AN EXPERIMENTAL DESIGN TO TEST WOLF REGULATION OF UNGULATES IN THE AISHIHIK AREA, SOUTHWEST YUKON

December, 1992

Yukon
Renewable Resources

TR-92-6

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Executive Summary

Moose and caribou in the Aishihik area of the southwest Yukon have declined to very low numbers in recent years. There is a risk that the moose and caribou populations could be driven even lower. Moose densities are currently among the lowest reported for northern interior populations. Both moose and caribou are important to 3 First Nations that have traditionally used this area for subsistence purposes. First Nations people have observed a decline in both moose and caribou populations in the area and have called for an ungulate recovery program.

Low recruitment is currently the problem for both ungulates. Wolf predation on adults and calves has been shown to be one of the major factors limiting the recovery of other northern caribou herds and moose populations. Other predators, including bears, may also be an important limiting factor to the small populations of both moose and caribou. Recent hunting restrictions and closures have not arrested the declines in woodland caribou in the Aishihik area of the southwest Yukon.

This study design calls for hunting closures on moose and caribou and an initial 2 year wolf control program that will be evaluated to determine if it has increased calf survival sufficiently to generate population growth of moose and caribou. If it has not, the program will be suspended. If it is has, the program should continue until 5 years when it will again be evaluated to determine if the population growth rate is acceptable. The long term population goals are for 2,500 caribou (up from 1200 to 1500) and 4,000 moose (up from 2000) in the Aishihik area.

The study is designed so that wildlife managers can learn by experimentally changing the wolf-prey system while monitoring other potentially important factors, including weather and range conditions. This could tell us: 1) why ungulate prey have declined in the area, 2) if and how wolves regulate the abundance of moose, caribou, Dall sheep and elk, 3) how weather, forage availability and other predators, including bears and humans, influences ungulate populations. In order to fully understand these systems each prey species will also be studied in areas where wolves are not reduced

(untreated 'control' populations). The long-term question that remains unanswered is: If ungulate populations grow after wolves are reduced will they again decline to low numbers due to strong wolf predation effects (ie. regulation). This is a critical problem to be solved for it poses the broader management question: Does wolf control have long-term effects, or are the benefits only short-term?

Acknowledgements

This study design was formed after a two-day workshop on wolf-prey dynamics held in Whitehorse, Yukon, October 3-4, 1992. Much of the theoretical aspects of this design were provided by A. R. E. Sinclair of the University of British Columbia, F. Messier of the University of Saskatchewan, and S. Boutin of the University of Alberta. The manuscript was reviewed by these 3 ecologists; Yukon Fish and Wildlife Branch staff including R. Farnell, D. Larsen, B. Gilroy, J. Carey, B. Smith, D. H. Mossop; P. Denison of the Yukon Fish and Wildlife Management Board, S. Gilbert of Yukon College , M. Williams of the Northwest Territories Renewable Resources and R. Breneman of Kluane National Park, and Doug Janz, B.C. Fish and Wildlife. Members of the Burwash and Champagne-Aishihik First Nations and R. Quock of the Council for Yukon Indians contributed to the design of this research through constructive discussions and advice.

Introduction

The Aishihik and Burwash caribou (*Rangifer tarandus caribou*) herds and moose (*Alces alces*) numbers continue to decline to low densities in the Aishihik area of the southwest Yukon. Both ungulates are particularly important to 3 First Nations who have traditionally used the wildlife in the area for subsistence. All caribou hunting has been closed since 1990 and closure was recently recommended for moose (Larsen and Ward 1991). Currently, low recruitment is the major problem for both ungulates. Wildlife managers are faced with a conservation dilemma. If they do not intercede and attempt to increase recruitment, both ungulate species will likely continue to decline to very low densities where natural recovery will not likely occur in the near future.

Wolf (*Canis lupus*) predation was an important factor limiting the recovery of northern caribou herds (Gasaway et al. 1983, Gauthier 1984, Seip in press, Bergerud and Elliot 1986, Farnell and Hayes in prep.) and moose populations (Gasaway et al. 1983, Ballard 1992, Larsen et al. 1989a, Hayes et al. 1991, Gasaway et al. 1992, Farnell and Hayes in prep.).

Despite a long history of wolf control in northern North America, wildlife managers still know little about the long-term dynamics of wolf-prey systems and how wolf control affects it. An important, unanswered question is - Will the temporary removal of wolves cause woodland caribou and moose populations to increase and then remain at a higher density? Or will they eventually return to low density due to wolf predation? The idea that ungulate prey can live at either stable low or high densities in areas where wolves are naturally-regulated (Haber 1977, Walters et al. 1981, vanBallenberghe 1980, Messier and Crete 1985), has been recently challenged (Gasaway et al. 1992, Seip 1992, Messier, in prep.). There has not been an empirical study conducted to test wolf regulation hypotheses (Boutin 1992).

This paper presents an experimental design to determine if wolves are an important limiting factor and whether they regulate ungulate prey numbers. It examines current theories about wolf-prey dynamics and summarizes the status of wolves and ungulate prey in the Aishihik area including: woodland caribou, moose, Dall sheep (*Ovis dalli*), and introduced herds of elk (*Cervus elaphus*) and wood bison (*Bison bison athabascae*). The experiment is designed to examine 5 competing hypotheses of population regulation. For each hypothesis there are predictions that can be tested among 4 ungulate species by deductively examining long-term population responses to wolf reduction. Untreated, 'control' populations of each prey species will be monitored to support or reject each hypothesis presented.

There is a broader issue of public ethics regarding wolf control as a management tool to restore wild ungulate populations (Seip 1992a). An independent planning team, composed of people sharing a wide range of wildlife views, debated these social issues. The Yukon Wolf Conservation and Management Plan was drafted after a series of 9 meetings between April and September 1992 (Yukon Wolf Planning Team 1992). The plan recognizes that there are conditions when wolf control may be considered to restore ungulate populations (see Appendix 1). The plan recommends that area specific plans are scientifically designed to allow wildlife managers to solve ungulate population problems, but also understand the type of wolf-prey system that exists and how wolf control influences the system. To achieve this requires an experimental approach.

Predator-prey Dynamics

How predators impact prey population dynamics depends on the relative number of prey they remove compared to the potential annual increment the prey are capable of producing in the absence of the predator (Seip 1992a, Messier, in prep.). Predation is a *limiting factor* for a prey population because it causes a change in population production or loss (Sinclair 1989, Boutin 1992). Its importance as a limiting factor depends on the mortality rate it exerts on the prey population, and whether predation-caused deaths were of individuals that would have survived otherwise (*additive*), or were predisposed to die of other causes before reproducing (*compensatory*-see Boutin 1992). For predation to *regulate* a prey population, it must tend to stabilize prey density over time (Solomon 1949, Fryxell et al. 1988, Skogland 1991.).

Predators can react in two important ways to increases in prey abundance (Solomon 1949); they can increase their numbers (*numerical response*) and individual predators can kill more prey (*functional response*). The functional response peaks at some prey density as each predator becomes satiated. The numerical response plateaus as some social limitation (ie. territoriality, competition) determines the upper limit of predator numbers (Solomon 1949).

Holling (1959, 1965) identified categories of functional responses of predators. For the type-III response, (sigmoid-shaped curve) a predator will initially have difficulty locating and killing prey at very low prey density, but as the number of prey increases, the predator will 'turn on' to the new prey resource and increase its predation encounters. The total predation response may increase exponentially through the multiplicative effects of the increasing numerical and functional responses of predators (Seip 1992a).

We assume that wolves have a type-III functional response (Walters et al. 1981) because they tend to selectively exploit the most abundant prey in their pack territories, they use alternative prey when primary prey becomes scarce, and they have a greater reproductive rate than their ungulate prey. In the type-III model, total wolf predation response (numerical and functional) is directly *density-dependent* at low prey density (removes an increasing proportion of prey as the density increases); *density-independent* at intermediate density (effect is not related to prey density); and *inversely density-dependent* (removes a decreasing proportion as density increases) at high density (Sinclair 1989, Pech et al. 1992, Seip 1992a). For wolf predation to be regulatory, it must have the characteristics of density-dependence.

Wolf-prey theoretical models

Despite the great number of wolf-prey studies done in the past few decades, there is still considerable debate about the limiting and regulatory effects of wolf predation on ungulates. Review papers that argue there is insufficient evidence for regulation include: Fowler (1987), Sinclair (1989), Skogland (1991) and Boutin (1992). Evidence for regulation is presented by

Gasaway et al. (1983, 1992), Ballard et al. (1990), Seip (1992a) and Messier (in prep.).

Predation impact can be quantified by the amount it alters prey population growth compared to other factors (Boutin 1992). How prey population dynamics respond to changes in wolf numbers depends on whether or not wolf predation is regulatory. If prey increase and remain at a higher, stable density after wolves recover, then predation is, by itself, not regulatory (Sinclair 1989, Sinclair et al. 1990, Pech et al.1992), and stable equilibria exist at both low and high prey densities (TWO STABLE STATES MODEL, Fig. 1.1). At the low stable density (*A*) the wolf predation rate is directly density-dependent and regulating the prey. At the higher density (*C*, Fig. 1.1) wolf predation is inversely density-dependent and is not regulating abundance (Pech et al. 1992). At the stable equilibrium *C*, competition for food mainly regulates numbers. An unstable equilibrium (*B*, Fig. 1.1) also exists where prey numbers will collapse to *A* if density falls below *B*, and erupt to *C* if density exceeds it (Pech et al. 1992). If prey eventually decline to a low density due to wolf predation, regardless of how high prey density was, then ungulate prey numbers are regulated at a single low equilibrium by wolves (SINGLE STABLE STATE MODEL, Fig. 1.3- from Messier in prep.). Messier (in prep.) analysed wolf predation rates and moose densities from various North American studies. He concluded that moose were regulated at low density by wolf predation, supporting the SINGLE STABLE STATE MODEL. There is evidence that non-migratory ungulate herds in the Serengeti plains of Africa are regulated at a single, low equilibrium by density-dependent lion predation (Fryxell et al. 1988).

The complexity of predator-prey systems increases where there are more than one predator and one prey species in the system (Skogland 1991, Messier, in prep., Boutin 1992, Seip 1992a). A low density, alternate prey of wolves (i.e. caribou) could become extirpated by inverse density-dependent (or depensatory) wolf predation (EXTINCTION MODEL, Fig. 1.5). In this model, wolf numbers could be regulated mainly by the abundance of a primary prey (ie. moose). There is an unstable equilibrium density *B*. for the alternate prey; below *B* the recruitment rate declines due to other density-independent factors (bears, other predators, weather). At low densities, alternate prey abundance continues to decline due to the impacts of density-independent wolf predation and other factors, precipitating the decline further until the prey eventually disappear.

If declining recruitment rates are plotted onto the SINGLE AND TWO STABLE STATES MODELS, a new low density unstable boundary *B* is formed (Figs. 1.9 and 1.10). A type III wolf predation response curve could lead to extinction of alternate, low density prey in both models.

A prey species that is naturally-regulated by environmental conditions at a wide range of densities may be only marginally limited by wolf predation. In this model, wolf predation is density-independent and cannot regulate prey density (STOCHASTIC MODEL, Fig. 1.7). For this to be true, the prey species must be relatively unattractive or invulnerable to wolf predation at a wide range of densities, or buffered by other prey species.

A prey species that is regulated by competition for food or space could be at a density that is mainly dependent on food resources (FORAGE/NUTRITION MODEL; equilibrium *C*, Fig. 1.1). In this model, wolf predation should be density-independent, and prey abundance should be regulated mainly by changes in food supply quantity, quality or availability. The recruitment potential of the prey should be inversely related to prey density.

On Isle Royale, wolf numbers remained high for a decade after moose declined sharply (Peterson and Page 1983). This *lag response* could amplify the total predation response of wolves at low prey density (Figs. 1.1., 1.3 and 1.5), until wolves eventually decline to stable densities that are regulated by ungulate prey biomass (Keith 1983, Fuller 1989) .Wolves in the boreal forest could be held at a higher density than is predicted by ungulate food supply; by 1) preying on cyclical snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*) or seasonally available migratory ungulates, or 2) through wolf social mechanisms (territorial overlapping, pack fracturing, dispersal).

Wolf-prey models and wolf control

During the 1970s-1980s large-scale reductions of wolf populations were used to try and help ungulates recover from low density (Gasaway et al. 1983, Bergerud and Elliot 1986, Ballard et al. 1987, Gasaway et al. 1992, Larsen et al. 1989b, Hayes et al. 1991, Farnell and Hayes in prep.) but none was carried out long enough to answer whether or not predation is regulatory. In some cases prey populations increased substantially when wolves were removed (Gasaway et al. 1983, Bergerud and Elliot 1986, Farnell and Hayes in prep.). This only implies that predation was limiting prey abundance- it is not evidence that it was regulating prey to a stable density (Sinclair 1989, Skogland 1991). To determine if wolves regulate prey, the system must be perturbed and studied until prey and wolves reach stable densities again.

The SINGLE STABLE STATE MODEL predicts that wolf control will produce a range of unstable equilibria points that wolf predation will eventually exceed, regardless of the period of wolf control (Fig 1.4). In this system, prey can only be maintained at a higher range of unstable densities through periodic or continuous wolf reduction. In the TWO STABLE STATES MODEL (Fig. 1.2) wolf control could lead to a stable higher density, depending on the reduction period. Short-term wolf control (1 year) may not allow the prey population to exceed the unstable density boundary *B*, and wolves will regulate prey back to the low density stable equilibrium *A*. Long-term wolf control could theoretically allow the prey population to exceed *B*, and enter the density phase where food supply should regulate prey density to the stable high density *C*.

In the EXTINCTION MODEL, reducing wolf populations could result in continued decline to extinction (Fig. 1.6) regardless of the period of wolf removal. The total wolf predation effect is reduced but it remains higher than the growth potential of the prey, which is declining with density due to unrelated factors. The EXTINCTION MODEL could describe an alternate prey response, for wolves should become extinct before a single, primary prey disappears. As the alternate prey declines to extremely low levels, other limiting factors beside wolf predation could become more important, including demographic and environmental stochasticity, or density-independent predation by bears.

For the STOCHASTIC MODEL to be true, any reduction in wolf numbers should have no important impact on prey dynamics, and not regulate density to any stable equilibria (Fig 1.8). This is because the prey is buffered by highly variable survival rates of calf and adult cohort, which are mainly caused by density-independent conditions (ie. weather). Predation may remove a large portion of the prey population if they become vulnerable, but most of the mortality is compensatory.

Knowing which system exists in nature is crucial for wildlife biologists. The type of system will determine the management strategies that can be used to recover different prey populations. If the TWO STABLE STATES MODEL is true, then one period of wolf control of sufficient duration should allow prey to reach a stable high density indefinitely, providing density exceeds *B*. If the SINGLE STABLE STATE MODEL is true, then wolf control will not sustain higher density prey for long, and prey will naturally return to low density. Wolf control must be conducted periodically to elevate and hold prey at a higher density. If the EXTINCTION model is true, then wolf control will have no impact on prey population dynamics at the low range of prey density. If the STOCHASTIC MODEL is true, there will be no impact at a wide range of prey densities.

Stochastic events may temporarily affect the other 3 models by influencing population composition and response rates. For example, severe weather could negatively affect all ungulate calf survival rates one year, which would depress or mask prey population responses to reduced wolf numbers. However, these events should be detected in both experimental and untreated control populations and model predictions could be altered accordingly.

Predictions of Wolf-prey Models

We propose to examine 5 competing hypotheses of wolf-prey dynamics using data from a wolf reduction experiment in the Aishihik area. We will test each model among woodland caribou, moose, Dall sheep, and elk. Each prey species may respond differently, if wolf predation is an important limiting factor or is regulatory. Our ability to examine and describe the wolf-prey system for each ungulate will depend on the rate and amount of change in prey density that happens after initial wolf reduction. For each of the models described, a series of predictions can be made:

SINGLE STABLE STATE MODEL

1). Wolf predation will be density-dependent at all ranges of observed prey densities where wolves have been culled.

2). An outbreak of the ungulate species should be induced experimentally by the removal of a large portion of the wolf population, while reproduction of prey does not change. The outbreak should be due to increases in the survival rates of both calves and adults.

3). Recovery of wolves after the removal experiment should result in the ungulate population declining to a stable, low density where density-dependent wolf predation is regulatory.

4). The ungulate population should not escape the low density state without a natural or artificial (control) decline in wolf numbers.

TWO STABLE STATES MODEL

1). Wolf predation will be directly density-dependent at the low range of observed ungulate prey densities, and will regulate prey density below the boundary density *B*.

2). At the higher range of prey densities above *B* wolf predation should be inversely density-dependent or depensatory, and should not regulate prey abundance.

3). An outbreak of the ungulate prey species could be induced experimentally by the removal of wolves, while prey reproduction does not change.

4). The natural recovery of wolves at the termination of the removal experiment should result in the ungulate population returning to a stable, low density where density-dependent wolf predation is regulatory, if the increased density does not exceed boundary *B*. If the increased density exceeds *B*, the prey population should escape density-dependent wolf predation and continue to increase to a high, stable density *C*, where forage/nutrition is regulatory.

5). The prey population should not escape the low density state without a natural or artificial (control) decline in wolf numbers.

6). At high equilibrium *C*, prey population size should be mainly regulated by intraspecific competition for food and space. Range quality should be depressed compared to low prey densities Physical condition and reproduction should be negatively affected.

EXTINCTION MODEL

1). Wolf predation is either non-regulatory (density-independent) or depensatory at all observed prey densities.

2). The experimental removal of wolves will not change the declining trend in prey numbers, and the prey population will continue to decline to extinction.

3). The experimental removal of wolves will not change the declining trend in the ungulate species's recruitment. The decline in recruitment should be due to a decrease in calf survival and not by changes in the fecundity rate. Decreased survival of calves and adults will be due to density-independent factor(s).

STOCHASTIC MODEL

1). Wolf predation is density-independent and non-regulatory at all observed prey densities.

2). The experimental removal of wolves will not change the population trend in the ungulate species, and the population size will fluctuate unpredictably and not be related to other factors.

3). The experimental removal of wolves will not affect either the ungulate. species's recruitment or adult mortality rate

4). Large-scale,die-offs of prey should happen stochastically, but not be related to wolf density. This should be manifest in a wide and unpredictable variation in the proportion of different age cohorts in the population over time.

FORAGE/NUTRITION MODEL

1). See prediction 6, two stable states model.

2). Wolf predation is density-independent and non-regulatory at high prey densities.

3). The experimental removal of wolves will not increase prey recruitment rates, adult survival rates, or prey population size.

Current views of northern predator-prey dynamics

There is evidence that wolf predation is an important limiting factor on certain northern ungulate populations (Gasaway et al. 1983, Larsen et al 1989a, Farnell and Hayes in prep., Messier in prep.), but it is often difficult to determine the additive or compensatory nature of wolf predation (Boutin 1992). Gasaway et al. (1992), Seip (1992a) and Messier (in prep.) examined wolf-prey systems and concluded that there is no evidence that prey can live at two stable equilibria if wolves are naturally-regulated. They argued that density-dependent predation by wolves will return prey to low density where a 'predator pit' is shallow or absent, restricting prey from increasing to a higher density. There is evidence that two stable states can exist in small mammal systems, based on experiments in Australia (Pech et al. 1992), but this has not been demonstrated for large carnivore-ungulate systems.

A population of wolves that is primarily supported by moose could theoretically extirpate small herds of woodland caribou, even without high bear predation on neonates. This could occur because density-independent wolf predation could remove an increasing proportion of caribou as density declines (Bergerud and Elliot 1986, Edmonds 1988, Seip 1992b, Farnell and Hayes in prep., Hayes and Gunson in prep.).

The synergistic effects of wolf and bear predation on adult and calf cohorts could have profound implications to wolf regulation theory (Messier in prep.). Evidence from black bear (*Ursus americanus*) studies in Alaska (Schwartz and Franzmann 1991) showed individual bear killing rates were independent of moose density. This is likely because bears are mainly regulated by non-ungulate food (Seip 1992a). There is evidence that brown bears (*Ursus arctos*) were important predators of neonatal caribou in Alaska (Adams et al. 1989) and northern British Columbia (Page 1985). In the case of northern moose, brown bear predation on neonates can be a strong factor limiting recruitment in the absence of wolves - especially at low moose densities (Ballard et al. 1981, Larsen et al. 1989a, Gasaway et al. 1992). If brown bear predation is also density-independent, then the combination of wolf/bear predation could theoretically lead to the extinction of both the primary and alternate prey of wolves, depending on how low prey density becomes. For ungulates to escape low density and eventually increase in wolf-bear systems, the annual wolf predation rate (% prey removed from population) must be strongly depressed to be below the potential recruitment rate (Hayes et al. 1991, Gasaway et al. 1992). This requires intensive wolf control throughout the year to reduce the impacts of wolf predation on calves that survive the neonatal period of bear predation (Larsen et al. 1989b, Hayes et al. 1991).

Perhaps the best case study to test wolf regulation is the ongoing research in the Finlayson area of the east-central Yukon (Farnell and Hayes in prep.). In this area, wolf numbers were reduced from 1983-89, then allowed to recover (1989-92). Moose and caribou populations increased 2-3 fold during the wolf control period. Both prey species continued to grow while wolves recovered to their pre-control population size in 1992. Monitoring numerical change in caribou and moose, and numerical and functional responses in wolves will allow assessment of wolf regulation hypotheses, and the efficacy of wolf control as a long-term management tool. The Finlayson study was not initially designed to examine wolf regulation, and it did not examine a series of *a priori* predictions. However, it does provide a time series of actual woodland caribou, moose, and wolf population data during and after wolf control. These data are incorporated into some of the wolf-prey models presented here.

STUDY DESIGN

To adequately test if wolves regulate prey, the experimental design must be flexible and broad enough to 1) address alternate regulation hypotheses, 2) separate and identify the predation impacts of wolves, brown bears and other predators, and 3) separate key ungulate species which could be experiencing different ecological conditions and limiting factors in the same area, at the same time. The study design must include: 1) a series of measurements that can sensitively detect changes in predator and prey population parameters, 2) legitimate 'control' populations that are experiencing similar ecological conditions and regulating factors, and 3) a long-term commitment to monitoring numerical change in prey populations, and both numerical and functional responses of predators.

Experimental area

Physiography, vegetation and human settlement

The 20,000 km^2 experimental area (Fig. 2) includes the Ruby Range mountains, and portions of the Kluane plateau and the Nisling River and Aishihik basins. The western boundary is formed by the Kluane Wildlife Sanctuary and Kluane National Park Preserve, which are in the northeastern flank of the massive St. Elias Mountains, the largest mountain range in North America . Study area terrain is rolling to undulating hills above 900 m a.s.l. The rugged, Ruby Range mountains (2,300 m a.s.l.) lie in the middle of the study area. The mountains are volcanic rocks, mostly lava and basalt, with large intrusive bodies composed of gradodiorite and quartz diorite (Oswald and Senyk 1977).

The area is mainly influenced by the orographic rainshadow effects of the glaciated St. Elias Mountains. Low elevations are arid, annually receiving 190-285 mm of precipitation. Average annual temperature is -4C; average January temperature is -20C (Haines Junction) to -31C (Burwash). Northern drainages flow to the Yukon River system. Southern drainages flow to the Alsek River, which drains into the Pacific Ocean. The area lies in the discontinuous, scattered permafrost zone. Soil drainage is generally poor in valley bottoms, with patterned fen and bog complexes common.

Treeline is at 1,200 m a.s.l. White spruce (*Picea glauca*) is common on well-drained sites below treeline. Black spruce (*Picea mariana*) is common in moist lowland sites. Aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are found on warm, drained sites or in recently burned areas. Lodgepole pine (*Pinus contorta*) is scarce except along the eastern edge of the region. The understory shrubs are willow (*Salix sp.*), dwarf birch (*Betula glandulosa*), soapberry (*Shepherdia canadensis*), alder (*Alnus crispa*) and ericaceous species. Shrub birch and willow communities are prevalent in the subalpine, extending into the alpine forb communities.

The experimental area is part of the traditional areas of 3 First Nations. There are 4 communities that border the study area totalling about 1,000 residents: Haines Junction, Canyon, Burwash Landing and Destruction Bay. Whitehorse (population 21,000) is 100 km east of the experimental area. Whitehorse residents use the area for hunting, fishing and non-consumptive wildlife activities. There are 3 active big-game outfitters that operate in the experimental area.

Traditional and local knowledge of wildlife

The people that used the study area became concerned about small numbers of caribou and moose in the area during the late 1980s. During hunting trips, members of the Champagne-Aishihik and Burwash First Nations noticed declining moose abundance in the Aishihik road area and a rapid decline in caribou, and some sheep populations, in the Ruby Range mountains. At the same time, brown bears were perceived to be more plentiful in recent times around some of the communities. First Nation elders say that bears began to increase after it became illegal to trade spring bear hides during the 1960s. Since then, the economic incentive to traditionally hunt spring bears has declined, and their numbers have increased. People in the study area noticed an increase in wolf-livestock problems, especially in the past 3 years. They felt that natural game populations had declined greatly in their area, forcing wolves to prey on domestic animals. Residents of the area felt the initial cause of the ungulate declines was overhunting; citing the antlerless moose season (cows and calves) from 1975-1981 as being a main factor. It is not clear that hunting was the causal factor for the decline in moose or caribou populations.

Wildlife populations

Moose, woodland caribou and Dall sheep are the important ungulate prey in the study area. Mule deer (*Odocoileus hemionus*) are also present, but are rare. A small herd of elk was introduced to the area in the 1950s (Yukon Fish and Wildl. Br. 1990a, 1990b) and wood bison were introduced in the 1980s (Hoefs and Reynolds 1989). Predatory mammals include wolves, brown bears, black bears, coyotes (*Canis latrans*), fox (*Vulpes vulpes*), wolverine (*Gulo gulo*) and lynx (*Lynx canadensis*). Golden eagles (*Aquila chrysaetos*) are potential predators of neonatal ungulates, especially caribou and sheep. The following is a summary of the status and trends of various large mammals in the experimental and untreated 'control' areas. The locations of experimental and untreated control populations of caribou are shown in Fig. 3a, moose in Fig. 3b and sheep and elk in Fig. 3c.

1. Woodland caribou

There are two discrete woodland caribou herds in the experimental area: the Burwash and Aishihik herds (Fig. 3a). Both herds primarily use alpine and subalpine areas of the Ruby Range throughout the year. Other woodland caribou herds in the Yukon winter exclusively in low elevation, shallow-snow areas of the boreal forest (Farnell et al. 1991). The Burwash herd ranges in the northeastern flank of the St. Elias Mountains in the Kluane Wildlife Sanctuary and a small portion of the Ruby Range west of Talbot Arm of Kluane Lake. The Aishihik herd historically occupied the remainder of the

Ruby Range, ranging past Aishihik Lake to the east, to Haines Junction in the south, and north to the Nisling River. Both herds declined in the past decade, and area residents, guides and outfitters felt that the Aishihik caribou herd declined sharply in the past 5 years.

a. Aishihik caribou herd

The Aishihik herd declined from at least 1,200-1,500 animals in 1981 (Larsen 1981), to 785 in April,1991 (Farnell and Gilroy in prep.), a 36%-47% decline. Recruitment in the fall has been below the ratio of 30-35 calves/100 cows that is required for woodland caribou herd stability (Farnell and Gilroy, in prep.). The fall calf/cow ratio was 29/100 in 1990, 9/100 in 1991, and 7/100 in 1992. In 1991 and 1992, most calves were lost within the first few weeks of birth, but causes of death were not known. Despite a 97% pregnancy rate, by June 15, the ratio was 11 calves/100 cows. Similar, low recruitment rates have been observed in some nearby Alaskan herds (Chisana, Mentasta, Delta) recently, but causes have also remained unknown.

In 1990, the number of bulls in the Aishihik herd was 28/100 females, one of the lowest sex ratios observed in Yukon caribou (Farnell and Gilroy, in prep.). In response, all bull hunting was closed before the 1991 hunting season, and First Nation hunting was voluntarily reduced at the same time. Since hunting closure was instituted, the bull/cow ratio has increased to 35/100 in 1992. Low bull ratios in other caribou herds have been related to higher predator-related mortality of male calves and adults (Bergerud and Elliot 1986) and selective male hunting (Bergerud 1980).

Adult survival rates can be accurately measured by census interpolation (Bergerud 1980), or from survival rates of radio-collared individuals. Census interpolation provides an empirical measure but it is limited by the precision of the census, harvest knowledge, and techniques for measuring recruitment. Unless conducted each year, census interpolation can only derive a mean annual adult survival rate between periods, and cannot show annual variations. Census interpolation cannot be used for the Aishihik herd because the 1981 survey was incomplete in its coverage.

A total of 28 adult caribou have been radio-collared in the Aishihik herd since 1990. Mortality rates from radio-collared caribou death rates are usually greater than rates extrapolated from census data due to biases related to sampling (Farnell and Hayes in prep). Between 14 March and 1 December 1992, 10 adults (7 cows and 3 bulls) died; for a 37% death rate, indicating high adult mortality. Based on low calf recruitment in the past 3 years and natural mortality of adults, the Aishihik herd is expected to be smaller now than in 1991.

Blood sera were collected from a sample of 50 cows in December 1991 to assess pregnancy rates (progesterone-nmol/1). If forage/nutrition is a factor regulating herd size, it could be manifest through a low fecundity rate and poor body condition of cows (Farnell and Gilroy, in prep.). The pregnancy rate was 92-96%, and body condition was good, suggesting that birth rate was likely high. Sinclair (1989) and Davis (1991, abstract only) argued that ungulate fecundity was constant at a wide range of densities, and was a less sensitive indicator of forage/nutrition effects than the survival rates of calves. If this is true, calf viability should be examined. In our view, calf survival is the most sensitive parameter of forage/nutrition stress, followed by birth rate, pregnancy rate and body condition and size of females and calves. Each parameter must be considered in conjunction with the other three.

Nutritionally-stressed caribou should be less capable of withstanding disease (Zarnke 1983). Of 71 animals tested for disease, none were infected with brucellosis, a pathogen that has detrimental impact on natality rates and future pregnancies (Zarnke 1983). Tests are pending for 9 other pathogens found in caribou. From condition and pregnancy parameters, we do not expect that forage or weather conditions in 1991-92 strongly limited survival of adults or productivity.

It is possible that late spring conditions in 1992 lowered calf survival in both the Aishihik and Burwash caribou herds by displacing cows from alpine calving areas to areas with higher predation pressure (Bergerud and Elliot 1986) and by perhaps exposing calves to severe weather occurrences, although there is little empirical evidence that neonatal calves are vulnerable to windchill (Miller and Gunn 1986).

Reported harvest of Aishihik caribou averaged 46 per year (range 29-67) from 1979 to 1989, with roughly equal numbers taken by non-resident and resident hunters. The licensed harvest of females has been prohibited since 1987. First Nation harvest is not known but was apparently light in recent years. An evaluation of the impact of hunting remains speculative in the absence of information on natural population performance (i.e. adult natural mortality and calf recruitment rates since 1981). Sport harvest in the five years surrounding the 1981 estimate (1979 - 1983) was 4% of the 1981 population, slightly in excess of the theoretical maximum within our general harvest management strategy (2 - 3%). As well, in the year preceding the 1991 population estimate, harvest was unjustified at 4% of the estimate. Harvest could have precipitated, and likely contributed substantially to the decline, given poor to modest levels of calf recruitment (Farnell and Gilroy in prep).

b. *Burwash caribou herd*

The Burwash caribou herd was studied from 1978 to 1982 (Gauthier 1984, Gauthier and Theberge 1986). With the aid of telemetry relocations the herd was estimated at 383-472 caribou in October 1981 (Gauthier 1984). Using a similar total count technique but without the benefit of radio-collars, herd size was estimated to be 143-156 caribou in October 1990 and 1991 (Farnell and Gilroy in prep.), a decline of more than 60%. Using mainly wolf scat techniques (Floyd et al. 1978) and census interpolation between 1980 and 1982, Gauthier and Theberge (1986) concluded that the Burwash herd was primarily limited by wolf predation on adults and calves. They estimated that wolf predation was responsible for 75% of total annual herd mortality in 1980-81 and 46% in 1981-82. The calf/cow ratio was 32/100 in 1990 and 30/100 in 1991. In 1992, only a fraction of the herd was counted (68 animals); no calves were recorded with 46 adult females.

Gauthier and Theberge (1985) measured the rate of neonatal loss during the early 1980s. Neonatal mortality in the first 2-3 weeks after calving was 40% in 1980, 13% in 1981 and 49% in 1982. They speculated that the adverse early-calving climate could have sharply increased calf mortality in the Burwash herd in 1982.

Reported harvest of Burwash caribou averaged 12 per year (range 7-17), most were taken by non-residents. Harvest rates by First Nation hunters from 1979 to 1989 are not known. Reported harvest rates ranged from 2-4% during 1979-89. In the 5 years around the 1981 population estimate (1979 - 1983) harvest was 3% of the 1981 population estimate. At 5% of the 1991 population estimate, the 1990 harvest is considered to have been unjustified. As with the Aishihik herd, human harvest could have precipitated and contributed significantly to the decline of the Burwash herd, given poor to modest levels of calf recruitment in recent years (Farnell and Gilroy in prep.).

2. Moose

Two areas in the experimental area, Aishihik and Onion Cr. (Fig. 3b) have been censused using a stratified random sampling areial survey techniques (Gasaway et al. 1986, Larsen 1982). At 60 - 114 moose/1000 km^2, densities are among the lowest recorded in the Yukon. The average density for the Yukon is 218 moose /1000 km^2.

Moose average density in the Aishihik area decreased from 107/1000 km^2 in 1981 to 79/1000 km^2 in 1990 (Larsen and Ward 1991); a decline of 23%. About 2/3 of the Aishihik survey area was re-censused in 1992. Density declined from 104/1000 km^2 in 1990 to 60/1000 km^2 in 1992 (Ward and Larsen in prep.); a further decline of 43%. Calf survival to 6 months was low (23/100 cows) in 1981, high in 1990 (52/100 cows) and low again in 1992 (13/100 cows). The recruitment rate (18-month-old yearlings) in November declined from 0.16 in 1981, to 0.12 in 1990, and 0.08 in 1992. The high calf survival in 1990 did not reverse the decline of the population, suggesting that wolf predation during the winter months may have removed most of the calves before they become yearlings. Hayes et.al. (1991) found that winter wolf predation on a neighbouring, low density moose population removed up to 60% of calves that were present in November. Recruitment rates below 0.14 usually indicate declining populations in Yukon and Alaska (D. Larsen, Yukon Fish and Wildl. Br., unpublished data).

The bull/cow ratio has been consistent at 66/100 in 1981, 61/100 in 1990, and 62/100 in 1992. These levels are considered sufficiently high to allow all reproductive females to be bred.

It is likely that brown bear predation on neonatal moose is an important limiting factor in the study area. Brown bears were important predators of moose in three nearby studies (Ballard et al. 1981, Boertje et al. 1988, Larsen et al. 1989a).

A moose cow hunting season was open from 1975-81 throughout the Yukon. There is no reliable information on the numbers of female moose taken although the proportion of the harvest was low (15%). Since 1981, an average of 16 moose (primarily males) were reported taken by First Nation and resident hunters in the 4,000 km^2 Aishihik moose survey area (Larsen and Ward 1991). Information about First Nation harvest of moose was not collected until 1987 (Quock and Jingfors 1988), and likely under-estimates true harvest rates. Based on minimum estimates, declining populations, and current recruitment rates, Larsen and Ward (1991) concluded that human harvest was not sustainable, removing 4-6% or more per year: they recommended a closure on moose hunting recognizing that this population was, at best, stable without hunting mortality.

Moose average density in the Onion Creek survey area was 114/1000 km^2 in 1992. Both calf/cow ratios (22/100 cows) and recruitment of 18-month-old yearlings in November (0.07) indicates that moose numbers in this more remote portion of the experimental area are currently in decline also (Ward and Larsen, in prep.). The reported harvest rates prior to the 1992 survey (1988 - 1990) have averaged 8 bull moose per year or 2% of the estimated population.

3. Dall sheep

Dall sheep have been surveyed in 1974, 1979, 1980, 1982 through 1986, 1989 and 1992 in various parts of the Ruby Range (J. Carey, Yukon Fish and Wildl. Br. unpubl. data). Population size have remained generally stable in the long-term, but large annual variations in sheep abundance in the region has been reported (Burles and Hoefs 1984). In 1992, sheep were counted and classified in 3 Game Management Subzones (GMS 5-31, 5-34, and 5-36, Fig. 3c). The total number of adults counted in the area declined from 746 in 1986, to 590 in 1989, to 562 in 1992. The smaller number in 1992 was almost entirely due to the absence of adult ram groups, which may have avoided the area due to high snowpack in the area during summer.

In this area of the Yukon, population size is thought to be related to stochastic variations in lamb survival that is linked to forage availability in winter (Hoefs and Bayer 1983-see sheep model parameters) and high neonatal mortality. It is believed that record snowpack during May (Water Resources 1992) caused regionally adverse conditions during 1992 lambing season. The ratio of lambs/nursery sheep (including adult ewes, yearlings and 2 year old rams) was very low (4-18/100), and well below the ratio of 36-46/100 observed in the 3 GMS in 1989 (J. Carey, Yukon Fish and Wildl. Br. unpubl. data).

Harvest of sheep is restricted to full-curl or 8 year old males for resident and non-resident hunters. Since 1987, an average of 110 sheep were annually harvested in the Ruby Range mountains: 37% by residents and 63% by guided, non-residents. In the 3 GMS surveyed in 1992, the average annual harvest was 17 rams; a 3% harvest rate. First Nation harvest of sheep is not well known. Subsistence hunting of both males and females was traditional in certain winter ranges along Kluane Lake during the 1980s.

4. Hutshi elk herd

The introduction of 49 elk to the southern Yukon in the 1950s resulted in the formation of two small groups: The Hutshi and the Takhini Valley herds (Fig. 3c). The Hutshi Lake herd ranges in the southeastern study area and has remained at 40-50 animals (Hoefs 1990). The herd showed a wide range of calf survival rates during the late 1980s (Yukon Fish and Wildl. Br. 1990a, 1990b). Only 1 calf born in 1987 survived to the spring of 1988. Six calves were recruited in 1988-89. In 1989, 12 calves (28%) were born, but their fate was unknown past that summer.

The Hutshi herd is growth limited, having not exceeded 50 animals since the introductions. Long winters, relatively low forage availability, predation and poaching are potentially regulating Hutshi elk. Both the Hutshi and Takhini Valley herds are below the the minimum viable population size of 50 required for large herbivores to preserve short-term genetic integrity (Reed et al. 1986). Both herds are at risk of extinction due to demographic and environmental stochasticity. Management plans for both herds call for populations of 100 animals each (Yukon Fish and Wildl. Br. 1990a and 1990b).

5. Wood bison

Wood bison were introduced to the study area during the 1980s as part of the Canadian wood bison recovery program (Hoefs and Reynolds 1989). A total of 120 captive bison have been released to the Nisling area on the northeastern corner of the study area. The objective is to establish a viable, free-roaming population of more than 200 animals in the Nisling River watershed and adjacent areas (Hoefs and Reynolds 1989). An additional 50-60 bison have been born on the Nisling range. Portions of the herd have dispersed from the core Nisling area to the Aishihik Lake lowlands, West Aishihik River and a section of grasslands along the Alaska highway right-of-way. Potential factors limiting wood bison include disease, genetic contamination, predation, range conditions, land-use conflicts, competition with other wildlife, poaching (Wood Bison Recovery Team 1987) and vehicle collisions. To date, the most important mortality factor is vehicle collisions. Predation by wolves has not yet been documented, and it is not likely that wolves will quickly switch to exploit wood bison in the area.

6. Wolves and wolf/prey biomass index

Wolves have been censused in 12 areas of the Yukon since 1983, using snow-tracking and radiotelemetry techniques (Hayes et al. 1989). Both methods provide a minimum count of wolves in mid-late winter. Wolves were censused by snow-tracking methods in a 15,000 km^2 area in the experimental area during 10-17 January and 3-7 March, 1992. A total of 22 packs were located (16 seen, 7 estimated from wolf tracks only), for a total population of 135-158 pack wolves. Wolf density was 10-11.6 wolves/1000 km2, which is typical of other mountain ranges in the southern Yukon (Hayes et al. 1991). Average pack size was 6-7 wolves, slightly below other areas (R. Hayes, unpubl. data).

Keith (1983) and Fuller (1990) found a strong relation between the densities of wolves and the biomass of ungulates in an area, showing that wolf numbers are determined by ungulate food supply. Fuller (1990) presented a linear equation that predicts the wolf density from a prey biomass/wolf index. We calculated the ungulate prey biomass/ wolf index for Aishihik using the following data:

No. of prey/1000 km^2	X relative biomass*	No. of wolves/1000 km^2
92 moose	6	
40 caribou	2	
88 Dall sheep	1	+10-11
		=65-72

* see Fuller 1989

Values of 65-72 represents the lowest prey biomass/wolf index among 27 wolf/prey studies in North America (Fuller 1989). Other studies range from 112-659, with most in the 150-300 range. Based on a linear equation (Fuller 1989: 21) the expected wolf density should be in the order of 3-4 wolves/1000 km^2. The actual density of 10-12/1000 km^2 indicates that the numerical response of wolves is lagging behind a decline in ungulate prey, and the wolf population is likely an important factor limiting ungulate populations in the area. It is possible that snowshoe hare were a buffer, alternate prey for wolves, and especially important to wolf pup survival. Hare numbers crashed in the study area during 1990-92.

7. Brown bear and black bear

Brown bears have not been studied in the area, but local residents say that bears have increased around some communities in the past few decades. Larsen and Markel (1989) estimate brown bear density at 13-22 bears/1000 km^2 in the Coast Mountains, immediately south of the study area.

Since 1973, the annual reported bear harvest from the 20,000 km^2 experimental area was 9 bears, ranging from 3-17. From 1985-1990, females were 39% of the reported harvest. Since 1990, females have been 23% of the harvest. Brown bears are presently being studied in the front ranges of the St. Elias mountains (Parks Canada-University of British Columbia). Black bears have not been studied in the southern Yukon, but were confirmed predators of neonatal moose in an adjacent study area (Larsen et al. 1989a). There is no estimate of black bear density anywhere in the Yukon.

8. Other predators

Golden eagles, lynx, coyote and wolverine predate on ungulates, especially neonates. Golden eagles have been surveyed in the southern portion of the experimental area (Windsor 1979; D. H. Mossop, Yukon Fish and Wildl. Br. unpubl. data) and adjacent areas (Hayes and Mossop 1982, 1983, Mossop 1988) where large eagle populations occur. About 120 pairs are known in the southern 25% of the experimental area. This suggests a minimum breeding population of 300 pairs, with a non-breeding component that may number 100-120 birds.

Golden eagles are important predators of neonatal caribou calves in the northern Yukon (Mauer et al. 1982). Sheep lambs are preyed upon for a short period following birth (Hoefs and Nette 1979). Preliminary data indicate golden eagles mainly prey on ground squirrels and ptarmigan (Hayes 1977).

Wolverine and coyotes are capable of killing ungulates including Dall sheep adults (M. Hoefs, Yukon Fish and Wildl. Br., pers. comm.) and caribou. Lynx are known to be important predators of caribou calves in Newfoundland (Bergerud 1971) and have killed caribou calves in the Yukon (R. Hayes, Yukon Fish and Wildl. Br.). Lynx abundance was high during 1990-1992, but they have declined following a crash in snowshoe hare in 1992 (B. Slough, Yukon Fish and Wildl. Br. pers. comm.). Coyote abundance also appeared to be highest in recent years, but little is known of this canid's population dynamics in the Yukon. It is possible that eagles, lynx and coyotes were responsible for a significant portion of caribou calf and sheep lamb mortality in 1992, following the decline in snowshoe hare.

Untreated control populations

We plan to intensively study the demography of the Wolf Lake herd as the primary untreated control population, following population dynamics through population censuses, radio-telemetry and composition counts, at the same frequency as the experimental Aishihik and Burwash herds. The Chisana, Klaza, Glenlyon, Southern Lakes and a previously unstudied herd in the Big Salmon range (Fig. 3a) will be also monitored each fall to determine composition and recruitment rates to compare to the experimental area herds.

1. Wolf Lake Caribou herd

The Wolf Lake herd ranges roughly 225 km to the east of the study area in the northern Cassiar Mountains (Fig. 3a). It was studied from 1984 to 1987, providing data on population size, composition, adult mortality, harvest, range and movements (Farnell and McDonald 1989). The range of the Wolf Lake herd is isolated from human settlement and roads, and annual harvest is light (<10 per year). Because wolves, moose, and bears are also lightly hunted in this remote area, the predator-prey system is considered to be naturally-regulated. The Wolf Lake herd has similar range use patterns to the Aishihik herd with the exception that it winters in lowland boreal forests, rather than in alpine areas.

In 1987 the Wolf Lake herd was estimated to be 664 (±154), and was considered stable with a calf/female ratio of 28/100 and an adult radio-collar death rate of 9.8% (Farnell and McDonald, 1989). The Wolf Lake herd had a highly skewed ratio of 29 males/100 females, similar to the Aishihik herd.

The Wolf Lake Caribou herd is at a very low density in relation to its range. According to local knowledge it was once a much larger population. The Aishihik herd was also much larger according to local knowledge.

Wolves were censused by aerial snowtracking techniques in the Wolf Lake area during 1985 (Hayes and Bowers 1987) and in 1987 (Hayes and Baer 1987). Density was 9-11 wolves/1000 km^2 in both years, similar to the experimental area in 1992. .

Monitoring of adjacent caribou herds

Although the Chisana herd and the Klaza herd (Fig. 3a). will be monitored, these herds may not be valid untreated controls because they range close to the boundary of the proposed experimental area. Wolves will likely be removed in some portions of their winter and summer ranges. However, monitoring these populations may provide valuable insight to the effects of wolf control beyond the experimental area.

The Chisana herd ranges to the west of the study area, in the northern flank of the St. Elias Mountains. This herd of about 1,300 animals (C. Gardner, Alaska Dep. Fish and Game, pers. comm. 1992), uses a high mountain summer range along the Alaska-Canada boundary, and winters on the lower eastern flanks of the St. Elias Mountains in the northern portion of the Kluane Game Sanctuary. The eastern range of the herd abuts the western range of the Aishihik and Burwash herds, but there is no evidence of overlap, based on current or historical (Gauthier 1984) radio-telemetry locations of the 3 herds. Because the Chisana Caribou herd ranges mainly in Park and sanctuary areas in Alaska and the Yukon, harvest is very light.

The Chisana caribou herd has been studied since 1987. The herd has been in decline, showing extremely low calf survival rates to early summer, especially in recent years. In July 1992, only one calf was observed in a count of 1,200 caribou. Wolves were studied in the Chisana winter range along the Kluane Game Sanctuary between 1985-86 by Sumanik (1987). Some predation on caribou was recorded. Wolf density was 7-8/1000 km^2.

The Klaza herd ranges directly to the north of the study area. Distribution, movements, demography and habitat were studied between 1987 and 1990 (Farnell et al. 1991). The herd was estimated at 486 caribou in March 1989. The adult natural mortality rate was 4.9%, derived from the death rate of 17 collared female caribou. Harvest estimates averaged 8.7 caribou from 1979 to 1988, or 1.8% of the 1989 population estimate. Calf recruitment varied from 11% in 1987 to 24% in 1988. The adult sex ratio ranged from 48 males/100 females in 1987 to 33 males/100 females in March 1989. The herd was thought to be at a stable, low density.

2. Mayo area moose population

The Mayo area moose population lies 250 km northeast of Aishihik in the Pelly River ecoregion (Fig. 3b). Moose were at a density of 139/1000 km^2 in 1988 (Larsen et al. 1989c). Calf survival to 6 month of age (61 calves/100 cows) and recruitment rate (.13) was similar to Aishihik in 1990, although somewhat higher than Aishihik in 1981 and 1992. Based on the low moose density in Mayo we expect calf survival and recruitment rates to be low over the long term, thus provide a valid untreated control population to measure moose responses to wolf population reduction. Wolves were surveyed in a 30,000 km^2 area in 1988 and 1989 in the same area (R. Hayes, unpubl. data); density was 10 wolves/1000 km, the same as in the experimental area in 1992. A small caribou herd (100-200, Ethel Lake herd) ranges in the Mayo moose control area. Mountain sheep are also present but uncommon.

3. Ladue River Area Moose Population

The Ladue area moose population lies 250 km northwest of Aishihik, along the Yukon Alaska border (Fig. 3b). Moose were at a density of 168/1000km in 1989 (Larsen and Ward 1991). This density is similar to those documented in the experimental area. Calf survival to 6 months of age (45 calves/1000 cows) was similar to Aishihik in 1990, and recruitment rate (.11) was similar to the 1992 experimental area results. As in the Mayo area, we expect calf survival in the Ladue area to be low over the long term, based on the low moose densities found there in 1989. Hunting pressure is minimal in this area. Sheep and caribou are present but in low numbers, although Forty Mile Caribou have recently (1984) occupied the area in winter. The herd started to re-occupy the Yukon in the winter since 1984. Numbers vary from very few to up to 7000 depending on the year. Wolves were not previously censused in the Ladue area.

4. Lake Laberge area moose population

A second untreated population is located east of Lake Laberge (Fig. 3b). Although no previous surveys have been conducted in this region, we expect the density to be less than 200/1000 km^2. Hunting pressure is minimal in this area. Sheep and caribou populations are also present in the area. Due to the lack of moose population information this is a priority management area and will be studied as part of ongoing moose population inventory studies beginning in 1993. Wolves were not previously censused in this area.

5. Primrose Mountain sheep population

We propose to monitor an untreated control population of sheep in GMS 7-23 and 7-30 (Fig. 3c). This sheep population experienced a 2-fold decline in wolf abundance during the mid 1980s, but has experienced naturally-regulated wolf densities since 1988 (Hayes et al. 1991). Lamb production and population size were not related to wolf density in this population between 1982-86 (Barichello et al. 1989) Sheep population composition and trend were not different from GMS 5-36 in our study area, which served as an untreated control in the same period.

6. Takhini elk herd

The Takhini Valley herd occupies a burned seral community along the Takhini River basin, west of Whitehorse (Fig. 3c). This introduced herd has been at 20-41 animals since it was first monitored in the 1960s. Similar to the Hutshi herd, calf survival has remained low and is thought to be the most important factor limiting the growth of both elk herds.

A minimum of 4 calves were produced in the Takhini herd in 1986 and 1987. Seven calves were produced in 1988, accounting for 21% of the herd size in June - none survived to 1989. In September 1992, 9 calves were counted, but by late October only 1 survived. Two elk (1 calf and 1 adult) were known to have been killed by wolves since 1991. Relatively low forage availability, winter severity, competing land uses, predation, vehicle accidents and poaching are potentially limiting the size of this herd. Wolf predation is thought to be the primary factor regulating low elk density in both herds.

Methods and Measurements

A. Wolf population reduction

Wolves will be shot by Fish and Wildlife Branch personnel from a helicopter, in a 20,000 km^2 area that encompasses the experimental ungulate populations described above. The annual winter wolf population will be decreased by 75-85% of the pre-reduction (1992) size . Density will be reduced from 11 to 1.5-3.0 wolves/1000 km^2. Wolves were removed at this rate for 7 consecutive years in a nearby population (Farnell and Hayes in prep.) without affecting the annual recovery rates of wolves (2.0-2.4). This was because ingress and reproduction were annually constant, and not affected by the number of years of control. The initial period of wolf reduction is 5 years, after which control should be re-evaluated depending on caribou and moose population responses. Thereafter, wolf reduction could continue until population objectives are met, given acceptable ungulate population growth rates continue.

Wolf carcasses will be retrieved for necropsy study. Samples of muscle tissue will be analyzed to indicate the importance of caribou in the winter diet, through the radiocesium method (Holleman and Luick 1978, Holleman and Stephenson 1981). Carcass studies will allow direct study of the impact of wolf control on the wolf population, including natural mortality rates (in first year), recruitment rates, dispersal, body condition, genetic composition, reproduction, sex ratio, age class changes and food habits (see Farnell and Hayes, in prep.). A serological survey of wolves will show the incidence of important wolf diseases, including rabies, canine hepatitis virus, canine distemper, parvovirus and brucellosis. A tissue sample from each wolf will be genetically analyzed through mitochondrial DNA fingerprinting (Lehman et al. 1992) to determine the effects of wolf control on the genetic composition of Aishihik wolves.

In accordance with Section 9.2.3 of the Yukon Wolf Conservation and Management Plan, an inter-agency agreement with Parks Canada will ensure the protection of Kluane National Park wolves from being shot in the experimental area. Wolf packs along the park boundary will be radio-collared and their status will depend on their territorial activities, denning locations, and predation impact on caribou in the experimental area. We recognize that moose populations along the Kluane National Park border, which are outside of the Aishihik caribou range, will continue to be preyed on by park wolves. Wolves in the Kluane Game Sanctuary will be afforded the same protected status. Wolves have been previously censused in each untreated control area (Hayes and Bowers 1987, Hayes unpubl. data) and will be periodically re-surveyed.

B. Brown bear studies

Brown bear investigations will be conducted beginning in 1994 to determine their potential impact on caribou and moose. It is planned to radio-instrument a total of 8-10 bears during 1994 and 1995 and intensively monitor their activities during the first two weeks after caribou calving (June 1995). Both males and females will be followed. As caribou and moose populations increase, bears will again be monitored intensively to determine whether bear predation rates on caribou and moose calves is density-dependent or not. Understanding the nature of bear predation is critical to testing the wolf regulation models and our understanding of the possible causes of the recent caribou and moose population declines in the experimental area. It is possible that density-dependent bear predation, by itself, could regulate caribou and moose densities to low levels.

C. Prey population parameters

Population parameters of four prey species and wolves will be monitored before, during and after wolf removal in the experimental area, and in one or more untreated control areas, depending on the ungulate species. The following are key parameters of ungulate and predator populations that will be monitored to detect changes between experimental and untreated control populations: 1) population censuses of ungulates and wolves, 2) recruitment and population composition trends, 3) adult and calf mortality rates, 4) physical condition and pregnancy rates of adult cows and 5) study of brown bear predation on caribou and moose calves.

1. Population size

Changes in density and composition of moose and caribou will be periodically measured using stratified random sampling techniques (Gasaway et al. 1986). In the experimental area, the Burwash and Aishihik caribou herds will be censused separately during March 1993. At the same time, the Wolf Lake caribou herd will be censused. Moose will be periodically censused in two regions of the experimental area (Aishihik and Onion Ck.) and compared to two untreated control populations, which will be censused in 1993. Sheep will be annually censused by total count in June, and elk population size will be estimated from total counts in late October. Elk counts will be radiotelemetry assisted.

2. Recruitment rate

Changes in the annual rate of recruitment will be measured for all 4 species in experimental and control areas using 3 techniques, including population census interpolation (all prey), ratio of calf/radio-collared cow for caribou (n=40 females) and and elk (n=6 females), and annual rut composition counts (caribou, elk). Annual moose recruitment will be measured by the proportion of calves observed in late winter moose composition counts. For caribou, moose and elk, we expect that the recruitment rate will increase in the first year, then decrease slightly as the proportion of non-breeding, immature animals increases in the population. This will depress the potential recruitment rate, until a large portion of these young animals reach breeding age and produce calves of their own. Recruitment rates should be greatest after 4-5 years when the breeding population should be skewed to middle-age, which is the age group with the highest fecundity.

3. Rates of adult cow mortality

Adult mortality rates of ungulates in the experimental and untreated control areas will determined by two techniques: 1) by census interpolation every 4-5 years for moose and caribou, and annually for elk and sheep; and 2) by periodically monitoring the survival of radio-instrumented female caribou and elk equipped with mortality-sensing transmitters. Monitoring will be in June-July, October, December and April. Age-specific mortality rates of sheep will be determined by monitoring age and sex composition in June by horn characteristics. For moose, we will not be able to measure annual adult mortality rates, but an average rate will be estimated from census interpolation after 5 years.

4. Pregnancy rates and physical condition of females

Pregnancy rates (blood progesterone-palpitation) and physical condition (morphological indices) of females will be assessed for cow caribou and elk in experimental and untreated control areas in February 1993. These measurements were previously collected from 50 Aishihik caribou in December 1991. We will periodically monitor changes in both parameters, by annually recapturing a small sample of females for radiotelemetry.

5. Peak of calving, mortality schedule and sex ratio of caribou and elk calves

This study design does not include the handling of caribou calves unless there is no substantial change in their annual survival rates. Survival rates of calves will be annually monitored in experimental and treatment areas by seasonally following radio-collared cow caribou and elk. For caribou, we will monitor birth rates of radio-instrumented cows during May and June to determine calving chronology. Mortality rates of associated, uncollared calves for both caribou and elk will be assessed at the same intervals as shown for adult mortality studies (see above). Sex ratios of caribou calves will be annually assessed during fall composition counts.

D. Weather variables

Deviations from normal weather patterns can have positive or negative effects on animal population dynamics. For the effects to be detectable in wide-ranging populations, the weather variations should be evident on a regional level. Weather stations in the experimental area are currently operated by Environment Canada at Burwash, Haines Junction, Otter Falls (Aishihik Lake), Braeburn and Carmacks. We expect these sites will provide an accurate, regional picture of annual weather patterns. Each station collects daily maximum and minimum temperatures, precipitation and monthly snow accumulations. Long term averages (over 20 years in some sites) can be compared with annual data to determine deviations from normal conditions. In addition to the 5 permanent stations, 8 snow survey courses are monitored by Water Resources (Dept. of Indian and Northern Affairs) in the Aishihik area. These will augment snow depth and density measurements collected by Fish and Wildlife Branch staff on important caribou and moose wintering areas. Important factors that could limit productivity and survival will be considered including:

1. Duration of snow cover and wind velocity; particularly related to conditions during ungulate birth periods.
2. Summer precipitation, as it relates to forage production.
3. Winter precipitation and wind, as it relates to forage availability.
4. Winter temperature and precipitation as an index of winter severity.

E. Food habits and range conditions

Forage/nutrition will be measured for caribou and elk by annual, late winter collections of fecal samples, and physical condition assessment of radio-collared females. Collections will be compared to previous ones made for caribou in 1990 (Farnell and Gilroy in prep.) and elk (R. Florkiewicz, Yukon Fish and Wildl. Br. unpubl. data).

E. Data collection

The Geographic Information System (GIS) is a tool that integrates and analyzes spatially-related information. For a study of this size, it is essential that data collection be coordinated and efficiently handled. Digital topographic maps at 1:250,000 scale are available to create study area base maps. Universal Transverse Mercator (UTM) coordinates will be be used to plot all geographic information such as census data, radio-collar locations, weather and snow data, and other wildlife information.

In addition to empirical data, subjective information about ungulate population trends and wolf abundance will be collected from residents of the study area each year. The Burwash and Champagne-Aishihik First Nations will maintain a record of band member accounts of ungulate distribution, abundance, and recruitment in various areas of the experimental area to compare to empirical survey results. Trappers will be asked for their estimation of changes in the abundance of ungulates, wolves and bears in an amended, annual trapper questionnaire.

F. Ungulate harvest

During the 5-year wolf reduction period all hunting of caribou and moose should remained closed. Any continuation of harvest should follow the guidelines recommended in the Yukon Wolf Conservation and Management Plan (Yukon Wolf Planning Team 1992). It is recommended that no more than 2% of the populations of moose or caribou should be harvested in all experimental and treatment areas to ensure that hunting does not affect the design. All harvest should be directed at males only. Elk harvest should remain closed for both the Hutshi and Takhini herds. There should be no change to the full-curl, male Dall sheep harvest regulations.

Ungulate Response Models

To project prey population responses to reduction in wolf numbers, we must predict how wolf predation will affect two important components of population dynamics: natality and mortality. We do not expect that wolf control will affect rates of ingress or egress of caribou, moose, sheep or elk .

1. Caribou

Natality and Mortality

Bergerud (1980) estimated an average birth rate of 86% for most North American caribou herds. Pregnancy rate was 92-96% in the Aishihik herd in 1991-92. Small caribou herds commonly have high adult and calf mortality rates. In northwestern Canada and Alaska where wolves were naturally-regulated, natural mortality rates of adult caribou were 6-9% (Gauthier 1984-this study area, Burwash herd), 22-25% (Edmonds 1988-Alberta), 18-21% (Bergerud and Elliot 1986-northern B. C.), 28% (Farnell and Hayes in prep.-Yukon.), 8% (Seip 1990-central B. C.), 7-19% (Davis et al. 1989) and 13-27% (Hatler 1985-northern B. C.).

In most years, the percentage of caribou calves in the fall (5 months old) population is the same as late winter (10 months), and is a suitable parameter for measuring population recruitment (R) (Gauthier 1984, Bergerud and Elliot.1986, Davis et al. 1989, Adams et al. 1989). This suggests that calves and cows experience equal survival rates during September to April, independent of their age (Adams et al. 1989). Where wolves or bears are common, herds typically lose 50% of the calf cohort before fall with most of the mortality happening during the first few weeks of life (Bergerud 1980, Bergerud and Elliot 1986, Gauthier 1984, Gauthier and Theberge 1986, Hatler 1985, Adams et al. 1989, Davis et al. 1989, Seip 1990, Farnell and Hayes in prep.). In low density caribou herds experiencing naturally-regulated wolf predation, populations will generally decline if calf recruitment is less than 30-35 calves/100 females during fall counts. Ratios were 17-28/100 in 3 declining or stable woodland herds in the southern Yukon (Farnell and Hayes in prep.), 28-41/100 in the Denali herd (Adams et al. 1989), 30/100 in the Wells Gray herd (Seip 1990), 9-45/100 in the Spatsizi herd (Hatler 1985), and 29-46/100 in the Delta herd (Davis et al. 1989). To offset natural mortality of adults, caribou recruitment should be about 10-12% (Fuller and Keith 1981, Bergerud and Elliot 1986), and higher if hunting mortality is substantial. Recruitment expressed as a percentage of the population should be carefully used, for it can vary depending on the degree that sex ratios of adults is skewed. For this paper recruitment will be expressed as the ratio of calves/100 females.

Wolf control has been conducted on the range of 3 relatively small caribou herds in Alaska (Delta herd -Gasaway et al. 1983), Yukon (Finlayson herd - Farnell and Hayes in prep.) and British Columbia (Level Mtn and Kawdy - Bergerud and Elliot 1986). Finlayson adult mortality fell from 28% to 11% after wolf control. Bergerud and Elliot (1986) reported 8% natural mortality when wolves were reduced and 12% after wolves recovered. After wolf control, fall calf/cow ratios increased 2-4 fold (up to 50-60 calves/100 females) in the 3 herds, while neighbouring or control herds did not increase substantially (Bergerud and Elliot 1986, Gasaway et al. 1983, Farnell and Hayes in prep.). After wolf control caribou increased at exponential rates of 0.06 in Level Mountain-Kawdy, 0.17 in Finlayson and 0.21 in the Delta herd (Davis et al. 1989).

Changes in harvest rates should only affect adult mortality because recruitment rates are not directly influenced by harvest. A 3 year hunting closure, by itself, did not cause the Delta caribou herd to grow (Gasaway et al. 1983). The Aishihik herd is likely still declining after 2 consecutive hunting season closures. The combined impacts of hunting closure and wolf control should best assist the recovery rates of caribou, as shown in Finlayson (Farnell and Hayes in prep.) and the Delta caribou herds (Gasaway et al. 1983).

Caribou response model

The impacts of wolves, bears, coyotes, lynx and golden eagles on caribou recruitment and adult mortality rates is not known. It is possible that predators besides wolves could be important, based on other caribou studies (Adams et al. 1989, Page 1985). Based on other studies where wolves were reduced, it is expected that the ratios of calves/100 females during October should increase to above 30-35/100 after wolf control, and adult mortality should be held at 5-10% in the Aishihik experimental herds. It is predicted that caribou calf recruitment and adult mortality will not change at the same rate in the untreated Wolf Lake herd before, during and following the wolf reduction period.

In this response model, it is predicted that both caribou herds in the experimental area will increase by a factors of 2.0 after 5 years of wolf control. This represents an annual average instantaneous rate of 0.15. Based on a 1992 estimate of about 600 animals, the Aishihik herd size should grow to 1,200 by March 1998. If other factors beside wolves strongly depress recruitment, and calf ratios remain below 30-35/100 females after 2 years of wolf control, then the reduction program should be suspended and re-evaluated. In order to test if the TWO STABLE STATES MODELS exists, caribou must be allowed to grow above the unstable boundary *B*. In this case, we do not know what this boundary density is. Because the Aishihik population declined from 1,500 caribou, it is likely that the boundary is above this. It is arbitrarily predicted that *B* is at 2,500 caribou, the *target* population size for the Aishihik herd. It is also predicted that when population size exceeds this number, then caribou will cease to be regulated by wolf predation. It is not possible that this caribou target will be achieved after 5 years of wolf control (1998). Continued wolf control should be considered depending on population growth rates observed to 1998.

Bergerud and Elliot (1986) showed that for most studied caribou herds, adult mortality is correlated with wolf abundance and recruitment. Their regression analysis indicated that caribou will decline to low density if wolf density exceeds 6.5/1000 km^2. Bergerud (1974, 1985) argued that caribou require refuge areas when moose biomass regulates wolf numbers to high density. It is predicted that if both moose and caribou densities increase after wolf control, caribou could exceed threshold boundary *B* of the TWO STABLE STATES MODEL. This should happen because wolf predation rates on caribou will be density-independent or depensatory, due to wolf selection for moose.

2. Moose

Natality and Mortality

Survival of prime-age animals plays a greater role in population growth than survival of either juvenile or old-aged animals (Eberhardt 1985). Female moose are most productive between 5.5 and 11.5 years (Markgren

1969). Natality rates could be increased by wolf control if the moose age structure changes towards middle-aged. In an adjacent, low density moose population that was skewed to old-age, Larsen et al. (1989a) documented a pregnancy rate of 84%, a birth rate of 114 calves/100 females and a 28% twinning rate. The Aishihik twinning rate was 8% in 1990 (Larsen and Ward 1991).

Data for natural rates of adult moose mortality range from 10-20% per year where wolves are common (Peterson 1977, Hauge and Keith 1981, Gasaway et al. 1983, Messier and Crête 1985, Hayes et al. 1991) and 4-11%/year where there are few wolves (Mytton and Keith 1981, Gasaway et al. 1983, Messier and Crête 1985). For our model we assumed 12% of adults were annually removed by wolves before wolf control, based on studies by Hayes et al. (1991) for a neighbouring population. We predict that this should fall to around 6% (Gasaway et al. 1983) after wolf removal, depending on the number of wolf groups in the area the following winter (Walters et al. 1981, Hayes et al. 1991, Farnell and Hayes in prep.). Survival of adults could be increased if packs are removed throughout the winter (Hayes et al. 1991).

The percentage of calves was high in 1990 but low in 1992. Yearlings were low in both years (Larsen and Ward 1991, D. Larsen, unpubl. data). Overwinter wolf predation on calves was high in two adjacent low density moose populations (Hayes et al. 1991, Hayes unpubl. data), and wolf predation could be responsible for the removal of most Aishihik calves during winter. The low recruitment and a combined, high natural and hunting mortality of adults can explain the moose population decline observed during the 1980s.

The maximum intrinsic rate of increase for moose is about 0.25 (Fryxell et al. 1988). The numerical response of moose to declines in wolf numbers has varied widely from a high of 0.23 to no change in 5 study areas (*see* Boutin 1992, Table 2) . The highest rates of increase were in areas where brown bears were not common (Gasaway et al. 1983-0.23). Where brown bears and wolves were sympatric, moose showed variable responses to wolf control. Moose increased sharply with intensive wolf control (Larsen and Ward in prep.-0.17); moderately with both bear and wolf removal (1.6 fold, Ballard et al.

1987), and slowly after wolf control (Gasaway et al. 1992-0.05, Larsen and Ward 1990-0.07).

Moose response model

For Aishihik, we do not know the impacts of bears, but assume that they will be an important factor limiting recruitment, based on studies in 2 neighbouring populations (Larsen et al. 1989a, Gasaway et al. 1992). It is expected that moose will grow at an annual exponential rate of 0.08-0.12 after wolf control, assuming that adult mortality could decline to about 6%, and the percentage of long yearlings could increase to 13-20%. Based on these projections, we expect that after 5 years of wolf control, moose density could theoretically increase to 88-106/1000 km^2.in the southern part of the experimental area (Aishihik) and to 173-208 /1000 km^2 in the northern part (Onion Creek). If bear predation on calves strongly depresses calf ratios below 40/100 adult females, or 16% calves in the early winter population, then wolf reduction should be suspended and re-evaluated. The moose density goal for the experimental area is at least 200/1000 km^2. This represents a population objective of 4,000 moose for the whole experimental area.

Messier (in prep.) argued that in the presence of wolves, moose should stabilize at a high density of about 1300/1000 km^2. If the growth rate is reduced by 5-10% because of density-independent bear predation, then a low density equilibrium is predicted. He estimated that wolves will regulate moose density to a single low equilibrium (200-400/1000 km^2; *A*, Fig. 1.3), if moose do not exceed 650/1000 km^2 (unstable boundary *B*, Fig. 1.1). We will incorporate these boundary densities in our model, but we do not expect that moose densities will exceed this boundary before wolf populations have recovered in the study area, unless wolf reduction is applied for a protracted period (>10 years).

3. Dall sheep

Natality and mortality

Dall sheep are uniparous (Hoefs and Bayer 1983) but annual pregnancy rates have not been well-studied. In two studies (Nichols 1978, Simmons et al. 1983) 84-100% of adult females and 43-75% of yearling females were pregnant in winter. Burles et al. (1984) compared 14 Yukon populations and found an annual range of 16-42 lambs/100 nursery sheep during early July, showing that a large number of neonatal lambs are lost during the first 2 months after birth. These variations have been related to winter forage availability that influences natality rates and survival rates of lambs over their first winter (Hoefs and Bayer 1983, Burles et. al 1984). Winter forage is primarily limited by snow depth. Severe winter temperatures may also influence survival by elevating energy requirements of sheep (Hoefs and Bayer 1983, Burles and Hoefs 1984, Burles et al. 1984, Barichello and Carey 1988). A weather-related, winter die-off of 25% was reported by Burles and Hoefs (1984) in Kluane Park, adjacent to our study area. Barichello and Carey (1988) reported a 40% decline in sheep in the central Yukon, relating it to severe winter conditions in 1 or more years. Winter die-offs were reported in Alaska by Murie (1944) in Denali National Park and by Nichols (1978) on the Kenai peninsula (40%). Extremely low lamb/ewe ratios in Yukon areas in 1992 were believed to be related to deep winter snow and cold spring lambing conditions in 1992 (J. Carey, Yukon Fish and Wildl. Br. pers. comm. , R. Breneman, Kluane Nat. Park pers. comm.).

Wolf predation on mountain sheep does not appear to be important, or regulatory (Gasaway et al. 1983, Sumanik 1987, Barichello et al. 1989, Hayes et al. 1991). In the Coast Mountains south of the study area, Hayes et al. (1991) found sheep were important to a few wolf packs, and there was a weak positive relationship between sheep kill rates and declining moose density. Sumanik (1987) argued that wolves that relied mainly on sheep were limited to low density because individual sheep biomass was low, and Dall sheep were less vulnerable to wolf predation compared to other prey. Burles and Hoefs (1984) observed especially high rates of predator-related mortalities during a severe winter. That winter, coyotes were the most important predator of adult sheep, followed by wolves. Burles and Hoefs (1984) speculated that sheep were alternative prey that coyotes switched to, following a crash in snowshoe hare and willow ptarmigan (*Lagopus lagopus*) populations.

Sheep response model

The large-scale reduction of wolves did not change sheep recruitment rates or population size in Alaska (Gasaway et al. 1983) or in the east-central Yukon (J. Carey, Yukon Fish and Wildl. Br., unpubl. data). We predict that the STOCHASTIC MODEL will best describe wolf-sheep dynamics in this experiment. Annual variations in lamb production and cohort survival rates, and population size should not be related to wolf numbers, but be related to regional stochastic events that will equally affect sheep demography in the experimental and untreated control areas at the same time.

4. Elk

Natality and mortality

Population characteristics of elk have been examined extensively (Picton 1961, Knight 1970, Flook 1970, Barimore 1980, Houston 1982, Taber et al. 1982). Elk are uniparous. Pregnancy rates of females older than 2 years is high (79-86%), and low (13%) for yearlings (Houston 1982). Because elk hide neonates for the first month of life, perinatal mortality losses are not well-understood. Black and brown bears have been found to prey heavily on elk neonates (Schlegel 1976, French 1989) removing a high proportion before winter. Barimore (1980, cited in Houston 1982) found the highest portion of calf mortality was overwinter. Houston (1982) found a high correlation between the number of calves alive in early winter and population recruitment. Where elk are abundant, wolves prefer them over other ungulates (Carbyn 1983).

Elk response model

It is reasonable to expect 20-50% of reproductive females will lose calves by fall, based on the literature and empirical data for the Takhini and Hutshi populations. Over the short period these two small herds have been monitored, overwinter calf survival has been 0-100% with evidence that wolf predation is the primary cause of mortality. There is no evidence to suggest that maternal condition or disease has been limiting recruitment (R. Florkiewicz, Yukon Fish and Wildl. Br. pers. comm.), or calf production and population growth is different between herds. Adult mortality was less than 10% during the late 1980s in the Takhini elk herd (R. Florkiewicz unpubl. data).

Elk population change and recruitment rates will be monitored by radio-instrumenting 6 females in each herd. Radio-instrumented and associated females will be periodically followed throughout the year, and calf and adult survival rates will be measured seasonally. Population size will be the total count of radio-tagged and associated females and other animals that are found during an intensive search of the known range of each herd during late winter. It is expected that female fecundity is 75% in both herds. It is predicted that 50% of Hutshi calves that are born will survive overwinter following wolf control. In the Hutshi herd, an estimated 20-30 females should retain 10-15 calves through the first winter after wolf control. Population size will increase each subsequent year, but recruitment rate (% of calves) will fall off after the first year when yearlings with low reproductive potential will become more common Based on an initial population model of 40 animals, equal sex ratios of calves and equal survival rates of immature and adult animals, it is predicted that the Hutshi herd will increase to 90-100 animals after 5 years of wolf control. Herd size should not change in the untreated control Takhini herd.

APPENDIX 1

Conditions to Implement and Continue Wolf Control

The draft Yukon Wolf Conservation and Management Plan (YWCMP) requires a series of conditions that must first be met before wolf control can be considered. It also sets out further conditions to continue wolf control, depending on ungulate population responses. The following are some of the important conditions, and how they apply to caribou and moose management problems in the experimental area.

To consider wolf control, there must be reasonable evidence that wolves are a primary limiting factor and the ungulate population must be either 1) threatened with local extinction, or 2) at low density and harvest must be closed for conservation purposes for at least 2 years (Section 9.1.1, 2, and 3: page 10). Hunting on the Aishihik herd was stopped in 1991 by all hunters. Biological studies of caribou are in their third year; the abundance of wolves and ungulates and the harvest of ungulates, wolves and bears are known. However, the number of bears are unknown (9.1.3 i) and it is not known how caribou calf survival is affected by bear predation (9.1.3 ii) . There is evidence from 3 other wolf reduction programs (Gasaway et al. 1983, Farnell and Hayes in prep., Bergerud and Elliott 1986) that caribou are primarily limited by wolf predation. Research in the experimental area identified wolves as the major factor limiting the Burwash caribou herd (Gauthier and Theberge 1986), and wolf/ungulate biomass ratios suggest wolves are presently an important factor limiting both caribou and moose in the area. However, other predators including coyote, lynx and golden eagles could also be important factors limiting caribou calf survival in recent years.

Brown bears are an important calf mortality agent in the Denali caribou herd in Alaska (Adams et al. 1989). This design does not include a population study of bears in the experimental area. This is mainly because of the cost and the long period of research that is required before there is sufficient empirical data on bears. Instead, it is proposed to directly study the impacts of brown bears on caribou calf survival beginning in 1994, if calf survival does not improve after wolf reduction.

The draft YWCMP makes 11 recommendations for implementation and follow-up to wolf control (Sections 9.3.1 to 9.3.11). It identifies helicopter-assisted hunting as the most effective means of controlling wolves. It also recommends that there be significant increases in calf survival rates after 2 years of wolf control or the program should be suspended. If calf survival is sufficient, then the program can continue to 5 years, when the ungulate population size must reach the predictions of the experimental design or the program will be suspended. We propose to continue wolf control if either caribou or moose show immediate and substantial increases (see caribou and moose response parameter). Caribou may indirectly benefit from increased moose densities (Bergerud and Elliot 1986), due to a displacement of wolf predation away from caribou. To meet the recommendations of the YWCMP, all moose hunting should be suspended in the experimental area. If only sheep or elk show a response after 2 years of wolf control, we propose to suspend the program.

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Fig. 1. Theoretical wolf-prey models in nature and after wolf predation response is depressed. A and C are stable state equilibria and B is a unstable boundary where wolf predation regulates prey back to low density (A), and food supply regulates prey to higher density (C). In perturbed models 1.2, 1.4 and1.6 there are two possible periods of wolf control: curve 1 is expected by short-term (one year) wolf control and curve 2 is longer-term (2 or more years). * is possible wolf predation effect caused by a time lag in wolf numerical response to declined prey density. In 1.9 and 1.10 the recruitment curve declines with density exposing a possible extinction outcome for both SINGLE AND TWO STABLE STATES MODELS.

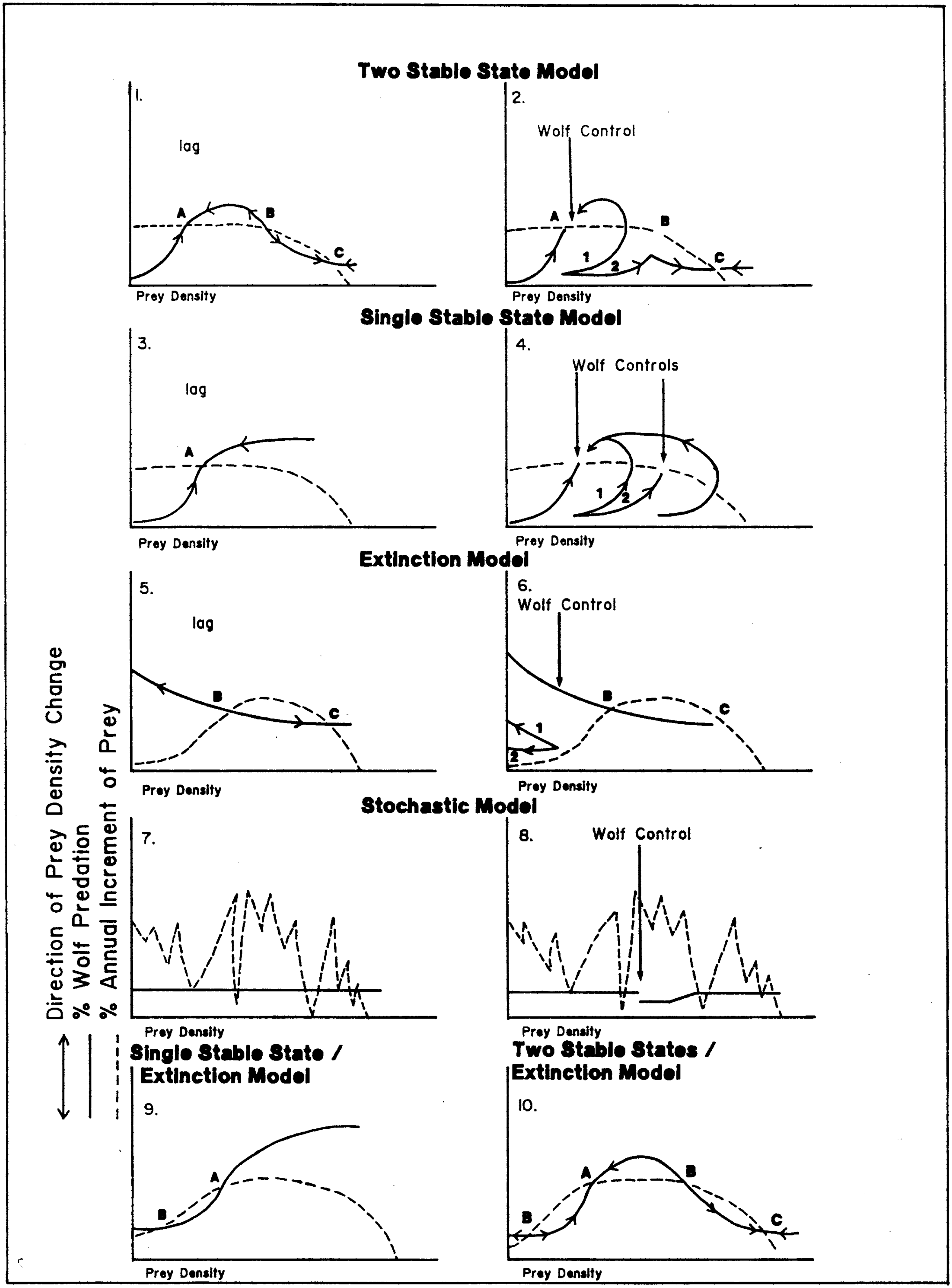

Two Stable State Model
1.
lag
A
B
C
Prey Density
2.
Wolf Control
A
B
1
2
C
Prey Density
Single Stable State Model
3.
lag
A
Prey Density
4.
Wolf Controls
1
2
Prey Density
Extinction Model
5.
lag
B
C
Prey Density
6.
Wolf Control
B
C
1
2
Prey Density
Stochastic Model
7.
Prey Density
8.
Wolf Control
Prey Density
Direction of Prey Density Change
% Wolf Predation
% Annual Increment of Prey
Single Stable State / Extinction Model
9.
A
B
Prey Density
Two Stable States / Extinction Model
10.
A
B
B
C
Prey Density

Fig. 2. Location of the Aishihik experimental area in the southwestern Yukon.

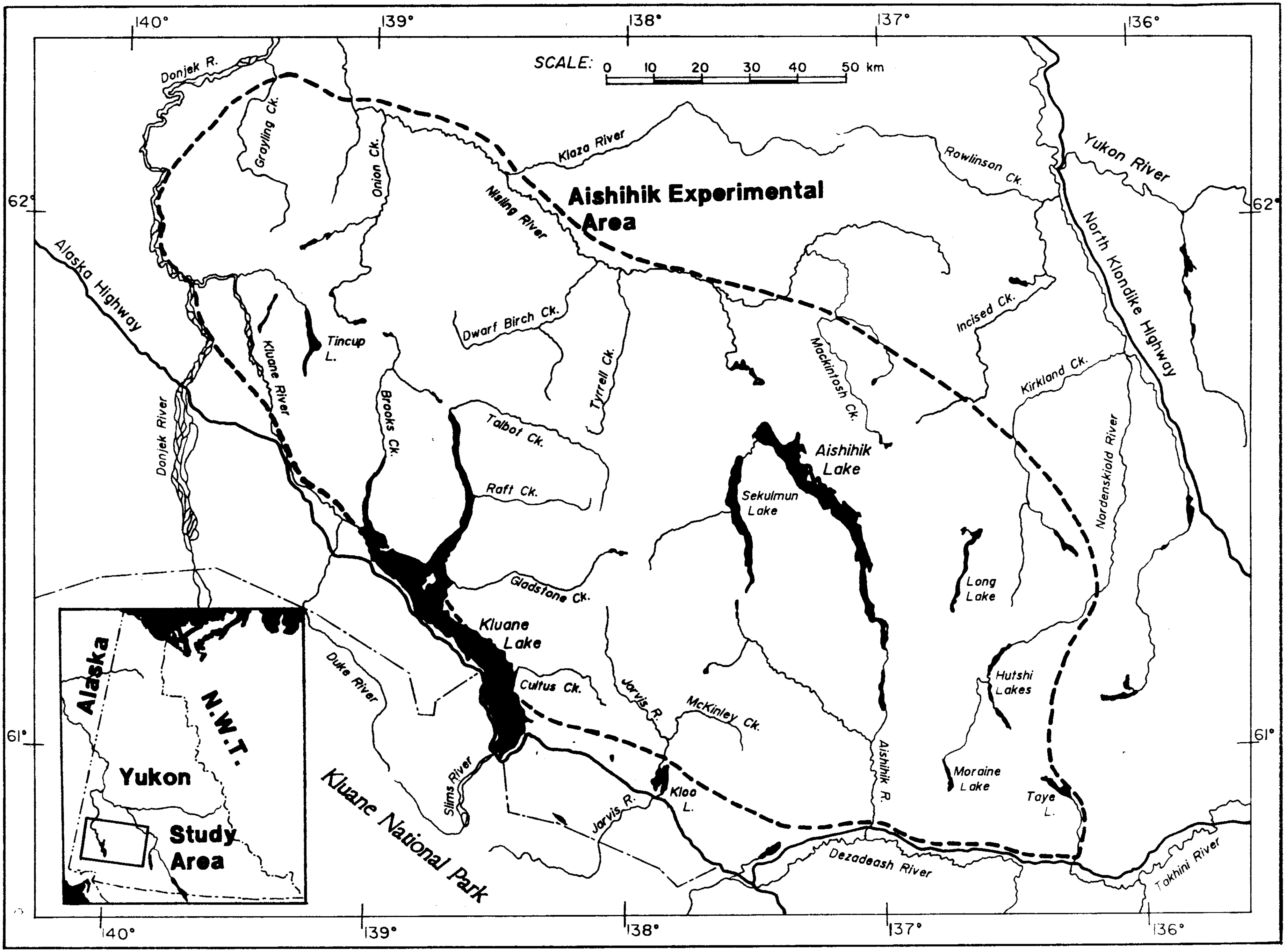

140°
139°
138°
137°
136°
SCALE: 0 10 20 30 40 50 km
62°
61°
Aishihik Experimental Area
Donjek R.
Grayling Ck.
Onion Ck.
Klaza River
Nisling River
Rowlinson Ck.
Yukon River
North Klondike Highway
Alaska Highway
Kluane River
Tincup L.
Dwarf Birch Ck.
Tyrrell Ck.
Mackintosh Ck.
Incised Ck.
Kirkland Ck.
Donjek River
Brooks Ck.
Talbot Ck.
Raft Ck.
Aishihik Lake
Sekulmun Lake
Nordenskiold River
Gladstone Ck.
Long Lake
Kluane Lake
Duke River
Cultus Ck.
Jarvis R.
McKinley Ck.
Hutshi Lakes
Aishihik R.
Slims River
Kloo L.
Moraine Lake
Taye L.
Kluane National Park
Jarvis R.
Dezadeash River
Takhini River
Alaska
N.W.T.
Yukon
Study Area

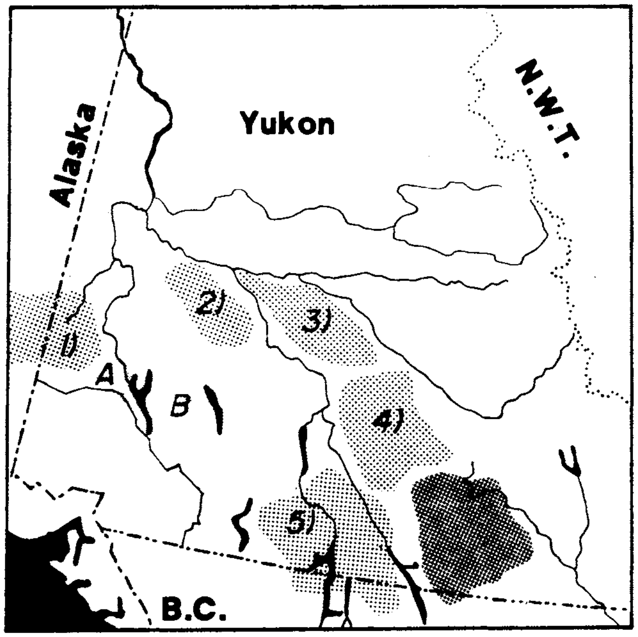
Fig. 3. Locations of experimental and untreated control study areas for caribou (3a), moose (3b), and sheep and elk (3c).

3a) Caribou

▩ *Primary Control Herd (Wolf Lake)*

☐ *Experimental Herds*
A)Burwash B)Aishihik

▒ *Adjacent Caribou Herds*
1) Chisana Herd
2) Klaza Herd
3) Glenlyon Herd
4) Pelly Herd
5) Carcross Herd

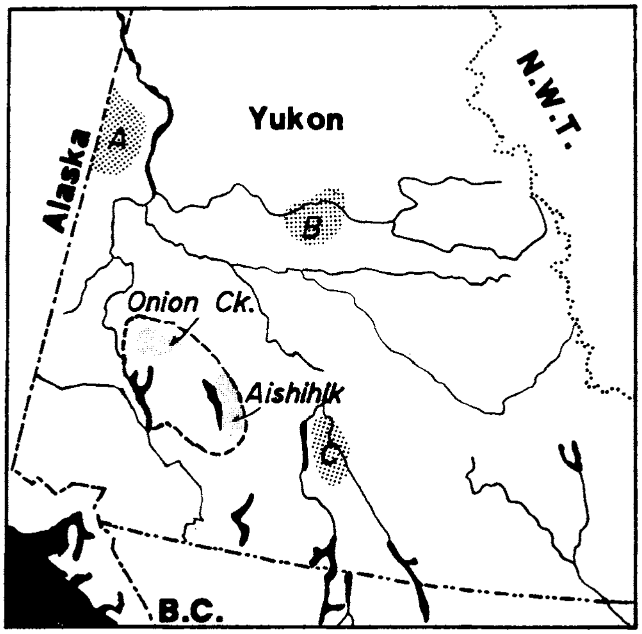


3b) Moose

--- *Boundary of Experimental Area*

☐ *Experimental Populations*

▩ *Untreated Control Populations: A) Ladue*
B) Mayo
C) Laberge



3c) Sheep and Elk

---*Boundary of Experimental Area*

☐ *Sheep Herds*

▩ *Elk Herds: A) Hutshi Elk Herd*
B) Takhini Elk Herd