al. [Alaska Department of Fish & Game (ADF&G), unpubl. data], a summer predation rate study on a pack of 8 wolves in Alaska. Moose calves are also subject to summer predation by other predators such as black and brown bears. Bear-caused calf mortality remains constant in the

simulations, independent of wolf population response (mMc). Winter wolf predation rates are based upon data from the Finlayson area in the central Yukon (Hayes 1995). I assumed that adults, yearlings, and calves are killed by wolves in a 2:1:1 ratio in the winter (eqs. 29-31). The summer moose population is incorporated annually into the system model.

Adult moose mortality due to wolf predation is assumed to be additive below a threshold of 2000 animals. Above that level, non-predation adult mortality is set at 3% of the adult population (eq. 25). Although moose dispersal may occur in the wild and may compensate for harvest in some populations (Labonté et al. 1998), it has not been included in the model.

Human harvest of adults is calculated as the removal of adults, irrespective of sex, from the winter moose population. For the simulations of the Aishihik moose population decline, a harvest rate of 120 moose per year was calculated between 1981 and 1990. This rate approximates the number of moose that were harvested in the study area during that period (Quock 1982, YTG unpubl.data). For other model simulations, adults are harvested as a percentage of the moose population at the end of summer. A "low" harvest is set at 2% of the annual population, and 5% is the "high" harvest rate (eq. 32).

Caribou sub-model

In the model, only the Aishihik caribou herd is represented, because the study area encompasses only small portions of the ranges of the Kluane and Klaza herds. Wherever

possible and unless otherwise indicated, caribou population parameters are derived from

Aishihik caribou herd population census data (YTG unpubl. data).

Like the moose population, the caribou population is evaluated at the end of

summer (eq. 22) and at the end of winter (eq. 23). Caribou are classified as either adults

or calves. I assumed that the calf mortality rate at 4-6 months of age does not differ from

the calf mortality rate at 12 months (Bergerud and Elliot 1986, Bergerud and Ballard

1988), and therefore, that the percentage of calves during the rut is a good estimate of

their recruitment. Adult caribou mortality due to wolf predation is assumed to be additive

when the herd is smaller than 1400 animals. In the model, 3% of the adult population is

removed due to other sources of natural mortality when the herd is larger than 1400

animals (eq.15a).

I assumed that wolf predation on caribou is heavily biased toward caribou calves

in the summer (Bergerud and Elliot 1986; FortyMile herd, ADF&G unpubl. data). To

derive the number of Aishihik calves killed over the summer, I subtracted the number of

calves present during the rut from the number of calves produced. I calculated the

number of calves produced as the number of adult cows in the rut multiplied by the

pregnancy rate. I assumed that prior to wolf control in 1992, wolf predation was

responsible for 55% of neonatal calf deaths, and that other predators and natural factors

were responsible for the remaining 45% based on the data from the FortyMile herd

(ADF&G unpubl. data). I averaged the number of wolf-killed calves over the years of

pre-wolf control data, and the number of other calf mortalities. Other calf mortalities

were held constant at that mean value in the model. The wolf-caused calf mortalities

were divided among the number and size distribution of packs on the Aishihik caribou calving grounds in January 1992, in order to determine calf predation by pack size (YTG unpubl. data). I assumed that in the summer, a pair represents one hunting unit, a medium pack represents 4 separate hunting units, and a large pack is equivalent to 6 hunting units. I calculated that each hunting unit kills 7.5 caribou calves per summer (eq.12).

I estimated wolf predation on adult caribou in the summer and on both age classes over winter. I varied predation rates while keeping the wolf population and caribou population parameters constant at 1992 levels until the Aishihik caribou herd percentage of calves in 1992 and population decline from 1981 to 1991 were approximated. The derived numbers of caribou killed by wolves over winter are approximately twice the number of moose killed over winter in the Finlayson area of the Yukon, and are in the same proportion by pack size (Hayes 1995). Wolf predation in the summer is responsible for very few adult caribou mortalities: in the model, wolves kill 75% fewer adults than calves (eq. 13).

As in the moose population sub-model, the number of caribou calves produced per year in the model is calculated according to the logistic equation. The natality rate is calculated as the pregnancy rate of adult cows multiplied by the percentage of adult cows in the Aishihik herd. There is evidence to suggest that the sex ratio of caribou herds becomes increasingly biased towards females when predation levels are high and recruitment is low (Bergerud and Elliot 1986, R. Farnell, pers. commun.) I therefore used the sex ratio from 1992 to calculate the natality rate when the population is below 1200

animals, and assumed that there are approximately 50 bulls per 100 cows when the population exceeds 1200 animals (eq.11a).

Harvest of adults is calculated as the removal of adults, irrespective of sex, from the winter caribou population. For the simulations of the Aishihik herd decline, 58 caribou were harvested annually between 1981 and 1990. This rate approximates the number of caribou that were hunted from the Aishihik herd in the study area during that period (Quock 1982, YTG unpubl.data). For other model simulations, adults are harvested as a percentage of the total number of adult caribou in summer. Low and high harvest levels are set at 2% and 5%, respectively (eq. 16).

Dall sheep sub-model

I have included only a subset of the study area Dall sheep population in the model, the Talbot Arm population, because the most complete census information is available for that group.

The initial sheep population in the model is 597 animals, which is the total count from 1992, at the beginning of the Aishihik wolf control program (YTG unpubl. data). I assumed that recruitment rate is equivalent to the percentage of yearlings in the population. The base recruitment rate (12.6%) in the model is the average of 5 years of YTG unpublished data for which there is information about yearlings. I assumed that weather and forage availability and quality are important factors for sheep population stability (Burles and Hoefs 1984), but have no field data with which to parameterize stochastic variability. Instead, I have used a random number generator which varies the

base annual recruitment rate by up to 50% every year (eq. 43). The adult annual survival rate is derived from a life table for the Talbot Arm population (Dehn 1997), adjusted upwards to account for wolf predation. The total number of sheep is calculated as the number of adults surviving the previous year added to the number of yearlings, minus the number of sheep killed by wolves and the number harvested by humans during the year (eq. 44). Simulation results presented are the mean population size, calculated from 10 simulations for each set of management options.

I assumed that the sheep population is too small to sustain predation by a large wolf pack, and that only lone wolves and a few small packs regularly kill sheep (Sumanik 1987). Due to the small biomass of sheep relative to other ungulate prey and the difficulty of hunting sheep, I assumed that sheep do not sustain wolf packs at levels high enough to maintain reproductive condition. However, sheep predation may supplement the diet of small packs over winter, when there are few or no small prey available to wolves. In the model, lone wolves kill 9 sheep per year, based on Sumanik's (1987) kill rate data. Small and medium packs kill 10 and 12 sheep per year, respectively (eq. 42), as I assumed that groups of wolves hunt alternate prey (caribou or moose) to supplement their diet. In the model, there is always at least one lone wolf hunting sheep, and I assumed that 10 % of the total number of wolf packs in the study area have access to sheep.

Human harvest of sheep varies from 8 to 12 sheep per year. This number approximates the level of harvest from 1991 to 1993 (YTG unpubl.data). The model does not distinguish age or sex classes of sheep. Hunters generally select for mature, full-curl

rams, whereas the model assumes that any sheep, including yearlings and ewes, may be removed. This may bias the effect of the hunting on the model population. I did not make the sheep sub-model more complex in terms of sex structure and age, however, because I was able to find very little data about the number of sheep killed by wolves of different pack sizes during winter (Sumanik 1987), none about wolf predation on sheep over the summer, and no data about age and sex specific survival rates before wolf predation. In addition, there is anecdotal evidence that ewes may have been harvested from the local sheep population during the 1980's (Hayes, 1992).

Weather

Stochastic weather variation is incorporated into the model as the random chance (6%) that the mean minimum temperature in Haines Junction and Burwash Landing, Yukon in March will be colder than 1.5 standard deviations from the 50-year average of mean minimum temperatures (Environment Canada, unpubl. data). A random number is calculated between 0 and 1. If the number is greater than 0.94, moose and caribou reproductive rates are reduced by 25% and 30%, respectively (eqs. 24b,11b). When weather is included in model simulations, I ran simulations 5 times for each management scenario and averaged the 25-year trajectories for moose and caribou populations.

Model validation

To test the model, I ran a simulation to emulate the moose, caribou and sheep population trends from 1981-1991. I used moose and caribou parameters from 1981

where available, and from 1992 where earlier data is not available. The distribution of

packs by size follows the 1992 wolf pack distribution. (Quock 1992, YTG unpubl. data).

RESULTS

Results of the model simulations are grouped according to management strategy.

These are:

(a) no active wolf management (nm); no wolves or ungulates are harvested

(b) lethal wolf control (lc, Years 2-6) with no or low levels of ungulate harvest (2%h)

  starting the year following wolf reduction (Year 7)

(c) lethal wolf control (lc) with high levels of ungulate harvest (5%h) starting Year 7

(d) wolf fertility control (fc) alone, starting in Year 1

(e) 5 years (Years 2-6) of lethal wolf control (lc) followed by fertility control (fc) starting

  in Year 5

(f) a combination of lethal control (lc) followed by fertility control in Year 5, with

  ungulate harvest starting in Year 7.

These options are simulated with and without stochastic weather variability (w). The

legend notation for a simulation with lethal control, fertility control, sheep harvest, and

weather would be (lc,1,0.6fc,12h,w). In this example, all of the small-sized wolf packs

on the caribou calving grounds and 60% of the small-sized wolf packs in the moose-

hunting sub-population in a given year would be sterilized, and 12 sheep would be

removed from the population each year. Caribou and moose reproductive rates would be

reduced by 30% and 25%, respectively, on a random basis throughout the 25 year

simulation. Table 3.2 is a key to the figure legends.

Overall, the model produces logical results which are consistent with the model's

assumptions. High rates of ungulate harvest and harvest when prey numbers are low

greatly reduces any benefits to prey populations derived from managing the wolf

population. Stochastic weather variability also dampens the effects of wolf management.

Figures 3.4 - 3.15 show examples of the model projections.

Model Validation

Figure 3.4 shows a simulation of the decline in ungulate populations that occurred

between 1981 and 1991.

Caribou.--

To simulate the conditions from 1981 to 1991, no wolf control is implemented

and 58 animals are harvested per year until 1990 (Quock 1992, YTG unpubl. data). In

this simulation, the caribou herd declines from 1340 animals in 1981 to 897 in 1990 and

667 in 1991. The average rate of decline is 4.6% per year. By contrast, the Aishihik herd

declined from between 1200 and 1500 animals to about 700 animals between 1981 and

1991, at an average annual rate of decline of approximately 4.4%. (a)

Moose.--

In the same 11 year simulation, the moose population declines by an average

2.1% per year when wolves are not managed and 120 animals are removed per year

(Quock 1992, YTG unpubl. data). From an initial population of 3000 animals in 1981,

the moose decline to 2347 animals by 1991(b). The population estimate for moose in the Aishihik area in 1991 was about 2000 animals, and the estimate for the actual rate of decline from 1981-1992 is 3.3% per year.

Sheep.--

The model predictions and the actual population estimates for the period between 1981 and 1991 are shown in Figure 3.4 (c). In the model simulation, the sheep population declines slowly at a harvest rate of 18 animals per year (Quock 1992, YTG unpubl. data) and without any management of wolves. On average, the population declines from 900 to 776 animals during the 11 year period, at an average annual rate of 1.3%. By contrast, the Talbot Arm sheep population decreased from 854 sheep in 1982 to 597 in 1992, an average decline of 2.7% per year.

No management

To simulate the Aishihik wolf-prey system without active wolf management, all parameters and initial population sizes were set to 1992 levels. Results are shown in Figures 3.5 and 3.6

Wolves.--

Without active wolf management, the total number of packs and the pack size distribution in the study area remain stable over most of the 25 year simulation (Fig.3.5). Within 2 years, the number of small-,medium-, and large-sized packs stabilizes at 4 (a),

12 (b), and 4 (c), respectively. Thus the model causes a small shift towards medium-sized packs and a reduction in the total number of packs from 22 to 20.

Caribou.--

The results from the model indicate that the Aishihik caribou herd would have been extirpated without active wolf reduction in 1992, when the herd numbered approximately 750 animals [Fig.3.6(a); ci750, nm). The model shows that even without any harvest, and unless wolf packs are removed, the caribou will decline to extinction when the initial herd size is smaller than a threshold of 1835 animals (ci 1835,nm).

Moose.--

The effect upon moose of not managing wolves is shown in Figure 3.6(b). In the model, the moose are also sensitive to a threshold density. Without any wolf management and no harvest, moose will increase slowly at any initial population size above 1900 (mi 1900,nm; mi1910,nm). Adding weather variability causes the moose to decline in 60% of the simulations, and so on average, moose will decrease slowly over time (nm, w).

Sheep.--

Figure 3.6 (c) shows that the sheep population, without active management and without harvest, demonstrates no predictable trend, and that on average, will remain fairly stable (bold face trend line). Due to the stochastic nature of the sheep sub-model, the population may increase, decrease, or fluctuate over the 25 year simulation period. The figure also shows the results of 10 runs of the model (regular type trend lines).

Lethal wolf control, low or no ungulate harvest

The effects of lethal wolf control and no or low levels of ungulate harvest are shown in Figures 3.7 and 3.8.

Wolves.--

In the model, five years of intensive wolf reduction causes a decrease in pack numbers during the wolf control period, but pre-control pack densities are reached within 5 years. Figures 3.7 (a), (b), and (c) show a shift to a stable pack size distribution of 4 small-, 10 medium-, and 6 large-sized packs.

Caribou.--

Model simulations of 5 years of wolf reduction predict that the caribou herd will increase to approximately 16,000 animals over 25 years (Fig. 3.8 (a): lc). An annual harvest of 2% per year slows the rate of population increase, but the herd reaches approximately 12,500 animals after 25 years (lc, 2%h). Incorporating stochastic weather variability and without harvest, a one-time wolf reduction, on average, causes a slow increase to about 9500 animals (lc,w). However, caribou decline beyond their capacity to recover in 40% of the simulations. In general, the caribou population recovery is sensitive to weather variation, and this effect is exacerbated by low levels of harvest (lc, 2%h,w).

Moose.--

In the model, lethal wolf reduction increases the rate of moose population growth [Fig.3.8(b)]. In all simulations where lethal control is applied, moose increase initially to approximately 3400. Inevitably, though, the population decreases to between 2000-2500

moose following wolf recovery. A modest increase is observed when there is no moose harvest, and there is no appreciable difference when weather variability is included (lc; lc,w). However, even a 2% annual harvest, combined with combined with weather variability (lc,2%h,w) will result in the population size stabilizing at approximately 2000 animals.

Sheep.--

A simulated 5 year wolf reduction causes the sheep population to increase, on average, by approximately 150 animals over 25 years [Fig. 3.8(c): lc]. Harvesting 8 sheep per year reduces the benefits of lethal wolf control, and the population increases on average by about 50 sheep (lc, 8h). The model projects that an annual harvest of 12 sheep will cause the population to decline, even when lethal wolf control is applied (lc,12h).

Lethal wolf control, high ungulate harvest

Figure 3.9 shows the effects of a 5 year wolf reduction combined with high levels of moose and caribou harvest.

Caribou.--

Following lethal wolf control, a constant annual harvest of 5% of the herd, with or without weather variability (a), nullifies any benefits from wolf reduction, and the population declines beyond recovery (lc,5%h; lc,5%h, w).

Moose.--

With lethal wolf reduction and a high harvest rate, moose will initially increase following lethal wolf control, but then will decline steadily with wolf population recovery [(b): lc, 5%h; lc 5%h, w].

Wolf fertility control

Simulation results of the effects of wolf fertility control upon wolves, caribou, moose, and sheep are depicted in Figures 3.10 and 3.11.

Wolves.--

When fertility control is applied to the original pack distribution and maintained throughout the simulation (Fig. 3.10), the pack size distribution shifts strongly towards small packs. When all small packs in the study area are sterilized (1,1fc), numbers are stable at 15 small (a), 2-3 medium (b), and 4 large packs (c). When low levels of fertility control are applied (60% of all packs: 0.6,0.6fc), small and medium pack numbers fluctuate periodically (a),(b). However, the maximum number of large packs at any level of fertility control is 5 (c).

Caribou.--

Figure 3.11 (a) shows that, in the model, no level of wolf fertility control alone can cause an increase in caribou numbers when the herd numbers were as low as they were in Aishihik in 1992 (700 animals). However, sterilizing small packs increases the rate at which a herd of 1800 or more will increase towards its carrying capacity of 20,000 animals (ci 1800, 1 fc).

Moose.--

Applying wolf fertility control increases the moose population in the model simulations [(b): 0.6fc; 0.8fc; 1fc), but increases are marginal and tentative when weather variability is considered (0.6fc, w) unless all small packs are sterilized (1fc,w).

Sheep.--

On average, sheep numbers in the model also increase when wolf fertility control is applied [Fig. 3.11(c): 0.6,0.8,1 fc). However, benefits to sheep decrease as the level of fertility control increases.

Lethal wolf control followed by fertility control

Figures 3.12 and 3.13 show the effects of combining an initial 5 years of lethal wolf control with long term fertility control. This sort of management strategy is considered feast0le for other canids (Vertebrate Biocontrol Centre, Australia).

Wolves.--

Five years of wolf control combined with fertility control in the 4th year of wolf reduction causes an initial reduction in pack number, followed by stable long term pack size densities [Fig. 3.12 (a),(b),(c)]. When 80% of all small packs are sterilized following wolf control (0.8,0.8), small, medium and large pack numbers stabilize at 10 (a), 6-7 (b), and 3 (c), respectively. Following lethal control, all levels of fertility control for both caribou- and moose- hunting wolves result in a maximum of 3 large packs after 25 years (c).

<u>Caribou</u>.--

Combining wolf reduction with any level of wolf fertility control above 50% will allow the herd to increase to at least 14,000 animals after 25 years [Fig. 3.13(a): lc,0.6/1 fc]. Adding the effects of weather variability slows the rate of increase and lowers the equilibrium herd size when only 60% of small pairs are sterilized (lc,0.6 fc,w), but in none of the simulations does the herd decline.

<u>Moose</u>.--

Applying lethal wolf control and any level of fertility control from the 4th year of wolf reduction causes the model moose population to stabilize between 2600-2950 animals, as shown in Figure 3.13 (b). These effects are not affected by weather variability.

<u>Sheep</u>.--

Figure 3.13 (c) shows that, following wolf reduction, sterilizing 60% of caribou- and moose- hunting small packs results in a decreasing sheep population (lc,0.6 fc). Sterilizing all small packs following lethal controls results in a modest increase in sheep numbers (lc,1fc).

Lethal and fertility control, ungulate harvest

The effects of harvesting ungulates following wolf lethal and fertility control are shown in Figure 3.14 and 3.15.

<u>Caribou</u>.--

In the model, a harvest rate of 2% of the caribou per year is sustainable when weather variability is considered, lethal control is applied, and all of the small packs on the calving grounds are sterilized [Fig. 3.14(a): (lc, 1fc,w,2%h)]. Similarly, a 5% harvest rate may be sustained under the same conditions [Fig. 3.15 (a): (lc,1fc,5%h, w)], but the population never exceeds 4000 animals, and the herd declines beyond recovery in 16% of the simulations.

<u>Moose</u>.--

For moose, adding levels of harvest of 2% [Fig. 3.14 (b)] and 5% [Fig. 3.15(b)] reduces the benefits of intensive wolf management in the long term. After 25 years, the model moose population will decrease at a harvest rate of 5% unless all of the small packs are sterilized and weather variability is not considered (lc,1fc,5%h).

<u>Sheep</u>.--

Figure 3.14 (c) shows that, regardless of intensive wolf management, an annual harvest of 8 or 12 sheep will cause the population to decline by approximately 50% over 25 years.

Table 3.2. Key to figure legends. Symbols used to abbreviate variable names are

explained.

Variable	Symbol	Meaning
Initial moose population size	mi	Moose population size input for Year 1
Initial caribou population size	ci	Caribou population size input for Year 1
No Management	nm	No active wolf management occurs. No human harvest of ungulates.
Lethal Control	lc	Wolf packs removed from Year 2 to Year 6
Fertility Control	(a,b) fc	Proportion of all small-sized wolf packs to be sterilized each year. Begins in Year 5 when combined with lethal control, begins in Year 1 when applied alone. "a" is the proportion of small-sized packs which hunt caribou, "b" is the proportion of small-sized packs which hunt moose
Human Harvest of Ungulates	h	Percentage (%) of adults harvested from the moose and caribou populations, removed over winter. A fixed number of sheep are removed each year (ie.12h=12 sheep/year)
Weather	w	Occurs randomly, acts to reduce caribou (30%), and moose (25%) calf production in a given year

Figure 3.4 Validation of the model prey population dynamics. The population estimates of caribou, moose and Dall sheep populations in the study area prior to wolf control (actual) were compared to the predicted changes in population size based on the simulation model (model). These are baseline simulations which assume no wolf control and historic levels of harvest of prey populations by hunters.

Caribou
Model Validation

(a)
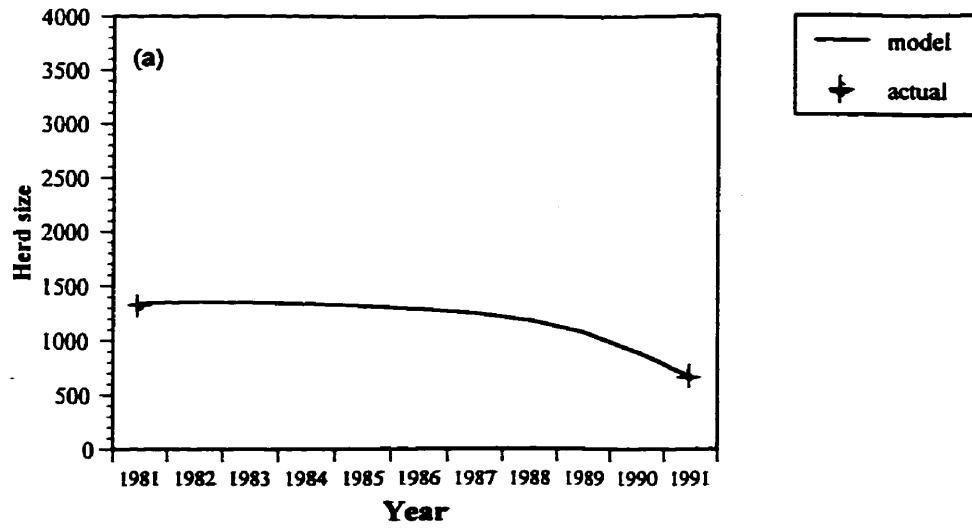
Moose
Model Validation

(b)
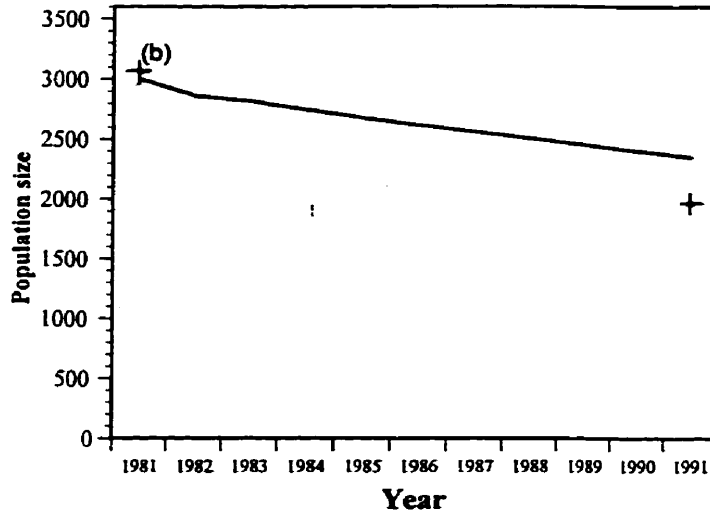
Sheep
Model Validation

(c)
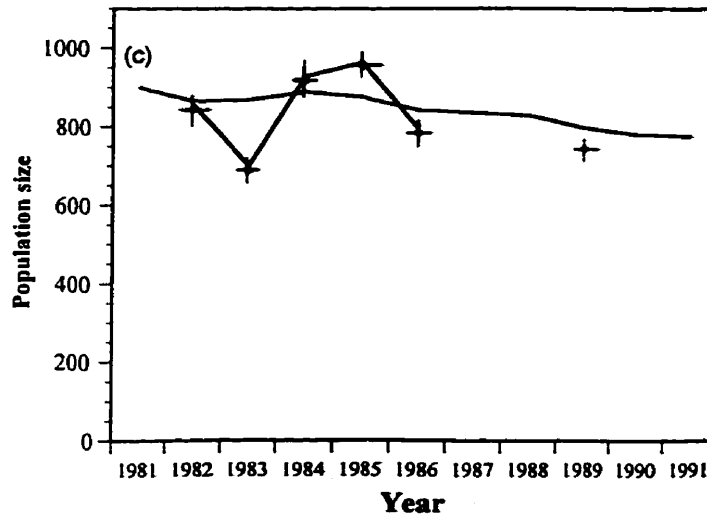
Figure 3.5 Simulation of the total number and distribution of wolf packs by size without

active wolf management (nm). All parameters and initial population sizes set to

observed 1992 levels.

Small-sized Wolf Packs
No Management
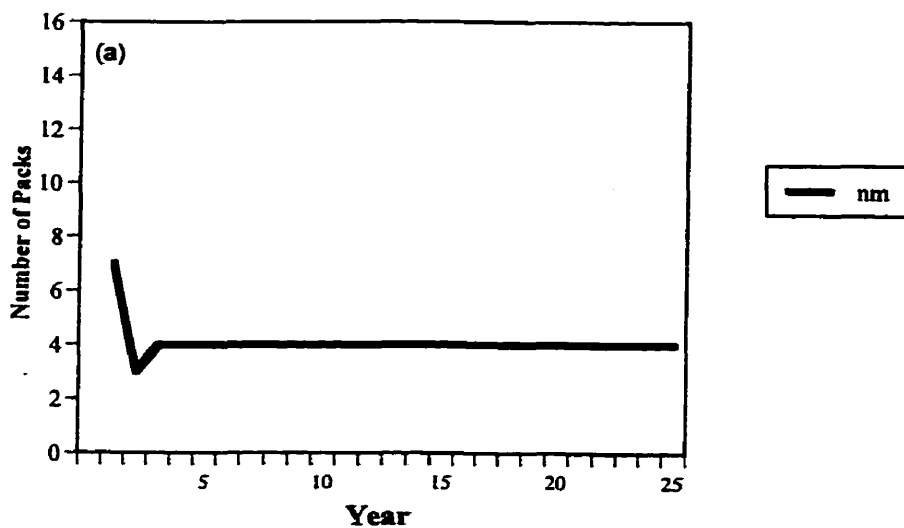
Medium-sized Wolf Packs
No Management
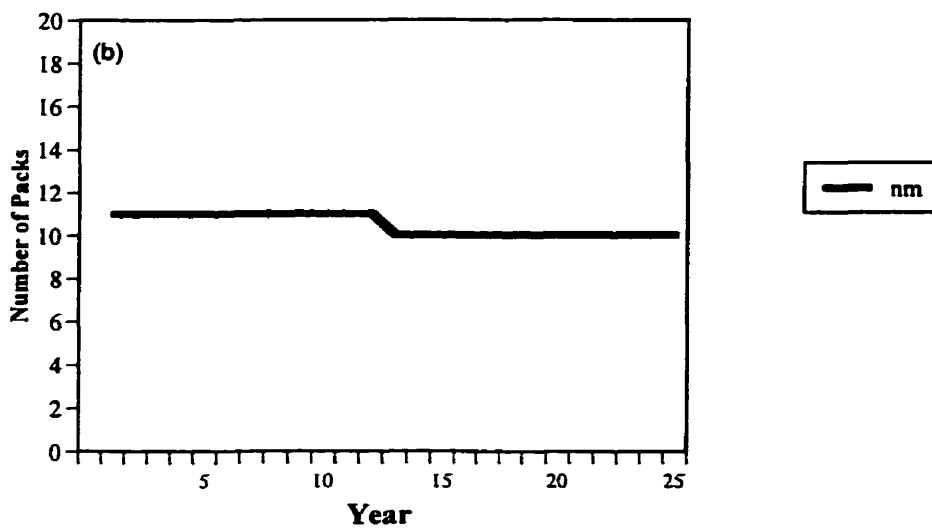
Large-Sized Wolf Packs
No Management
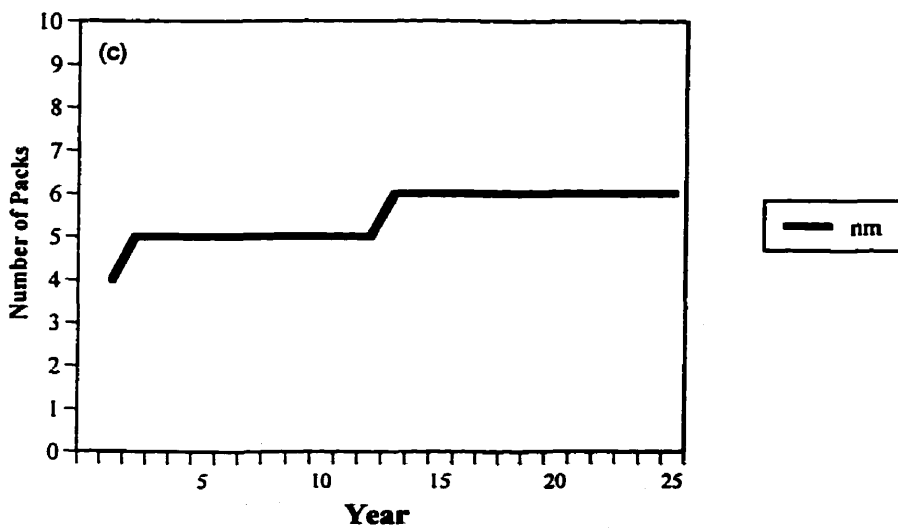
Figure 3.6 Simulation of the changes in prey population size under various simulations without active wolf management (nm). (a) The threshold initial caribou population size (ci), below which the population declines to extinction is 1835 (ci 750, ci 1835). (b) The threshold initial moose population size, below which the population declines to extinction is 1900 (mi 1900, mi 1910). The stability of this threshold population size is influenced by weather (w), which randomly reduces caribou and moose recruitment in a given year. (c) Outcome of ten model runs (weather variation is always incorporated) and the mean (solid line) of Dall sheep population dynamics. All other parameters set to observed 1992 levels.

Caribou
No Management

(a)

Legend:
- nm, ci 750
- nm, ci 1835

Moose
No Management

(b)

Legend:
- nm, mi 1910
- nm
- nm, w
- nm, mi 1900

Sheep
No Management

(c)

Legend:
- model runs (1-10)
- mean of model runs
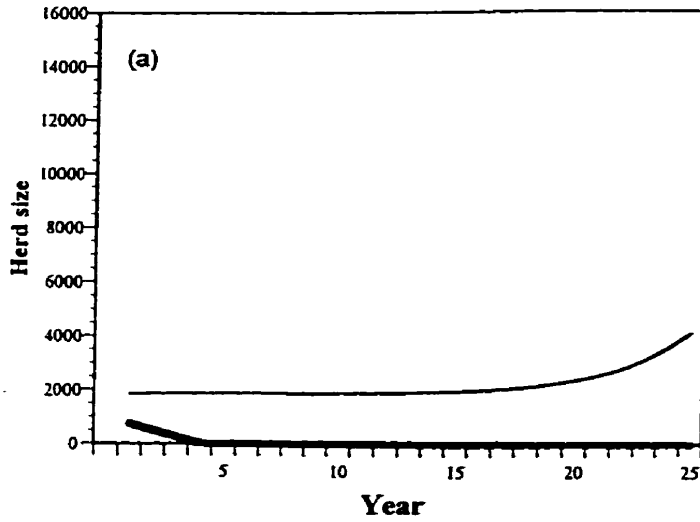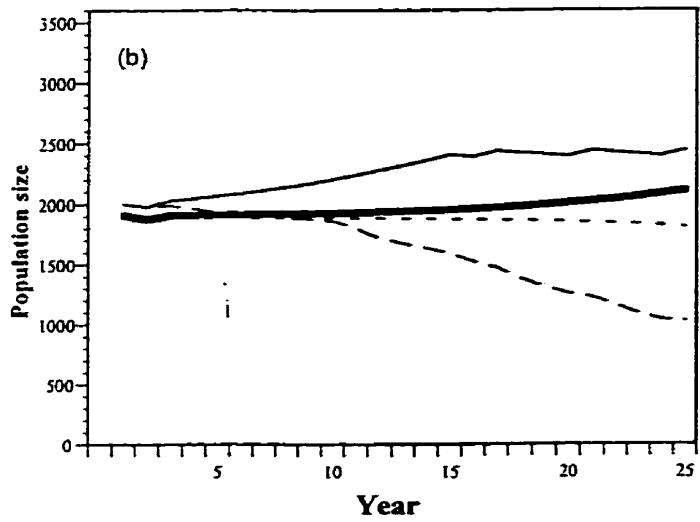
Figure 3.7 Simulation of the total number and distribution of wolf packs by size with

five years (Years 2-6) of intensive lethal control (lc), as in the Aishihik wolf reduction

program. All other parameters and initial population sizes set to observed 1992 levels.

Small-sized Wolf Packs
Lethal Control

(a)

Medium-sized Wolf Packs
Lethal Control

(b)

Large-sized Wolf Packs
Lethal Control

(c)
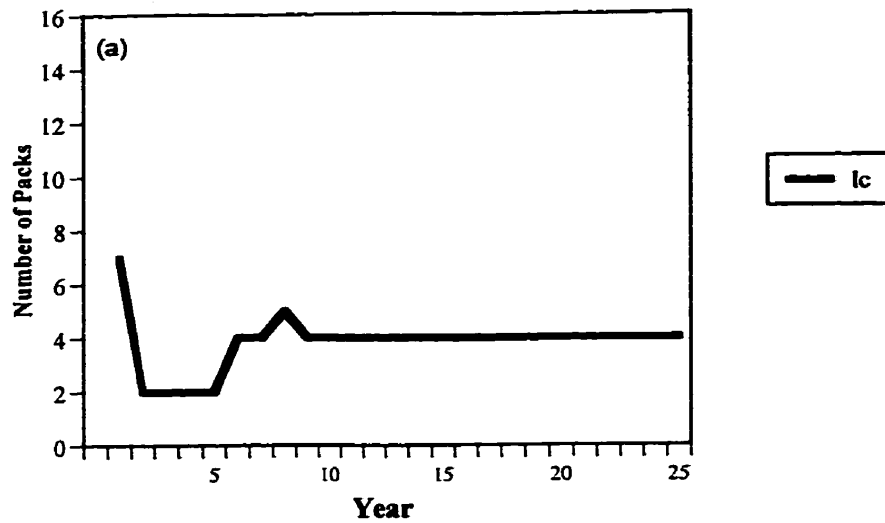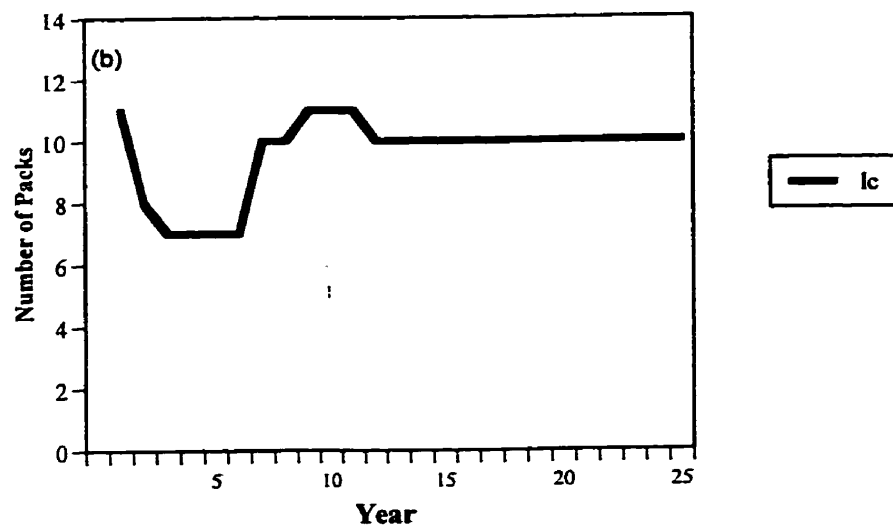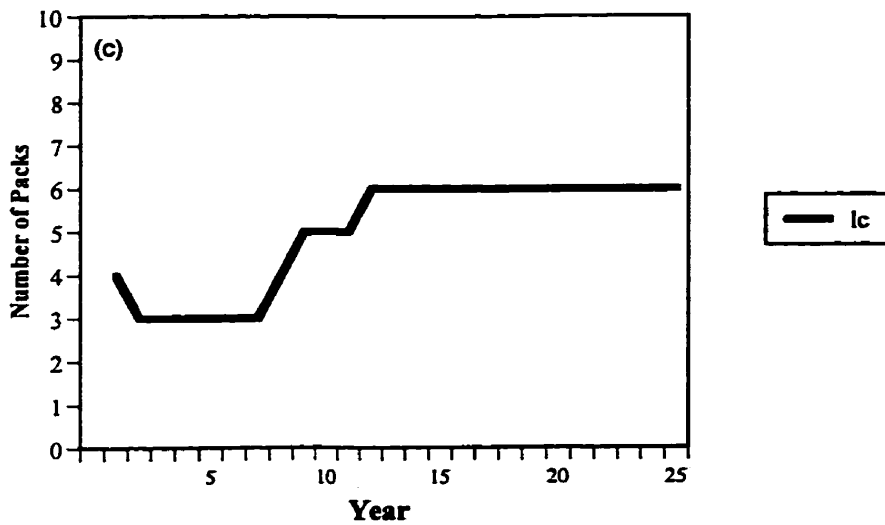
Figure 3.8 Simulation of the changes in prey population size under various simulations

with five years of wolf lethal control (lc: Years 2-6). Human harvest (h) is absent or low

starting in Year 7 (2% h: 2% of winter adult populations removed per year for caribou

and moose; 8h/12h: 8 or 12 individuals removed per year for sheep). Weather (w)

randomly reduces caribou and sheep recruitment in a given year. (a) Caribou, (b) Moose,

and (c) Dall sheep. All other parameters and initial population sizes set to observed 1992

levels.

Caribou
Lethal Control, Low or No Harvest

(a)

Legend:
- lc, w
- lc
- lc, 2% h
- lc, 2% h, w

Moose
Lethal Control, Low or No Harvest

(b)

Legend:
- lc, 2% h, w
- lc, 2% h
- lc
- lc, w

Sheep
Lethal Control, Harvest

(c)

Legend:
- lc, 12 h
- lc, 8 h
- lc

Figure 3.9 Simulation of the changes in prey population size under various simulations

with five years of wolf lethal control (lc: Years 2-6). Human harvest (h) is high (5% of

winter adult populations removed per year) starting in Year 7. Weather (w) randomly

reduces recruitment in a given year. (a) Caribou and (b) Moose. All other parameters

and initial population sizes set to observed 1992 levels.

Caribou
Lethal Control, High Harvest

(a)

Legend:
- lc, 5% h
- lc, 5%h , w

X-axis: Year
Y-axis: Herd size

Moose
Lethal Control, High Harvest

(b)

Legend:
- lc, 5% h
- lc, 5% h, w

X-axis: Year
Y-axis: Population size

Figure 3.10 Simulation of the total number and distribution of wolf packs by size with different levels of fertility control (proportion of small-sized packs affected in each sub-population) applied throughout the simulation (fc). For example, (1, 0.8 fc) indicates that 100% of caribou-hunting small packs and 80% of moose-hunting small packs will be sterilized each year. All other parameters and initial population sizes set to observed 1992 levels.

Small-sized Wolf Packs
Fertility Control

(a)

Legend:
- 0.6, 0.6 fc
- 1.0, 0.8 fc
- 0.8, 0.8 fc
- 1.0, 0.8 fc
- 1.0, 1.0 fc

Medium-sized Wolf Packs
Fertility Control

(b)

Legend:
- 1.0, 0.8 fc
- 0.6, 0.6 fc
- 0.8, 0.8 fc
- 1.0, 1.0 fc

Large-sized Wolf Packs
Fertility Control

(c)

Legend:
- 0.8, 0.8 fc
- 1.0, 0.8 fc
- 0.6, 0.0 fc
- 1.0, 0.8 fc
- 0.6, 0.6 fc
- 1.0, 1.0 fc
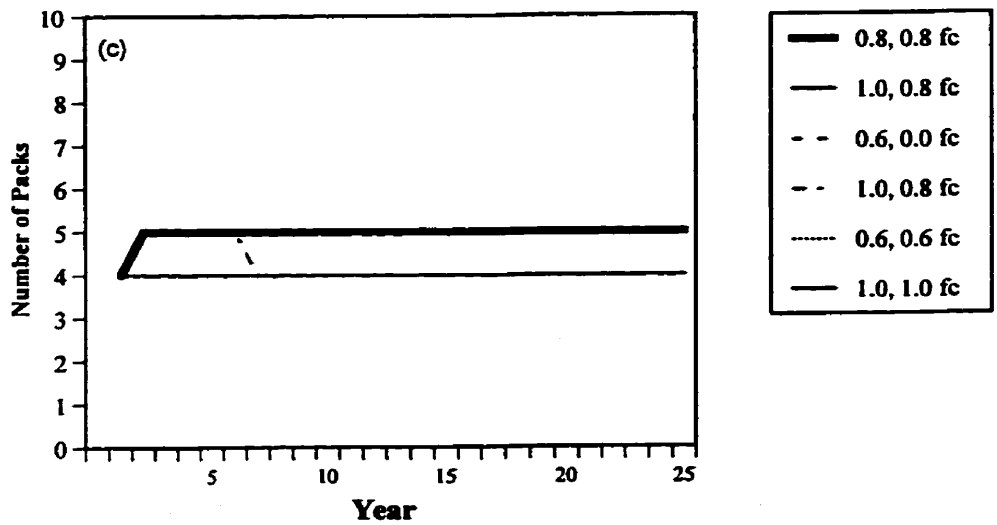
Figure 3.11 Simulation of the changes in prey population size under various simulations

with wolf fertility control applied throughout the simulation with no human harvest of

ungulates. Levels of fertility control are represented as the proportion of small-sized

packs that are sterilized every year. Weather (w) randomly reduces caribou and moose

recruitment in a given year. (a) Caribou: initial population size is 750 animals (ci 750) or

1800 animals (ci 1800), (b) Moose, and (c) Dall sheep. All other parameters and initial

population sizes set to observed 1992 levels.

Caribou
Fertility Control

(a)

Legend:
- 1.0 fc, ci 750
- 1.0 fc, ci 1800

Moose
Fertility Control

(b)

Legend:
- 1.0 fc
- 1.0 fc, w
- 0.6 fc, w
- 0.8 fc, w
- 0.8 fc

Sheep
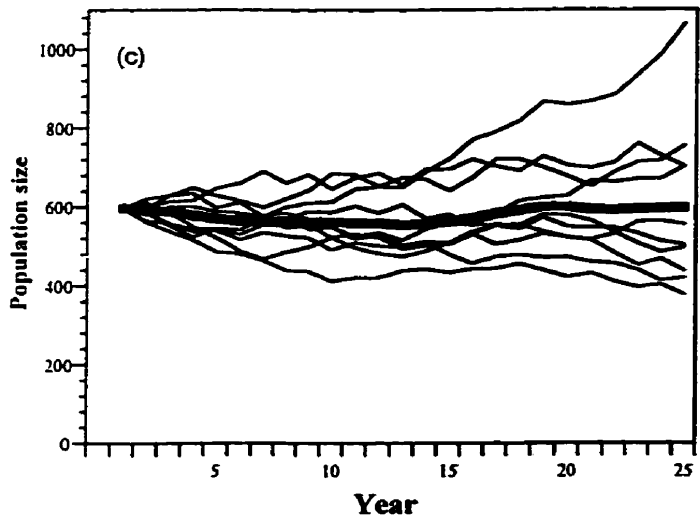**Fertility Control**

(c)

Legend:
- 1.0 fc
- 0.6 fc
- 0.8 fc
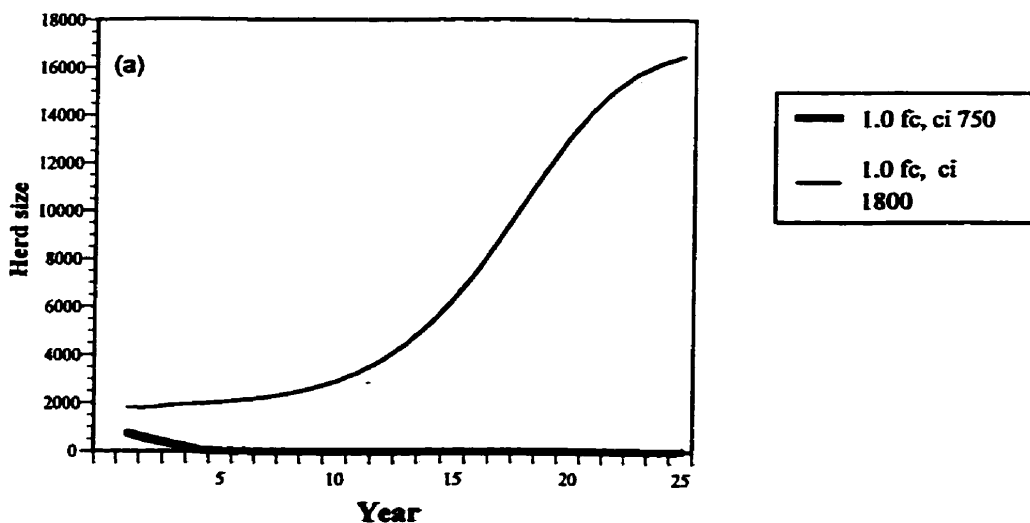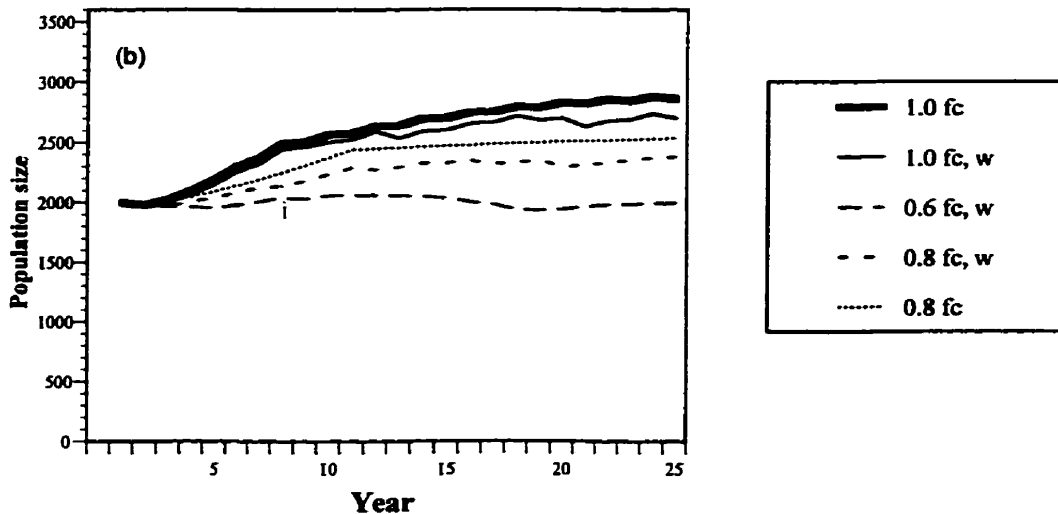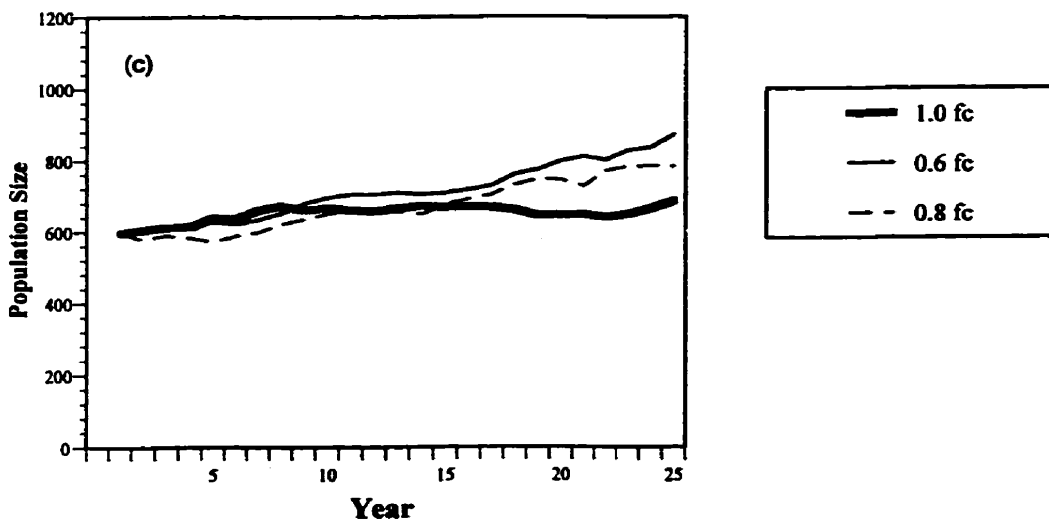
**Figure 3.12** Simulation of the total number and distribution of wolf packs by size with

five years (Years 2-6) of lethal control (lc) followed by different levels of fertility control

(proportion of small packs affected in each sub-population) applied from Year 5 (fc).

Figure legend notation as in Figure 3.10. All other parameters and initial population sizes

set to observed 1992 levels.

Small-sized Wolf Packs
Lethal Control, Fertility Control

(a)

Legend:
- lc, 0.6, 0.0 fc
- lc, 1.0, 0.0 fc
- lc, 0.8, 0.8 fc
- lc, 0.8, 0.4 fc
- lc, 0.8, 0.0 fc

Medium-sized Wolf Packs
Lethal Control, Fertility Control

(b)

Legend:
- lc, 0.6, 0.0 fc
- lc, 1.0, 0.0 fc
- lc, 0.8, 0.8 fc
- lc, 0.8, 0.4 fc
- lc, 0.8, 0.0 fc

Large-Sized Wolf Packs
Lethal Control, Fertility Control

(c)

Legend:
- lc, 0.6, 0.0 fc
- lc, 1.0, 0.0 fc
- lc, 0.8, 0.8 fc
- lc, 0.8, 0.4 fc
- lc, 0.8, 0.0 fc
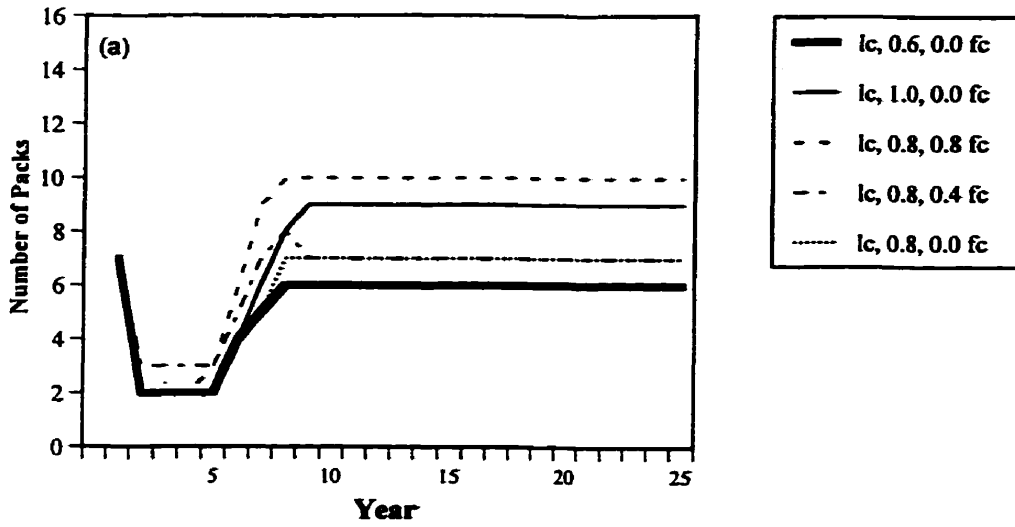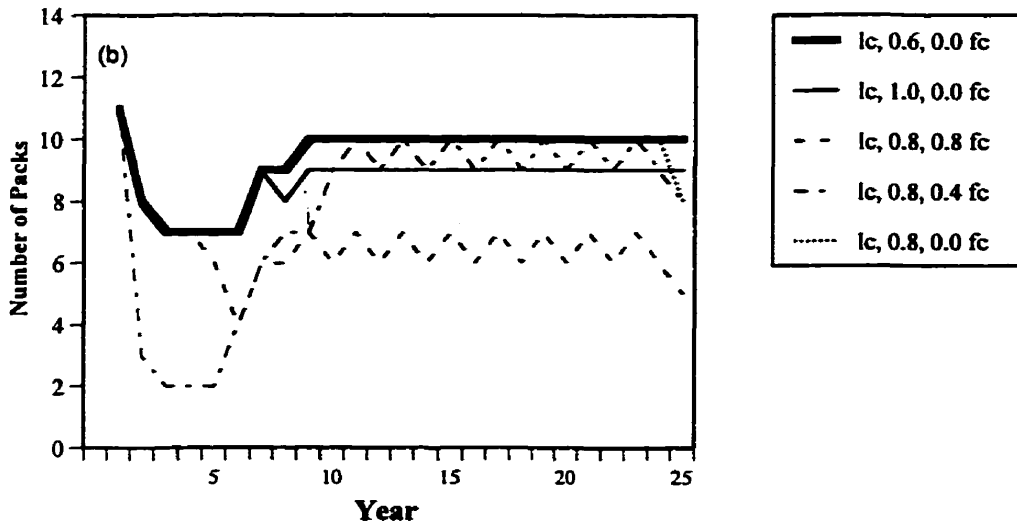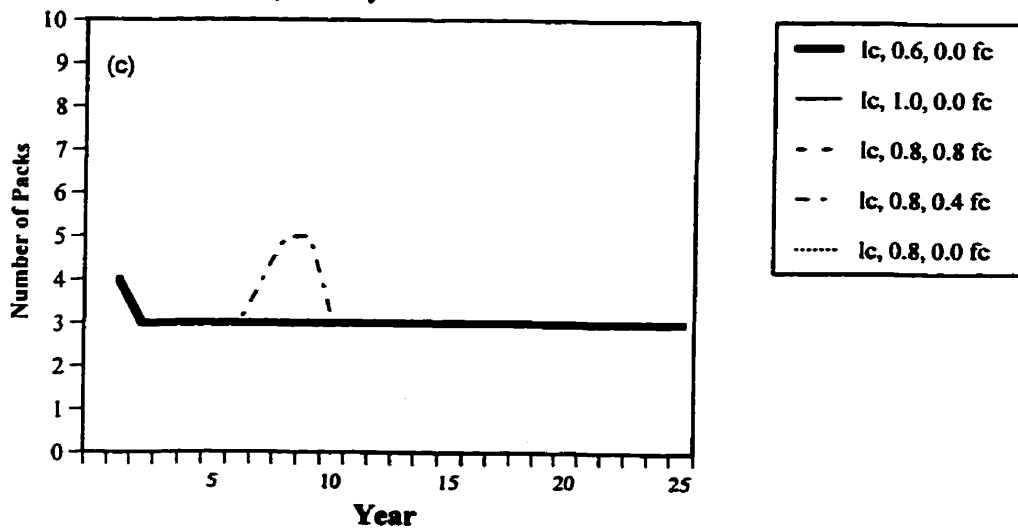
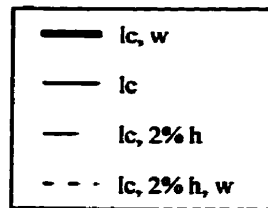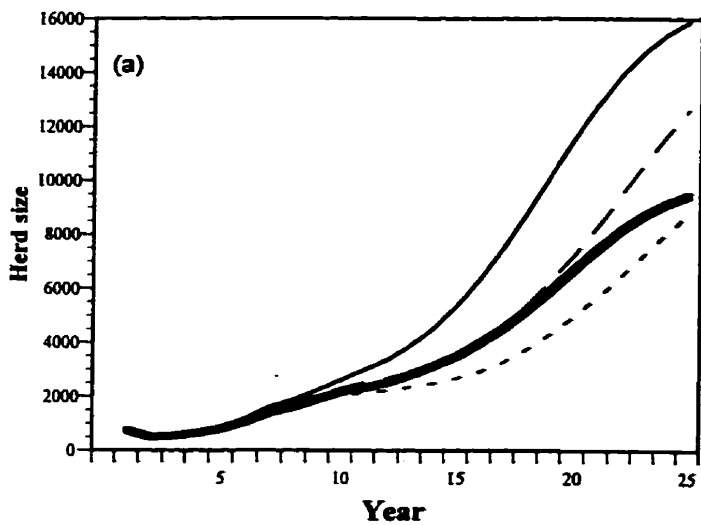**Figure 3.13** Simulation of the changes in prey population size under various simulations with five years of wolf lethal control (lc: Years 2-6), followed by different levels of fertility control (proportion of small-sized packs affected) applied from Year 5 (fc). No human harvest of ungulates. Weather (w) randomly reduces caribou and moose recruitment in a given year. (a) Caribou, (b) Moose, and (c) Dall sheep. All other parameters and initial population sizes set to observed 1992 levels.

Caribou
Lethal Control, Fertility Control

(a)

Herd size / Year

Legend:
- lc, 1.0 fc
- lc, 1.0 fc, w
- lc, 0.6 fc
- lc, 0.6 fc, w

Moose
Lethal Control, Fertility Control

(b)

Population size / Year

Legend:
- lc, 1.0 fc, w
- lc, 0.6 fc
- lc, 0.6 fc, w
- lc, 1.0 fc

Sheep
Lethal Control, Fertility Control

(c)

Population Size / Year

Legend:
- lc, 0.6 fc
- lc, 1.0 fc
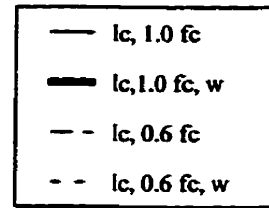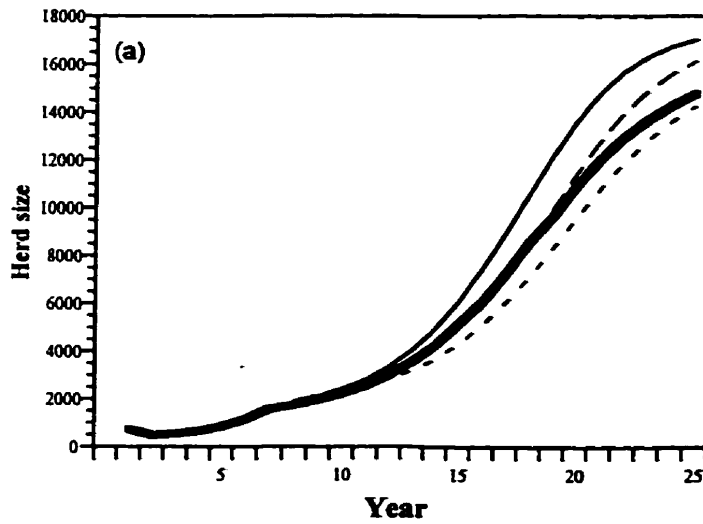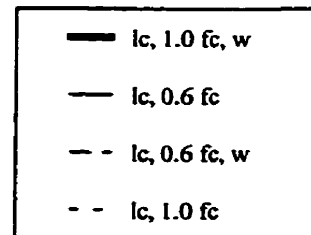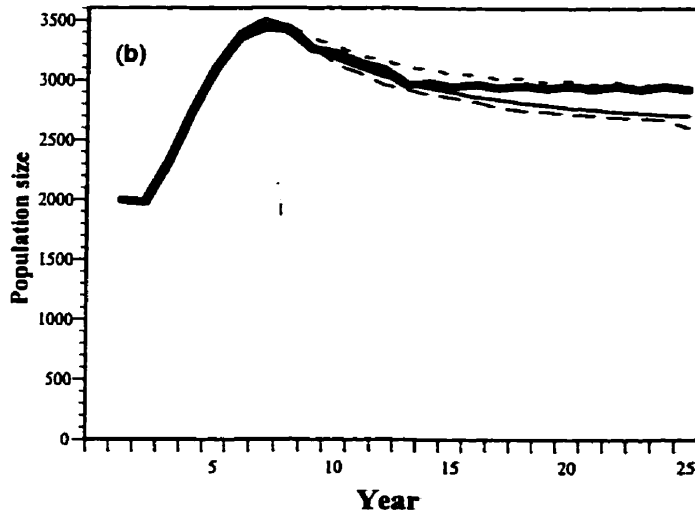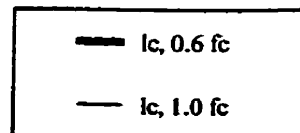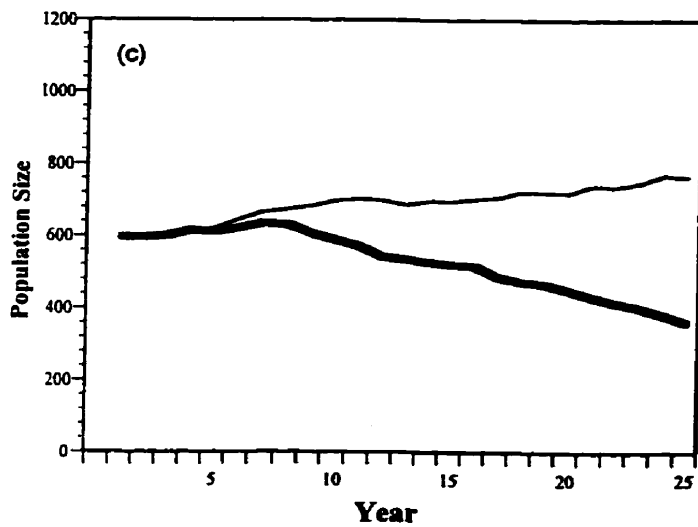
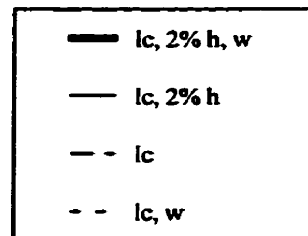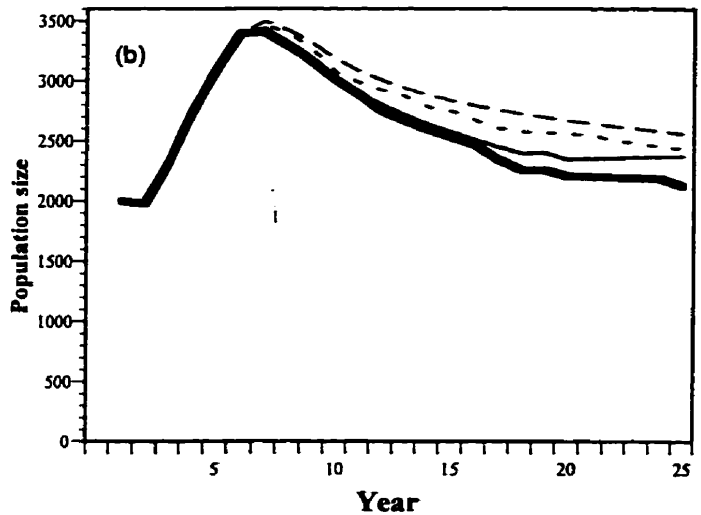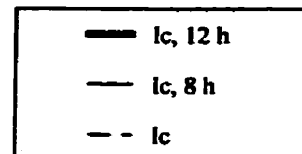**Figure 3.14** Simulation of the changes in prey population size under various simulations

with five years of wolf lethal control (lc: years 2-6), followed by different levels of

fertility control (proportion of all packs affected) applied from Year 5 (fc), and low levels

of human harvest of ungulates starting in Year 7 (2% of adult winter populations per year

for caribou and moose, and 8 or 12 individuals per year for sheep). Weather (w) random

reduces caribou and moose recruitment in a given year. (a) Caribou, (b) Moose, and (c)

Dall sheep. All other parameters and initial population sizes set to observed 1992 levels.

Caribou
Lethal Control, Fertility Control, Low Harvest

(a)

Legend:
- lc, 1.0 fc, 2%h
- lc, 1.0 fc, 2%h, w
- lc, 0.6 fc, 2%h, w

Moose
Lethal Control, Fertility Control, Low Harvest

(b)

Legend:
- lc, 1.0 fc, 2%h
- lc, 1.0 fc, 2%h, w
- lc, 0.6 fc, 2%h, w
- lc, 0.6 fc, 2%h

Sheep
Fertility Control, Harvest

(c)

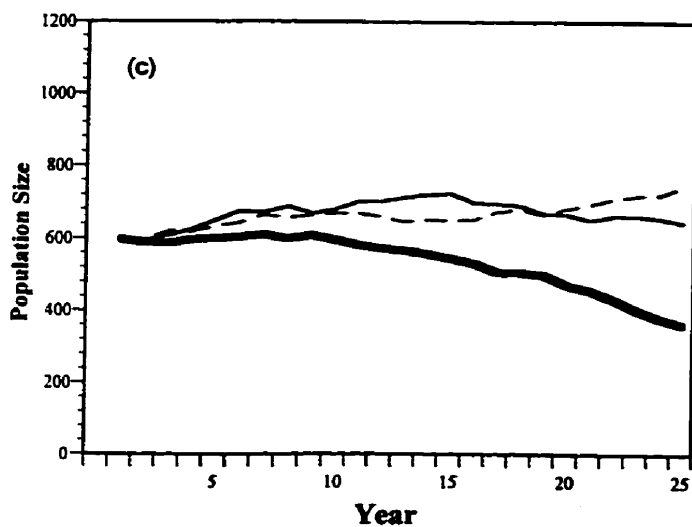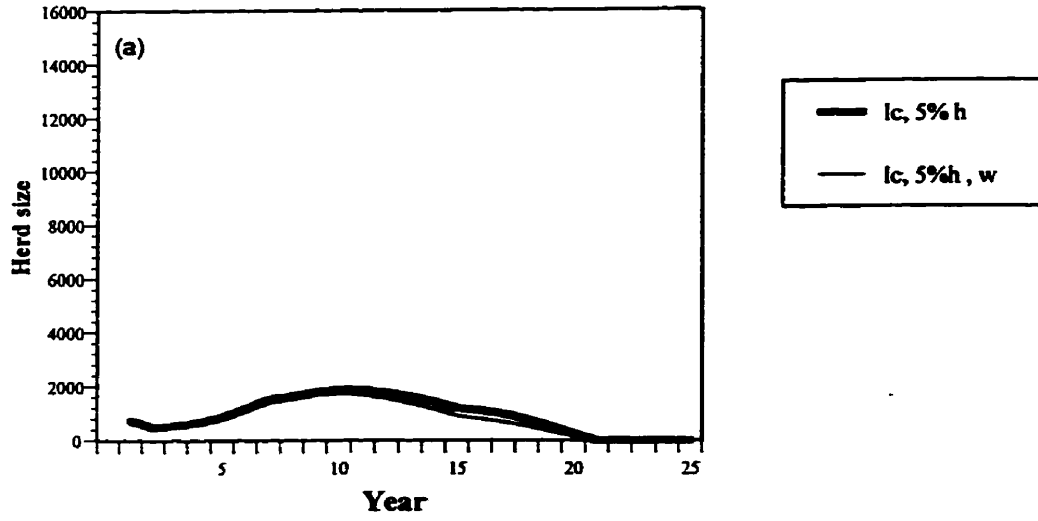Legend:
- lc, 1.0 fc, 8 h
- lc, 1.0 fc, 12 h
- lc, 0.6 fc, 12 h
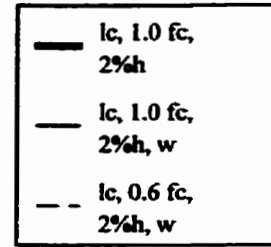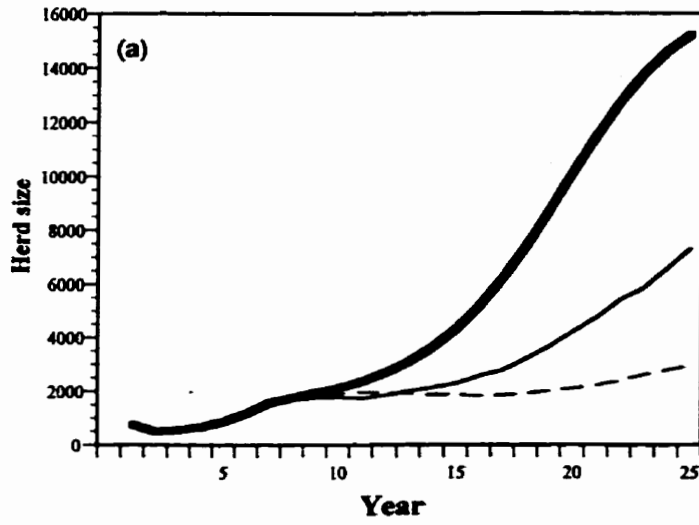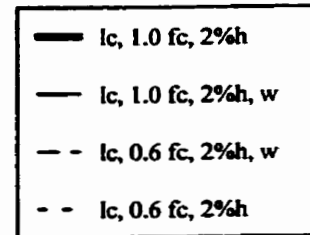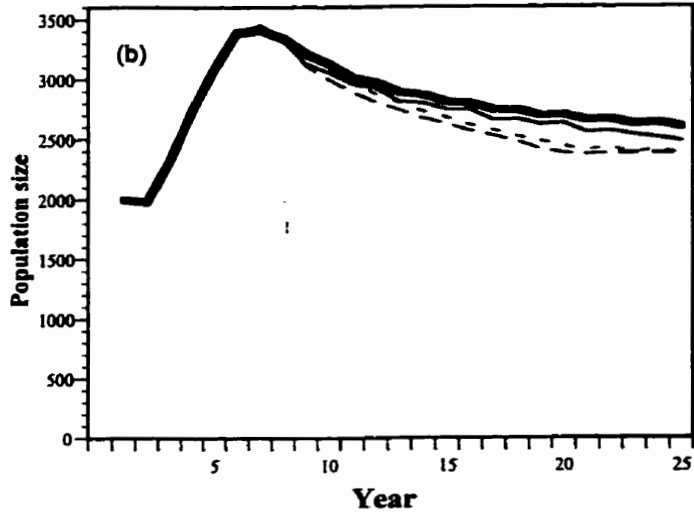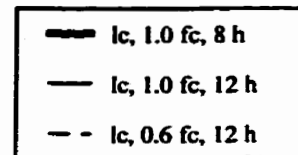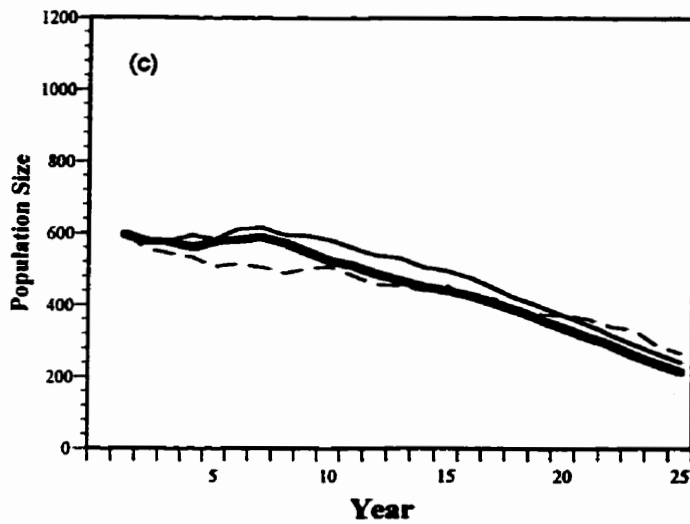
Figure 3.15 Simulation of the changes in prey population size under various simulations with five years of wolf lethal control (lc: Years 2-6), followed by different levels of fertility control (proportion of small-sized packs sterilized each year) applied from Year 5 (fc). High levels of human harvest of ungulates (5% of winter adult populations per year), starting in Year 7. (a) Caribou, and (b) Moose. All other parameters and initial population sizes set to observed 1992 levels.
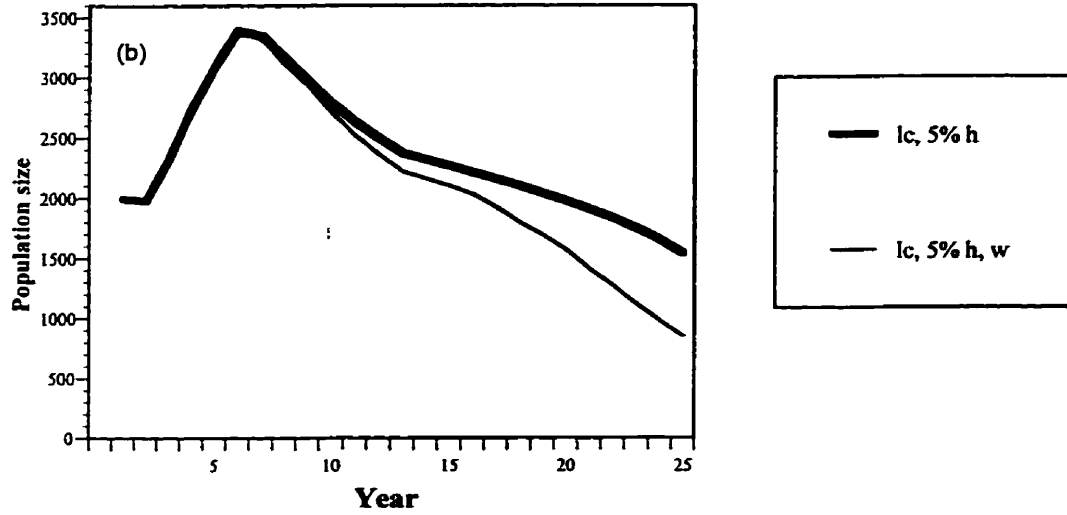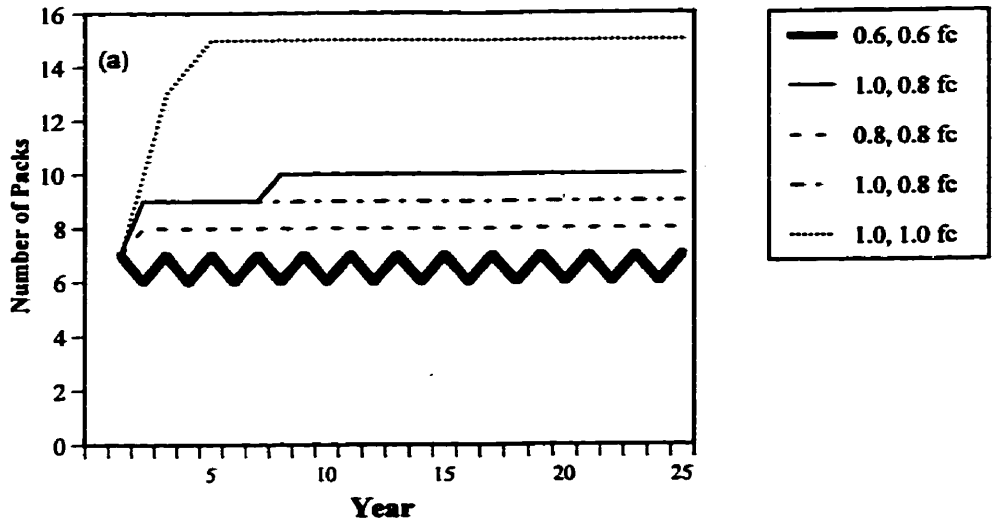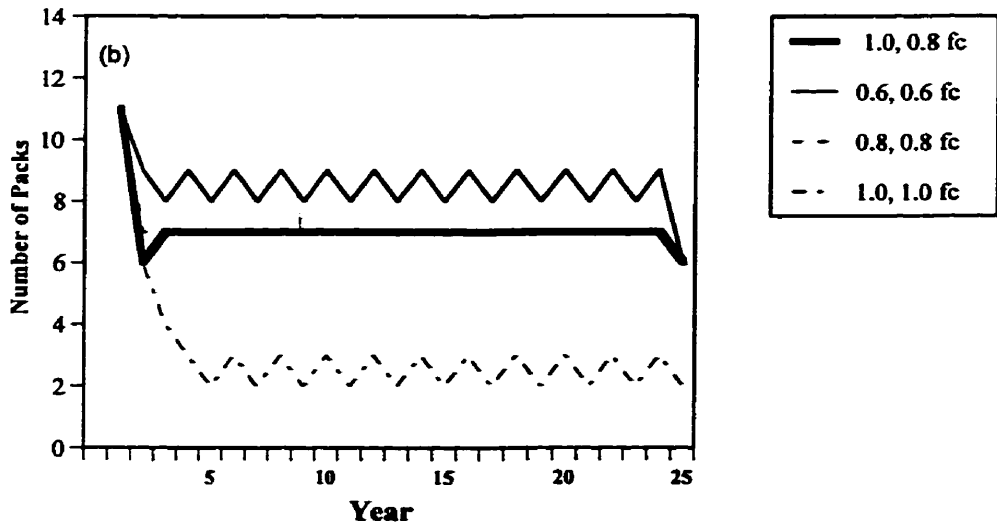
Caribou
Lethal Control, Fertility Control, High Harvest

(a)

Legend:
- lc, 1.0 fc, 5%h
- lc, 1.0 fc, 5%h, w
- lc, 0.6 fc, 5%h
- lc, 0.6 fc, 5%h, w

Moose
Lethal Control, Fertility Control, High Harvest

(b)

Legend:
- lc, 1.0 fc, 5%h, w
- lc, 0.6 fc, 5%h
- lc, 0.6 fc, 5%h, w
- lc, 1.0 fc, 5%h
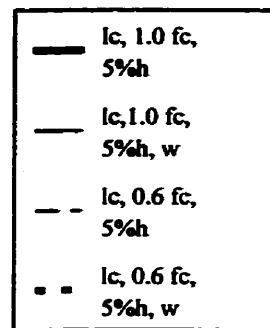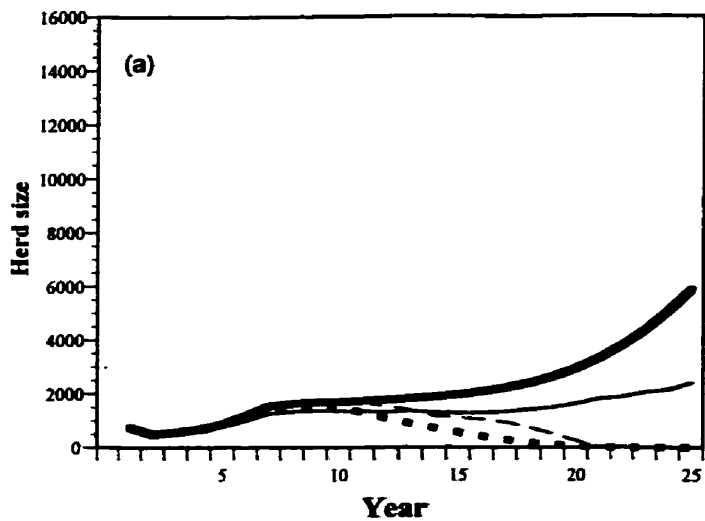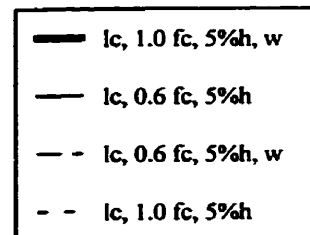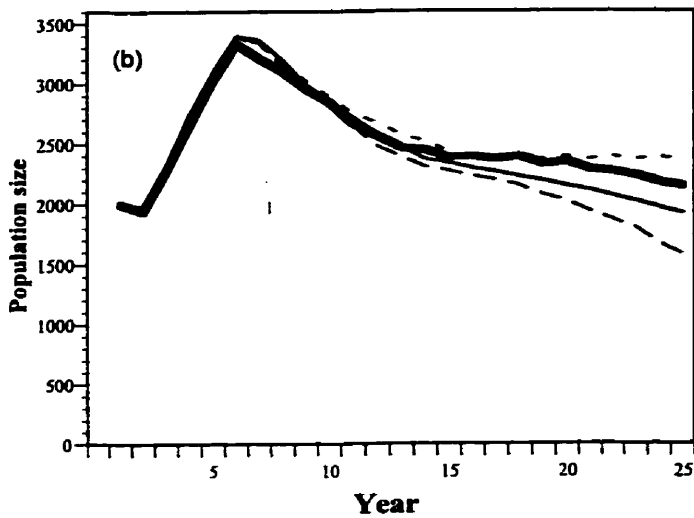
DISCUSSION

The model outcomes vary dramatically depending upon the wolf management strategy, ungulate harvest level, and weather variability. However, there are several consistent patterns that emerge with each management strategy.

No management

The 'no management' scenario implies that wolves and their prey are naturally regulated and that no harvest or other human interference occurs. This is an important simulation, because it demonstrates the mechanisms of the model, and lends insight into wolf-prey interactions and the population dynamics of the individual prey populations. Yet there are likely few, if any, examples of naturally regulated pristine wolf-prey systems in nature (Peterson and Page 1987, Van Ballenberghe 1987, Van Ballenberghe and Ballard 1994, Crête and Manseau 1996). This scenario, then, is not considered to be a realistic management alternative, but a necessary modelling exercise.

In the model 'no management' simulations, moose appear to be regulated by wolves at a low equilibrium population size between 2000 and 2400 animals. Increases in moose density are matched by corresponding increases in wolf pack size and wolf pack number. Even below the threshold of 1900 animals, moose decrease very slowly. Above the threshold, moose are not likely to decline as long as they are lightly harvested.

For caribou, however, wolf reduction is required to prevent a rapid decline below a threshold of 1800 animals. There does not appear to be a stable, equilibrium density for caribou. Recruitment is either sufficient to compensate for adult mortality, thus allowing

caribou to increase, or else the herd will decline steadily. This may be a realistic trend. Bergerud and Elliot (1986) observed negative recruitment for caribou herds in British Columbia, and cited 5 studies from other herds where moderate to high wolf numbers were correlated to caribou recruitment below 10%. They also suggested that stable population sizes do not generally occur in caribou, due to rapid changes in mortality and recruitment rates which can result from relatively small changes in predator abundance.

The Dall sheep population, on average, remains relatively stable with no harvest and no wolf management. Even when the stochastic nature of yearling recruitment is considered, the low level of wolf predation should not have an effect on the sheep population. Indeed, there is very little evidence from the literature to suggest that wolf predation has a significant effect on sheep calf survival and population dynamics (Burles and Hoefs 1984, Sumanik 1987, Boyce 1995, Scotten 1997). Scotten (1997) reported that in the Central Alaska Ranges, wolves killed only 1 lamb out of 23 known mortalities. He reported that coyotes and eagles were responsible for the majority of lamb deaths due to predation.

Lethal control

The model projections show that lethal wolf control can dramatically increase calf recruitment and initiate rapid population growth in moose and caribou. These effects, however, are short lived. Moose may increase from 2000 animals to 3500 during wolf control, but immediately begin to decline as the wolf population begins to recover. This

return to low moose density following wolf reduction suggests wolf regulation of moose at low densities.

For caribou, removing large packs from the caribou calving grounds enables the herd to increase to near the critical threshold density where they can continue to increase without further management. This suggests that the caribou population is limited by wolf predation on calves. Indeed, cow to calf ratios dramatically increased in both the Finlayson and Aishihik herds when lethal wolf control was applied. However, the results from the model suggest that if severe weather causes poor recruitment before this threshold is reached and after the wolf population has recovered, the herd will decline. Thus 5 years of wolf control is not sufficient to guarantee long term herd growth.

Lethal control causes a small average increase in the sheep population, but the population size after 25 years does not exceed population levels reached in several of the simulations with no wolf management. Due to the low level of wolf predation upon sheep, I expected that wolf reduction would have a minimal impact on the sheep population. Indeed, a recent evaluation of the Aishihik wolf control program concluded that it did not affect the sheep population (YTG unpubl. data).

Fertility control

Fertility control changes the pack size distribution of wolves from medium- to small-sized packs. Unless preceded by pack removal, fertility control will not reduce the number of large-sized packs in the area. When caribou populations are below critical threshold densities, they will continue to decline until most wolf predation upon calves is

reduced. It is interesting to note that increasing the level of fertility control (and thus increasing the number small-sized packs in the area) decreases the average amount by which the sheep population will increase. This is because, in the model, only lone wolves and small- and medium-sized packs hunt sheep. By increasing the number of small sized packs, the number of sheep killed by wolves increases. This may be an artifact of the structure of the model, but it is not entirely unrealistic. Highly exploited or managed wolf populations are characterized by pack instability (Haber 1996), and the average pack size in recovering wolf populations is generally low (Hayes 1995). Under these conditions there may be more small-sized packs and more lone wolves. These wolves may be more likely to hunt sheep opportunistically, whereas larger wolf packs could not likely be supported by sheep alone (Sumanik 1987). It is possible that manipulating wolf populations to increase caribou and moose may decrease sheep survival.

My model shows that, combined with lethal control, fertility control can be useful. For caribou, fertility control appears to allow the herd enough time to increase past the threshold density where wolf predation can remove most of the recruitment. For both moose and caribou, fertility control combined with lethal control seems to "buffer" the population from the effects caused by a year of poor recruitment due to weather. With a high level of fertility control, the moose population does not return to a low equilibrium between 2000-2400 following wolf mortality control, but rather stabilizes near 3000 animals. At first glance, this appears to be a higher equilibrium density, but it is not what Messier's (1994, 1995, Chapter One) predation-food model predicts. If the higher moose density was determined by carrying capacity (mk), moose would stabilize at 5000

animals, the mk value in the model. Rather, it appears that the model moose population is ultimately limited by moose reproductive capacity. Another explanation is that the low population was below the low density equilibrium caused by the lag effect of wolves in response to declining prey density (Peterson and Page 1983). It is also possible that wolves were not reduced for a long enough period to allow moose to increase to a high population density which would allow them to escape regulation by predators.

It is less clear what the effects of combining the two techniques are for sheep. A moderate increase is observed when all small-sized packs are sterilized following wolf control, but sterilizing 60% of the small packs causes a definite decline. These results may simply demonstrate the effect of the large stochastic variability in recruitment (J. Carey, pers. commun.) built into the sheep sub-model, or the effect of increased numbers of wolves.

Human Harvest

For all of the prey populations, constant annual harvest rates can lead to decline. A 2% harvest can generally be supported by caribou and moose populations following wolf management, but a 5% harvest will almost invariably cause the populations to decrease. This prediction supports observations from the Yukon, where harvest levels have traditionally been high (YTG unpubl. data). Similarly, harvesting 12 sheep per year for 25 years will cause sheep population decline. Due to the lack of age and sex specificity in the model, the effect of these harvest rates may be exaggerated in the model. However, the population trend is probably reasonable. Removing a proportion of a

population or a set number of animals every year, regardless of the population size or recruitment in any given year, can be very risky, as it does not include inevitable annual variation in recruitment or survival rates. One or two years of poor recruitment could mean that non-predation adult mortalities cannot be supported, and thus cause a population decline. Even at the seemingly low level of 2% of adults per year, harvest can cause the caribou population to decline to a level from which it will not recover without lethal wolf control. Numerous examples from fisheries have demonstrated the risks inherent with a quota or a maximum sustained yield (MSY) approach to harvest (Krebs 1994). One of the potential pitfalls of this approach is that initial population declines due to harvest may represent the gradual population decline to 1/2 K if harvest is set at the MSY, but that initially this decline is hard to distinguish from that observed when the population declines to extinction when the harvest rate exceeds MSY (Caughley and Gunn 1996). The implications are that managers must be very aware of yearly variation in population indices, and that a conservative harvest strategy is warranted.

Weather

Climate variability is large in northern environments and the effects of weather in the model add a necessary stochastic element. Without this random variability, the model would project that five years of lethal wolf control would be sufficient to guarantee long term population growth for caribou. One year of reduced recruitment, however, can mean the difference between continued population growth and irretrievable decline below

threshold population densities. The effect is less pronounced for moose, but still important near the low threshold population size.

Of all of the variables in the model, weather is the true unknown. Managers must be very aware and sensitive to its potential effects when considering how to manage prey populations. The exact effects of severe weather conditions upon prey populations are not known, but must be anticipated. I have chosen unusually cold temperatures in March as a factor which reduces recruitment, but there are many possible factors that could have a similar effect, or increase ungulate mortality including: snow depth, late snow/ice melt, change in forage availability, and oestrid fly harassment (Fuller 1989, Boertje et al. 1996, Del Guidice 1998). Cautious and conservative management will be required to compensate for these unpredictable effects.

Limitations of the model

A limitation of the model is the lack of sex and age structure for the prey populations. Harvest is removed from the adult population over winter, but there is no way to specify the sex of harvested animals. Managers, faced with declining ungulate populations, would most likely limit harvest to mature bulls, and thus the model simulations of harvest may show a greater adverse effect than would occur if only mature bulls were harvested. Nonetheless, adding the complexity of sex and age structure without having reliable data about sex-and age-specific fecundity and survival rates or how they are affected by wolf predation, would only weaken the predictions from the model.

In many of the simulations, the caribou herd declines to extinction. This occurs because I assumed that wolf packs on the calving grounds are supported by moose density. There is no functional response of wolves to caribou density, thus predation rates are fixed. This may be a valid assumption (Dale et al. 1994), but in reality wolves might switch from caribou to alternate prey at some very low density of caribou. Nonetheless, the implications of the model projections are valid. Where the caribou herd declines to several hundred animals in the model, the herd may be too small to recover because it is no longer a viable population that can be harvested and will not support large numbers of predators. The Chisana herd in Alaska is a possible example of an unharvested herd that has declined rapidly to several hundred animals, apparently due to predation (ADF&G, unpubl. data). This may be explained by a lag in wolf numerical response to declines in prey density (Ballard and Larsen 1987, Peterson and Page 1988). There is also evidence to suggest that wolves may hunt preferred prey until they are extirpated when alternate prey are available (Bergerud and Elliot 1986, Mech 1986, Dale et al. 1994).

The most important limitation of the model is one which is true of all models. The projections of a model are only as realistic as the assumptions that define it and the accuracy of its parameters and inputs. I believe that the results from this model are reasonable and realistic. My results are consistent with population trends that have been observed for the Aishihik ungulate populations before and after wolf control (YTG unpubl. data). Although empirical projections can not be relied upon to predict what will happen in the real system, the trends are apparent, and models can help in the

understanding of wolf-prey interactions and of the effects of stochastic natural variation and human management. The model is an ideal way to generate hypotheses and to tentatively explore possible management alternatives before accepting the risks of applying them to the real populations.

Significance of model

This model is unique in that the wolf population is structured by pack size. This takes pack social dynamics and territoriality into account, and allows recent information about wolf kill rates by pack of different sizes to be incorporated (Hayes et al. 1991, Thurber and Peterson 1993, Dale et al. 1995, Hayes 1995). Perhaps the most important benefit of structuring the model this way is that the effects of applying wolf fertility control and mortality control can be simulated in a way that is consistent with management practices. Wolf control typically involves removing whole packs, or reducing pack sizes to 1 or 2 animals, rather than the random removal of individuals from the population. Similarly, the Aishihik fertility control program focused on small-sized packs on the caribou herd range, not randomly selected individuals throughout the study area (Chapter Two).

Other important characteristics of the model are the use of field and demographic data for its parameters, the inclusion of seasonal differences in wolf predation on calves and adults, stochastic weather variation, and the interactions between the wolf population and the three prey populations. Furthermore, it is the first model that examines the

effects of wolf fertility control on a wolf population, as well as upon the ungulate prey populations.

General conclusions

In this chapter, I have presented a model that incorporates wolf social and territorial behaviour, wolf-prey interactions, stochastic variation, and various wolf management and ungulate harvest scenarios. The projections lend insight into wolf-prey dynamics, as well as demonstrate the possible long term population level effects of both lethal wolf control and wolf fertility control. The results may be applicable to other wolf-moose-caribou systems where wolf predation is an important factor limiting ungulate population growth.

APPENDIX 3.1. -EQUATIONS AND PARAMETER VALUES FOR WOLF-PREY

SIMULATION MODEL

Wolf sub-model

Maximum number of territories

      (cT): caribou hunters: Default = 7 territories on summer calving grounds
           If moose population at winter's end (mPw)<1000, 6
                                    >5000, 8

      (mT): moose hunters: Default = 15 territories throughout experimental area
      (except for calving grounds)
                       If mPw <1000, 7
                              >5000, 19

Territorial vacancies (Vac):   (eq. 1)
          = T-(Sm+Md+Lg winter distribution of packs)

Immigration efficiency (Ie):
      =% of vacancies that are filled the following season
      = 1 unless following mortality control
      = 0.25 during mortality control, 0.5 year following last removal, then 0.75, 0.9, 1

Percentage of vacancies filled, by pack size(fils, filmd, filL):
      fils   = 0.6
      filmd = 0.4
      filL   = 0

Vacancies filled by small, medium, large packs (vac fild sm, vac fild md, vac fild l) (eq.2)
      (assume infinite pool of in-shifters, dispersers, colonizers, fill in summer)
      (a) =Ie*fils*(Vac previous winter)
      (b) =Ie* filmd*(Vac previous winter)
      (c) =Ie* filL*(Vac previous winter)

Territorial vacancies filled (Vac filled)
      =vac fild sm + vac fild md + vac fild l   (eq.3)

Pack reproduction by pack size (Rs, Rm, Rl):
      =% of packs of each size that successfully raises pups
      Rs = 72 % of small packs
      Rm = 0.55 % of medium packs
      Rl = 0.4 % of large packs

<u>Wolf sub-model (cont'd.)</u>

Dispersal by pack size (Ds, Dm), over winter:

Dispersal of small packs (Ds) = death or splitting, results in a territorial vacancy
(0.14)

of medium packs (Dm)=dispersal of 2 yr olds, pack size stays constant
(0.3)

of large packs =pack size stays constant unless splitting

Maximum number of large packs(cTm or mTm for caribou or moose hunters):

caribou hunters: If cPw   >1000 = 2
                           >6000 = cT
                           <1000 = 1

moose hunters: If mPw   >1000 = 3
                           >3500 = 5
                           <1000 = 1

Pack splitting (Split):   (eq. 4)

= If winter large packs exceed maximum large packs: L(w) - (cTm or mTm)

Lethal wolf control (lc, removal of whole packs in winter):

Simulated Aishihik wolf removal

Caribou hunters (remove all winter packs)

	Sm	Md	L
Year 1	3	3	1
Year 2	1	1	
Year 3	1	1	
Year 4	1	1	
Year 5	1	1	

Moose hunters

	Sm	Md	L
Year 1	6	3	
Year 2	6		
Year 3	3	1	
Year 4	2	1	
Year 5		2	

Wolf sub-model (cont'd.)

Fertility Control (F is "on" =1 or "off" =0)
Small packs do not reproduce, stay in territory as a small pack, small pack dispersal/death rates apply
Applied from Year 4 onward if combined with lethal control, from Year 1 if applied alone

Percentage of small packs sterilized (fc):
The % of all small packs in a given year that do not reproduce when F=1

Number of small packs in summer (Sm(s)):   (eq. 5)
  (a) With fertility control: = Sm(w) * fc + vacfild sm
  (b) Without fertility control: = Sm(w) * (1-Rs) +vacfild sm

Number of medium packs in summer (Md(s)):   (eq. 6)
  (a) With fertility control: =Md (w) * (1-Rm) +(1-fc)*Sm(w) + vac fill md + Split
  (b) Without fertility control =Md (w) *(1-Rm) +Sm(w)*Rs + vac fill md + Split

Number of large packs in summer (L(s)):   (eq. 7)
  =L(w) + Md(w)*Rm + vac fill L - Split

Number of small packs in winter (Sm(w)):   (eq. 8)
  =Sm(s) -Ds*Sm(s) - Sm(lc) +Md(s)*Dm

Number of medium packs in winter (Md(w)):   (eq. 9)
  =Md(s) - Md(lc) - Dm*Md(s)

Number of large packs in winter (L(w)):   (eq.10)
  =L(s) - L(lc)

Number of lone wolves all year:
  = Lo, applies only to sheep sub-model, unaffected by management action, = 1

Number and size distribution of packs that determine prey distribution:
  caribou predation = Sm(s), Md(s), L(s) from caribou hunter sub-model
  moose predation = Sm(s), Md(s), L(s) from moose hunter sub-model
  sheep predation = Lo, Sm(s), Md(s) summed from both wolf sub-models* sAC
         (% of packs that hunt sheep = 0.1)

Caribou sub-model

Initial population size, cPi (1992): 750
Percentage calves in population cRy (1992): 14.6%
Carrying capacity (cK): 20,000

Stochastic weather effect (w):
    -6% random chance that winter is severe in March:
    w is "on" = 1, "off" = 0

Natality rate , pregnancy rate as % of total population (cRp):   (eq.11)
    (a) if population <1200=1992 % adult cows * 97% pregnancy rate = 0.7
                     >1200=1997% adult cows * 97% pregnancy rate = 0.5
    (b) -with stochastic weather variation   cRpw = (6% random chance)*0.7*cRp
    (random chance that pregrancy rate is reduced by 30%)

Wolf summer predation on calves (Wsc)   (eq.12)
    = 7.5*Sm + 30*Md + 45*L

Wolf summer predation on adults (Wsa)   (eq.13)
    = 2*Sm + 4*Md + 7*L

Wolf winter predation on calves (Wwc):   (eq.14)
    = 27*Sm + 36*Md + 50*L

Wolf winter predation on adults (Wwa):   (eq.15)
    = 27*Sm + 36*Md + 50*L

Non-predation caused adult mortality, in winter (cAm)
    if population>1400 = 3% * adult population at the end of summer (cAs)   (eq.15a)

Other sources of calf mortality, in summer (cMc):
    if caribou population at the end of winter (cPw) >1350 = 145
                                             <1350 = 100

Adult harvest from winter population (cH):   (eq.16)
    (a) "Low" level harvest   = 2%* cAs
    (b) "High" level harvest   = 5%* cAs

Adults surviving at the end of summer (cAs):   (eq.17)
    = cAw + cCw - Wsa

Calves surviving at the end of summer (cCs):   (eq.18)
    = Calves produced -cMc - Wsc

Caribou sub-model, cont'd.

Calves produced: (eq.19)
      (a) -without stochastic weather variation $= cRp*cPw*(1-cPw/cK)$
      (b) -with stochastic weather variation $= cRpw*cPw*(1-cPw/cK)$

Number of adults surviving at the end of winter (cAw):   (eq.20)
      $= cAs - Wwa - cH - cAm$

Number of calves surviving at the end of winter (cCw):   (eq.21)
      $= cCs - Wwc$

Population at the end of winter (cPw):   (eq.22)
      $= cAw + cCw$

Population at the end of summer (cPs):   (eq.23)
      $= cAs + cCs$

Moose sub-model

Initial population size, mPti (1992): 2000
Percentage calves in population mCi (1992): 8%
Percentage yearlings in population mYi (1992): 11%
Percentage adults in population mAi (1992): 81%
Carrying capacity (mK): 5,000

Stochastic weather effect (w):
    -6% random chance that winter is severe in March:
    w is "on" = 1, "off" = 0

Natality rate, including twins, as % of total population (mRp):   (eq.24)
    (a) =1992 -54 % adult cows * 138 calves/100 cows = 0.65
    (b) -with stochastic weather variation   mRpw = (6% random chance)*0.75*mRp
    (random chance that pregnancy rate is reduced by 25 %)

Non-predation caused adult mortality, in winter (mAm)   (eq.25)
    if population>2000 = 3% * population at the end of summer (mPs)

Wolf summer predation on calves (Wsc)   (eq.26)
    = 12.3*Sm + 16*Md + 20.8*L

Wolf summer predation on yearlings (Wsy)   (eq.27)
    = 3*Sm + 4*Md + 5.2*L

Wolf summer predation on adults (Wsa)   (eq.28)
    =1.5*Sm + 2*Md + 2.5*L

Wolf winter predation on calves (Wwc):   (eq.29)
    = 6.3*Sm + 8.1*Md + 10.6*L

Wolf winter predation on yearlings (Wwy):   (eq.30)
    = 6.3*Sm + 8.1*Md + 10.6*L

Wolf winter predation on adults (Wwa):   (eq.31)
    = 12.6*Sm + 16.3*Md + 21.3*L

Other sources of calf mortality, in summer (mMc):
    = 75

Adult harvest (mH), from winter population: (eq.32)
    (a) "Low" level harvest   = 2% * mAs
    (b) "High" level harvest   = 5% * mAs

Moose sub-model (cont'd.)

Adults surviving at the end of summer (mAs):　　　　　　　　　　　　　(eq.33)
$$= mAw + mYw - Wsa$$

Yearlings surviving at the end of summer (mYs):　　　　　　　　　　　　(eq.34)
$$= mCw - Wsy$$

Calves surviving at the end of summer (mCs):　　　　　　　　　　　　　(eq.35)
$$= Calves \ produced \ -mMc - Wsc$$

Calves produced:　　　　　　　　　　　　　　　　　　　　　　　　(eq.36)
(a) -without stochastic weather variation $= mRp*mPw*(1-mPw/mK)$
(b) -with stochastic weather variation $\quad = mRpw*mPw*(1-mPw/mK)$

Number of adults surviving at the end of winter (mAw):　　　　　　　　(eq.37)
$$= mAs - Wwa - mH - mAm$$

Number of yearlings surviving at the end of winter (mYw):　　　　　　　(eq.38)
$$= mYs - Wwy$$

Number of calves surviving at the end of winter (mCw):　　　　　　　　(eq.39)
$$= mCs - Wwc$$

Population at the end of winter (mPw):　　　　　　　　　　　　　　　(eq.40)
$$= mAw + mYw + mCw$$

Population at the end of summer (mPs):　　　　　　　　　　　　　　　(eq.41)
$$= mAs + mYs + mCs$$

Sheep sub-model

Initial Talbot Arm sheep population (1992): 597
Base Recruitment Rate (sRy): 12.6 % yearlings
Percentage of wolf packs with access to sheep (sAC): 10%
Annual adult survival rate before wolf predation (sS): 92%

Stochastic weather factors (sw):
- augments or decreases annual recruitment rate
= annual random % change of up to 50%

Wolf predation (W): (eq.42)
$$=9*Lo + sAC*(10*Sm + 12*Md)$$

Sheep Harvest (sH):
= 8-20 sheep per year

Yearlings (sY):
(eq.43)
$$= (sRy + sw) \bullet sT$$

Total population size, accounted annually (sT$_{+1}$): (eq.44)
$$= sY + sS*sT - W - sH$$

CHAPTER FOUR: GENERAL DISCUSSION - THE FEASIBILITY AND FUTURE OF FERTILITY CONTROL

Managing problem animal populations effectively has been problematic in the past and represents a challenge for the future. Traditional methods of population control such as culling are often only short term solutions, and can be inhumane, expensive, non-species-specific, and controversial (Bomford 1990). Methods used to control wolf populations, in particular, vary widely both in their degree of public acceptance and their long term ecological effectiveness (Cluff and Murray 1995, Mech 1995, Haber 1996, Mech et al. 1996a). Fertility control represents another management alternative to mortality control of wolves, but there has been very little research into its application for wild wolf populations (Mech et al. 1996a).

Wolf fertility control in Aishihik, Yukon

This study contributes new information about the potential for the use of fertility control to manage wolf populations. In Chapter Two, I presented results from an experiment which tested whether surgical sterilization alters wolf social and territorial behaviours. This information is crucial to understanding the effects of wolf fertility control. Sterilization of wolf pairs from small-sized packs could potentially slow the rate of wolf population recovery following wolf reduction, and reduce the wolf predation rate upon ungulates and its impact on ungulate calf survival. These 'benefits', however, are

contingent upon unaltered wolf behaviour: sterilized wolves must maintain and defend their territories, remain with their mates, retain dominant breeding status, and yet not produce pups. I presented behavioural data from 7 sterilized wolf packs which were monitored for up to 52 months, spanning up to 4 breeding seasons. I did not find any evidence to suggest that wolf social and territorial behaviour is affected by surgical sterilization. Thus, at the level of individual wolves, fertility control by surgical sterilization is a feasible technique. At the population level, surgery is perhaps not as appropriate due to the expense and logistical difficulties associated with live capture and removal to a controlled environment for the procedures.

Equally important to evaluating the merits of fertility control of wolves is an understanding of the long term, population level effects of wolf sterilization upon wolves and their prey. Long term monitoring of the wolf, moose, caribou, and Dall sheep populations in the Aishihik study area will provide the only experimental data of its kind. In the interim, a population simulation model can help to project and anticipate these effects, and to inform future management decisions. In Chapter Three, I presented a population simulation model which incorporated the social biology of wolves, the basic processes which determine the populations dynamics of wolves, moose, caribou, and Dall sheep, and the relationships between those populations. The value of the model is improved by its parameters, which are almost all derived from census data from populations in the study area. It can thus be used investigate the effects of mortality control, lethal control, hunting, and random weather variability. The projections from the model suggest wolf fertility control may enhance the long term benefits of a mortality

control program, and can be applied strategically to improve caribou calf survival and the population growth rate. The results also imply, however, that wolf fertility control alone can not be used to help recover prey populations which have declined to critically low numbers. The model prey populations are sensitive to stochastic factors such as weather variability and are extremely vulnerable to constant hunting pressure regardless of wolf management techniques.

The short term wolf behaviour results and the long term population simulation projections lend insight into the usefulness of wolf fertility control as a management tool, as well as contribute to our understanding of predator-prey interactions. The results from this study suggest that sterilization of wolves may help to maintain viable ungulate populations without some of the ecological and human social problems associated with lethal wolf control.

Wolf fertility control in other wolf-prey systems

The results of the wolf behaviour study are directly applicable to other territorial wolf populations. In the Aishihik wolf population, we sterilized wolves by tubal ligation and vasectomy, but any other contraceptive method would be acceptable providing it does not induce changes in hormonal cycling and associated social and territorial behaviours. Ideally, wolves could be sterilized without the expense, trauma, and risks associated with capture and surgery. Immunocontraception, induced by porcine zona

pellucida (PZP) or other immunogens, may be a promising alternative to surgery (see

Chapters One, Two, Table 1.2). If immunocontraception can provide reliable

contraception without behavioural side effects, sterilizing wolves will become possible on

a larger scale than is currently feasible using surgical techniques. The immunogen could

be delivered remotely by a dart from the air or delivered in baits at den sites, thus

eliminating the need even for immobilization and handling. This technology is currently

being developed for red foxes at the Vertebrate Biocontrol Centre in Australia and for

coyotes in Utah (M. Holland pers. commun.)

Wolf fertility control is a feasible management tool for the Aishihik wolf

population. Aishihik caribou calf recruitment is strongly limited by wolf predation, and it

was possible to remove wolf packs from the caribou calving grounds to increase calf

survival rates over summer. Due to the limited size of the calving grounds and the

relatively small number of wolf packs that range on them, we were able to sterilize a

majority of the wolf pairs and small packs which recolonized the area following lethal

control. However, wolves live in highly varied ecosystems throughout the northern

hemisphere. Their ability to limit or regulate prey populations depends upon prey

population characteristics such as migratory behaviour, population size, and vulnerability

to wolf predation, as well as upon alternate prey species availability, the occurrence of

prey refuges, the presence of other predators, the effects of compensatory prey mortality,

and stochastic factors such as extreme weather conditions (Bergerud et al. 1983, Ballard

et al. 1987, Ballard and Larsen 1987, Skogland 1991, Eberhardt and Pitcher 1992, Van

Ballenberghe and Ballard 1994).

Wolf control, lethal or otherwise, will only benefit ungulate populations where wolves have a significant limiting effect on their prey. Accurate and detailed information about the factors limiting specific prey populations is required before wolf control can be considered. The model may be used to evaluate wolf management in other wolf-caribou-moose systems, provided that area-specific data can be obtained for input as parameters. Where wolf predation is an important limiting factor, it is important to know the number of prey killed by wolf pack, by pack size, and possibly, by season. The location of calving grounds or other important prey habitat must also be determined.

In this study, fertility control was used to shift the pack size distribution in the study area from medium- or large-sized packs prior to wolf control, to small-sized packs or pairs. The projections from the model show that, for the declining Aishihik caribou herd, large packs had to be removed from the calving grounds for the population to rebound, and that fertility control is most effective following wolf pack removal. In the Southwest Yukon, entire wolf packs were removed by aerial shooting and ground snaring in a government sponsored wolf kill program. It is unlikely, however, that such programs will be initiated in the future. Public opposition to large scale lethal intervention has led managers to search for other alternatives. For fertility control to be effective for the recovery of small-sized caribou herds, for example, large packs must first be reduced in size or removed altogether. This may be achieved by translocation of subordinate wolves away from their territories. In rural or northern communities, this may also be accomplished by public wolf trapping. Managers in Alaska have begun a program which combines public trapping, translocation of sub-adult wolves, and wolf fertility control in

order to increase the Fortymile caribou herd (C. Gardner, Al. Dept. Fish & Game, pers. commun.). However, in areas where there is no public interest in the trapping or hunting of wolves and there is opposition to other wolf removal techniques, fertility control may not be a viable option.

Fertility control for other species

Due to their long life expectancies (relative to small mammals), their territorial nature, and their social hierarchy and monogamous mating system, wolves appear to meet all of the ecological and logistical requirements for successful fertility control. Other species, however, may possess characteristics which make them unsuitable for management by this technique. In some species, compensatory responses such as reduced juvenile and adult mortality, decreased dispersal rates and increased immigration may occur. In cases where reproductive rates are density-dependent, fertility control may only serve to determine which animals, and not how many, will reproduce (Bomford 1990). For very short-lived species, in large populations, it may not be possible to sterilize enough individuals over time in order to reduce the population size or curtail population growth. Nonetheless, fertility control may be effective for species with high recruitment rates such as the European rabbit, where mortality factors including disease and predation regulate the target population at low densities (Newsome and Hik, unpubl. data).

Fertility control models have been used to assess species suitability to fertility control techniques. Eagle et al. (1993) suggested that sterilizing dominant males would not likely reduce the size of a feral horse population due to the potential for females to move between bands of males, or the potential for sub-dominant males to breed. For red foxes, the effectiveness of fertility control may be compromised by environmental variability (Pech et al. 1997), and immigration (Bubela et al. unpubl. data).

Once a species is determined to be suited to management by fertility control, there are many practical problems to consider. Depending on the method chosen, these may include: difficulty of application of contraceptive treatment or of dissemination of the anti-fertility agent, possible contamination of the food chain by consumption of treated animals or accidental treatment of non-target animals, the ecological implications of releasing genetically altered strains of viruses (vectors) into the environment, the genetic implications of restricting breeding, public acceptance, and economic cost. Several studies have reported unsuccessful results due to side effects caused by the sterilizing agent (Munson 1993), or logistical difficulties (Botti 1985, Frank and Sajdak 1993). Garrott (1995) recommended that the effects of specific fertility control techniques upon target and non-target species should first be determined using modelling and small pilot experiments within populations that are isolated or closed to immigration and emigration, if possible. Clearly, potential compensatory mechanisms need to be well understood.

Ethical concerns

In addition to the considerations of all of the biological, ecological and practical issues that are involved with fertility control, there are certain ethical concerns that must also be addressed. The concept of fertility control may appear to many be more ethical, humane and politically tractable than some forms of lethal control (Bomford, 1990, Cluff and Murray 1995), but many others believe that fertility control compromises animal rights, or that natural ecosystems should not be interfered with in any manner. Some opposition to any form of intervention into wild ecosystems seems inevitable, because wildlife population control will always involve conflicts of varying values and beliefs (Gill, in press). It is crucial to acknowledge that the very determination of when a population is overabundant is a subjective value judgment (Garrott, 1995). Nonetheless, there is widespread agreement that, at least in a few cases where there are grave conservation concerns, some form of population management is warranted. Here I address the ethical issues which pertain exclusively to wildlife fertility control.

Given that wildlife management increasingly takes the form of intervention into wildlife populations, is fertility control less disruptive and more acceptable than other methods such as culling, hunting and displacement? Depending upon the contraceptive method chosen, the answer may be 'yes'. Cohn (1996) examined the history of research into and the application of fertility control techniques, and noted that there appears to have been a shift towards more ethical treatment of animals. This is especially relevant with the development of immunocontraceptives that can be remotely delivered and that

cause very few if any physiological or behavioural side effects. It would seem as though the physical and social disruptions caused by fertility control to target animal populations are fewer than by lethal control. Cohn (1996) suggested that a move to fertility control in wildlife management is a recognition that animals have a right to exist in the wild and is therefore "a step in the right direction". Mathews (1991) agreed that contraceptives currently represent "the most benign forms of population control for wildlife", but raised concerns that sterilized animals can no longer be considered to be wild, and that applying fertility control represents "a dramatic intensification of our power to direct the course of Nature". Indeed, some have expressed concerns that fertility control involves intervention into natural evolutionary processes (Anonymous, 1993).

Accordingly, the application of fertility control to wildlife populations should not be taken lightly, and management decisions regarding what treatments will be applied to which populations must be made wisely, carefully, with a long term vision, and through an ongoing public process (Gill, in press).

The future of wildlife contraception

While fertility control may seem initially to be a viable solution to problem wildlife issues, it is clear upon closer examination that the issues to be considered are as complex, and in some cases, as controversial as those pertaining to lethal control and other more traditional forms of population management. Gill (in press) noted that there

are four major areas of ideological conflicts associated with wildlife contraception : anti-management sentiment, anti-hunting sentiment, animal rights sentiment, and animal welfare sentiment. The author predicted, however, that the most pressing concerns will involve the practical issues of applying fertility control: where, when, and under which circumstances. These are fundamentally ecological questions. Indeed, Warren (1995) stressed the need for researchers and wildlife managers to join forces and consolidate efforts and funding if we are to be able to achieve publicly acceptable, ecologically responsible, scientifically sound and logistically feasible management objectives.

There is now substantial research that has examined potential contraceptive agents and techniques. The vast majority of this work has been applied to either laboratory animals or captive populations (Tables 1.1, 1.2). The relatively few studies that have applied contraception to wild animals have largely been short term studies and have not examined the effects of fertility control upon the population dynamics of the target species, nor its effects upon the ecosystems in which target populations play an integral role. Any future research should aim to fill this significant gap in our knowledge of this potentially valuable management tool.

CONCLUSION

At present, there are very few tools available to wildlife managers with which to regulate wild animal populations when and where such actions are deemed necessary. All available techniques have drawbacks which must be considered. Associated with

each are ecological, practical, ideological and ethical grounds for objection. There will therefore always be some public opposition to the management strategy chosen. Regardless, the volume of recent research and contraceptive programs that have been implemented over the last several decades indicates that, increasingly, more investigators and wildlife management agencies are willing to attempt to overcome some of the hurdles associated with fertility control in order to test the merits of this non-lethal technique. This study adds to the our knowledge about the potential for the use of fertility control in wildlife management.

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