Response of Caribou, Moose and Dall Sheep to Reduction of Wolves in the Aishihik Area, Yukon

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Abstract

We conducted a large scale, controlled experiment to study the responses of declining woodland caribou (*Rangifer tarandus*), moose (*Alces alces*), and Dall sheep (*Ovis dalli*) to a 5 year reduction in wolf (*Canis lupus*) numbers in the Aishihik area in the southwestern Yukon. We monitored 3 caribou herds, 3 moose, 1 Dall sheep, and 3 wolf populations as contemporary controls. We tested hypotheses that wolf predation was the major factor limiting recruitment, adult survival, and population size for the 3 ungulates in the Aishihik area. Caribou productivity, forage quality in winter, disease, snow depth, snowmelt phenology and migration were also assessed. For moose, we also examined snow depth and summer growing season.

We found evidence that wolf predation strongly limited recruitment of caribou and moose, and survival of adult moose. We found only weak evidence that wolf predation limited adult survival of caribou. We found no evidence that Dall sheep recruitment or adult numbers responded to reduced wolf numbers.

Wolf predation and human hunting were the probable main causes of caribou and moose declines before our study. Reduction in hunting contributed to the increase in the treated Aishihik caribou herd, but lower predation by wolves was more important than harvest reduction to the moose increase in the Aishihik area.

We hypothesize that woodland caribou herds are linked to the population dynamics of low-density moose in the Yukon. We conclude that natural predation is the main force maintaining low abundance of moose, and that harvest rates should be set conservatively at 0% to 5% for moose and caribou.

To increase the sustainable harvest of ungulates, we propose 3 methods to reduce the losses of ungulates to predators: sterilize wolves, hunt and trap wolves, and allow wildfires to modify moose and caribou habitat.

We evaluate large scale wolf-prey experiments and identify design problems including replication of predator treatments, hunting as a confounding second treatment, and the difficulty in randomizing effects in management experiments. We recommend smaller scale, replicated experiments be applied to continue to examine the long-term effects of predation.

Introduction

There is compelling evidence that predation by wolves (*Canis lupus)* is a primary force limiting moose *(Alces alces*) and caribou *(Rangifer tarandus)* in Alaska (Gasaway et al. 1983, 1992; Ballard et al. 1987, Boertje et al. 1996) and the Yukon (Gauthier and Theberge 1985, Farnell and McDonald 1988, Jingfors 1988, Hayes et al. 1991, Hayes and Harestad 2000*a*). Nevertheless, it is difficult to determine the additive or compensatory nature of predation without proper experimental designs (Gasaway et al. 1983, Boutin 1992, National Research Council 1997) or empirical wolf-prey models (Thomas 1998, Messier 1994, Hayes and Harestad 2000*a*).

One way to study predation is to reduce its effect on a selected prey population and monitor other 'control' populations where predation is not altered (Gasaway et al. 1983, 1992). Using this design, quantitative predictions can be tested against observed responses. In most wolf reduction studies, wolf numbers are not reduced long enough, prey and wolf responses are not adequately followed, or the experimental design is inadequate to expose the relative effects of wolf predation compared to other limiting factors (National Research Council 1997).

In the Aishihik (Ay-shee-ak) area of the southwest Yukon, people first became concerned about declining numbers of caribou, moose and Dall sheep (*Ovis dalli*) during the 1980s (Hayes 1992, Allen 1994, Johnson 1994). By 1990, R. Farnell (Yukon Department of Renewable Resources, unpublished data) reported declines of about 50% in both the Aishihik and Kluane caribou herds compared to earlier studies (Larsen 1981, Gauthier and Theberge 1985). Moose declined by more than 60% between 1980 and 1992 (Larsen and Ward 1995), and Dall sheep numbers also decreased in the area (J. Carey, Yukon Department of Renewable Resources, unpublished data). Based on ungulate and wolf densities in the Aishihik area in 1992, Hayes (1992) estimated a ratio of 65 to 72 ungulate prey biomass units per wolf - lower than any value reported in the literature (see Fuller 1989). Gauthier and Theberge (1985) estimated that wolf predation was responsible for 46% to 72% of the annual mortality of the Kluane caribou herd. In addition to predation, local people believed overhunting was partly responsible for the declines in caribou and moose (Hayes 1992, Allen 1994, Johnson 1994).

Our study was preceded by a series of political and societal events that influenced the research design. In 1992 the Yukon government solicited from a citizens' team a plan to manage wolves in the Yukon. The Yukon Wolf Conservation and Management Plan (Yukon Wolf Planning Team 1992) provided ethical and scientific guidelines for managing wolves, including conditions for conducting wolf reductions. The plan restricted our study in 2 important ways: 1) by limiting wolf reduction to a single treatment area, increasing pseudoreplication error (Hurlbert 1984); and 2) by requiring that hunting be closed during wolf reductions, adding a second confounding treatment effect. Our experimental design was based on a public workshop that included academic ecologists, other biologists and members of the public (Government of Yukon 1992). The study design (Hayes 1992) included a series of hypotheses and predictions about ungulate responses based on previous wolf reduction studies in Alaska (Gasaway et al. 1983, 1992) and the Yukon (Farnell and McDonald 1988, Larsen et al. 1989).

In this paper, we report on a 5-year wolf reduction experiment. We compare temporal responses of moose, caribou and Dall sheep in the Aishihik area with untreated, control populations. We address other possible explanations for observed responses and discuss management models and implications of our research. We also examine the benefits and limitations of experimental approaches to studying large-scale wolf-prey relations.

Experimental Design and Hypotheses:

Our experimental approach was to each year reduce wolves in a large area to about 20% of their pre-treatment density, and then compare population size, recruitment, and adult survival of woodland caribou, moose, and Dall sheep with control populations. We compared wolf numbers in Aishihik with 3 control areas where wolves were counted 1 winter during the same period.

We examined other explanations for ungulate responses by studying the effects of disease, winter food habits, and productivity on caribou herds, and by examining the influences of summer weather, snow depth, and changes in harvest on both caribou herds and moose populations.

A series of hypotheses about ungulate responses to wolf predation were tested, and we compared responses to predictions made earlier by Hayes (1992, see our Table 10). The notation of Campbell and Stanley (1966) was modified to represent our experimental design (Tables 1 and 2).

Hypotheses

Caribou H1: Wolf reduction caused calf survival rates to increase in the Aishihik herd. To test for this we compared the ratio of 4-month-old calves per 100 cows in the Aishihik herd, and in 3 control herds before and during wolf reduction.

Caribou H2: Wolf reduction caused the Aishihik herd to increase. To test this hypothesis we compared changes in size of the Aishihik herd with changes in the control herds through the same period.

Caribou H3: Wolf reduction caused adult survival rates to increase in the Aishihik herd. To test this we 1) compared survival rates of radio-collared adults in the Aishihik herd with rates in 2 control herds, and 2) used census interpolation to estimate average survival during treatment.

Moose H1: Wolf reduction caused moose recruitment to increase in the Aishihik area. We compared the proportion of 9 month-old calves in the Aishihik area with those in 3 control areas.

Moose H2: Wolf reduction caused moose densities to increase in the Aishihik area. To test this hypothesis we compared moose densities in 2 survey blocks within the Aishihik area (Aishihik South and Onion Creek) with those of moose in 2 areas (Mayo and Big Salmon) before and during treatment.

Moose H3: Wolf reduction caused survival rates of adult moose to increase in the Aishihik area. We tested this hypothesis by comparing survival rates of adult moose in the 2 survey blocks in the Aishihik area with the rates in 2 control areas at the end of treatment.

Dall sheep H: Wolf reduction caused adult Dall sheep numbers and lamb recruitment rates to increase. We compared annual total counts and proportion of lambs in the Ruby Range treatment area and the Rose Lake control area.

Study Areas

Our study areas were the Aishihik wolf treatment area and 10 control areas where we monitored wolves or ungulates (Fig. 1). Our large-scale study did not follow classical experimental design (see Hurlbert 1984) because treatment and control areas were not randomly selected; population trends in control areas did not influence our selection.

Our criteria for selecting control areas were:

1) Recent wolf reduction programs in the Yukon could not affect control areas (Larsen et al. 1989, Farnell and McDonald 1988).
2) Caribou herds had to be of similar size to the Aishihik herd or less than 1,500 animals, and we had to be able to annually sample about 30% of each herd for composition. At the outset of the study, we had adequate pre-treatment data to

consider 11 woodland caribou herds (Farnell et al. 1998) as potential controls. Farnell et al. (1996) found caribou of southwest Yukon were ecologically different than the rest of the territory, based on behavior and biogeography. Of the 4 potential control herds in the southwest Yukon, we rejected the Kluane and Klaza herds because wolves were reduced on parts of their range during our study. Thus, the Ibex and Chisana herds were the only 2 suitable herds remaining. We selected the Wolf Lake herd because it bordered the southwest Yukon ecotype, and was naturally limited with little human activity in its annual range. Table 3 shows the pre-treatment status of caribou study herds.

3) Moose densities had to be similar to those in the Aishihik treatment area or less than 200 moose/1,000 km^2. Because there were few annual pre-treatment data on moose throughout the Yukon, we arbitrarily chose 3 control areas that were sufficiently distant to ensure they were not affected by our wolf treatment. Table 4 shows the pre-treatment status of moose populations.
4) We chose the sheep control area to follow the experimental design of Marcstrom et al. (1988). This allowed us to increase the robustness of our analysis by including data from a previous wolf-sheep experiment (Barichello et al. 1989).

Aishihik Treatment Area:

Physiography, Climate and Vegetation

The 20,000 km^2 Aishihik treatment area (Fig. 2) lies mainly within the Ruby Ranges ecoregion (Ecological Stratification Working Group 1995). The Ruby Range climate is characterized by short, cool summers and long, cold winters. Winter temperature inversions are common, giving milder temperatures at higher elevation. The mean annual temperature for the area is about -3°C. Mean summer temperature is 10°C and mean winter temperature is -17°C. Average annual precipitation is semi-arid, ranging from 250 to 300 mm. The terrain consists of rugged mountains rising to 2304 m asl and rolling hills over 900 m asl. Discontinuous permafrost is extensive, decreasing to sporadic along the western portion. Lower slopes and valley bottoms are forested with white (Picea glauca) and black (P. mariana) spruce in a matrix of dwarf willow (Salix spp.), birch (Betula glandulosa), and ericaceous shrubs. Black spruce, willow, birch and mosses (Sphagnum spp.) are usually found on poorly drained sites. Alpine fir (Abies lasiocarpa) inhabits higher subalpine sections. Alpine communities consist of mountain avens (Dryas spp.), dwarf willow, birch, ericaceous shrubs, graminoid species, and mosses.

Wildlife

We studied wolf numbers and moose recruitment each winter throughout the entire Aishihik treatment area, and changes in moose abundance in the Aishihik South (2,000 km^2) and Onion Creek (3,400 km^2) count blocks (Fig. 2). Each year we monitored Dall sheep recruitment and total adult numbers in the 1,600 km^2 Ruby Range study area (Fig. 2). In addition to moose, caribou and Dall sheep, the Aishihik area included introduced herds of less than 50 elk (Cervus elaphus) and 400 to 500 wood bison (Bison bison) (R. Hayes, Yukon Department of Renewable Resources, unpublished data). Black bears (Ursus americanus) are present, but their densities are unknown in the Yukon. Brown bear (U. arctos) density was estimated at 22 bears/1,000 km^2 in the ecoregion (Yukon Department of Renewable Resources, unpublished data). Lynx (Lynx canadensis) and coyote (Canis latrans) were both abundant to 1990, but by 1992 both predators had crashed (O'Donoghue et al. 1997) following a snowshoe hare (Lepus americanus) decline (Boutin et al. 1995). Wolverines (Gulo gulo) were present at unknown densities. Golden eagles are known to nest at high densities in the study area (Windsor 1979).

Control Study Areas:

Figure 1 shows locations of control study areas. In the Pelly Mountain ecoregion we studied wolves (6,800 km^2), caribou (9,700 km^2 in the Wolf Lake area), and moose (2,700 km^2 in the Big Salmon area). The Pelly Mountains ecoregion has annual temperatures similar to the Aishihik area, but receives twice as much precipitation (500 to 1000 mm). The ecoregion is generally mountainous, with elevations over 1500 m asl. The alpine community consists of dwarf willow and birch, ericaceous shrubs and lichens. In mesic lowland areas, forests are dominated by lodgepole pine (*Pinus contorta*).

Two populations were monitored in the Yukon Southern Lakes ecoregion, including the Rose Lake sheep area (800 km^2), and the Ibex caribou herd (4,000 km^2). This mountainous ecoregion is different than the Aishihik area because it does not have black spruce, and grassland communities dominate the south-facing lower elevations. Like the Pelly Mountains and Ruby Range ecoregions, most of the area is dominated by alpine. Precipitation and temperature are similar to the Aishihik area.

Wolves (15,700 km^2) and moose (3,000 km^2) were monitored in the Mayo area, a part of the Yukon Plateau-North ecoregion. This ecoregion is mountainous, with broad u-shaped valleys containing white spruce forests up to 1500 m asl. The Mayo area receives 300 to 600 mm precipitation per year. Winters are generally colder than Aishihik, with a mean temperature of -20°C.

The Chisana caribou herd ranges in a 13,000 km^2 area in the St. Elias ecoregion. The terrain is highest of all study areas, with glaciated mountains surrounded by permanent ice and snowfields. At the lower elevations, mean temperatures are warmer in the winter than in the Aishihik area. Precipitation is similar and permafrost is also discontinuous. Lower valleys have vegetation communities similar to the Aishihik area. Dwarf willow and birch, heather (*Phylladoce empetriformis*), graminoid species and lichens dominate the alpine community.

Wolves were counted in the Tatchun Hills area (10,000 km^2), part of the Yukon Plateau-Central ecoregion. Mean annual temperature is similar to the Aishihik area, but seasonal temperatures are more extreme. Mean summer temperature is 12°C and mean winter temperature is -19°C. A significant feature in the Tatchun Hills is the extensive grasslands on all low-elevation, south-facing slopes. Sedge tussocks (*Carex* spp.) and mosses are common in wetter drainages, similar to the northern portions of Aishihik area.

The Ladue moose control area (2,000 km^2) is in the Klondike Plateau ecoregion. Temperatures and precipitation are similar to the Aishihik area, except the average winter temperature is slightly colder at -23°C. Northern boreal forests occupy lower slopes and valley bottoms. Open black and white spruce with aspen and, occasionally, lodgepole pine, are most prevalent in the warmer boreal sections. Black spruce and paper birch (*Betula papyrifera*) prevail on slopes underlain by permafrost; balsam poplar (*Populus balsamifera*) is found along floodplains. Subalpine dwarf birch and willow stands extend from valley bottoms to well above treeline.

Methods

Estimating Wolf Abundance:

We estimated the total number of wolves in the Aishihik area every winter and in each of the 3 control wolf areas once during our study (Table 1). We estimated total numbers by snow-tracking wolves from Piper PA-18 and Maule M7 fixed-wing aircraft in late winter (January-March) following methods of Hayes and Harestad (2000*a*). We followed wolf snow trails until we found wolves or until the trail split, giving a minimum count for unseen packs.

We used height of land to set the boundaries of all wolf study areas, and then estimated wolf density and mean pack size for each area (6,800 to 20,000 km^2). For unseen packs, we estimated an upper and lower pack size based on wolf track sign. To derive total wolf numbers, 10% was added to the number of pack wolves to account for unseen single wolves (Mech 1973, Boertje et al. 1996, Hayes and Harestad 2000*b*).

Wolf Reduction:

Wolf reduction began in February 1993 and ended March 1997. Our objective was to annually reduce the number of wolves to about 20% of the number counted in the Aishihik area in February 1992. Most wolves were shot from Bell 206B helicopters. Other wolves were trapped by the Yukon Government or by private trappers, using neck snares or leg hold traps. Wolf sterilization was also used between 1994 and 1997 to experimentally reduce the reproduction of up to 6 wolf groups each year. Spence et al. (1999) described the capture and surgical methods used for male vasectomies and female uterine horn ligations. Spence (1998) studied the behavior of surgically sterilized wolves compared to untreated wolves in neighboring Kluane National Park. She found no difference in home range use or survival rates.

To prevent Kluane National Park wolves from being accidentally killed we established a 920 km^2 buffer area within the Aishihik area (Fig. 2). Conditions to decide the fate of boundary wolf packs were set by an agreement between Canadian Parks Service and the Yukon Government (Carey et al. 1994).

Estimating Caribou Abundance:

We used total counts (Valkenburg et al. 1985, Farnell and Gauthier 1988) and stratified random block sample methods (SRB; Farnell and Gauthier 1988) to estimate caribou abundance. We initially chose methods based on the ecological herd type (Farnell et al. 1996). To estimate initial herd sizes for alpine-wintering herds we used a total count in March 1994 for the Aishihik herd and October 1990 for the Ibex herd. We attempted to count the Aishihik herd in 1993, but found it to be overlapping on 2 neighboring herds' winter ranges. In 1994, the herds were well separated, and we were able to complete a total count. We estimated the 1993 (pre-treatment) herd size by removing the number of calves seen in 1994 and assuming 10% annual adult mortality (see results). We used a total count to estimate Chisana herd size in June 1992, 1993, 1995, and 1997. During these counts, we used locations of radio-collared caribou and searches from fixed-wing aircraft to establish boundaries of count areas. Two helicopter crews then counted all caribou within the bounded areas. Estimates of annual abundance were also derived for the Chisana herd using a population model (P. Valkenburg and D. Reed, Alaska Department of Fish and Game, Fairbanks, Alaska, unpublished data).

In March 1993 and 1998, we used SRB methods to estimate the size of the Wolf Lake herd, a forest-wintering herd that was more difficult to count than the other herds (Farnell et al. 1996). As the study progressed, we used SRB methods to estimate the Aishihik herd in 1997 and the Ibex herd in 1998 to assess the accuracy of previous total counts and to establish confidence intervals whenever possible. In all cases SRB counts were done at high enough intensity that most animals in each herd were observed. We compared herd size estimates for the Aishihik (1993 and 1997), Wolf Lake (1993 and 1998), Chisana (1993 and 1997), and Ibex (1990 and 1998) herds. Mean rates of annual increase, adult survival and recruitment were estimated after methods of Hatter and Bergerud (1991). Because pre-treatment estimates of the Aishihik (1993) and Ibex (1990) herds were based on total counts we determined whether those estimates were included in the 90% confidence interval around the SRB estimates at the end of treatment for the Aishihik herd in 1997 and the Ibex herd in 1998. We compared the results of the Wolf Lake estimates using a 1-tailed Student's *t* test to test the pooled variance from the 1993 and 1998 estimates.

Estimating Caribou Calf Recruitment and Adult Sex Ratio:

Each October, we estimated that 28% to 100% of the caribou in each study herd were sampled to determine calf recruitment (calves per 100 cows) and adult sex ratio (bulls per 100 cows) (Appendix 1). We used radiotelemetry to locate caribou groups and then classified them from a helicopter. We studied changes in composition of the Aishihik and 2 control herds for 3 years before (1990 to 1992) and 5 years during (1993 to 1997) treatment (Table 1). There were no pre-treatment data for the Wolf Lake herd.

Each annual ratio of calves per 100 cows was averaged over years before or during treatment and the 90% confidence interval was calculated using a bootstrap procedure (Manley 1997). We also estimated the differences between calves per 100 cows before treatment and during treatment, and between Aishihik and control areas using the bootstrap procedure. We performed bootstrapping in a 2-step fashion. First, we sampled with replacement a random set of 3 pre-treatment years and a set of 5 treatment years. Then, for each of the years selected, groups of caribou were sampled with replacement from all groups counted that year. After the 2 steps were completed, the ratio of calves per 100 cows was calculated for each year. Then the pre-treatment and during-treatment ratios were averaged, and their difference calculated. These 3 numbers formed the output of 1 resampling cycle.

We then repeated the entire process 2,000 times, and used the resulting distributions to estimate the bias-corrected confidence intervals and to compare the difference of the ratios to zero (i.e., no difference before and during treatment periods). We used 1-tailed tests to compare recruitment during treatment with the pre-treatment period because we expected the Aishihik ratio to be higher after wolves were reduced. We used 2-tailed tests to compare Aishihik recruitment with control herds during the same periods.

We determined differences between the Aishihik and Wolf Lake herds in the net loss of calves from July to October during treatment years. July composition surveys followed the same methods as October composition surveys. For logistical reasons, we could not compare all 3 control herds with Aishihik. We chose the Wolf Lake herd because it was our best example of a naturally-limited herd, and there was a substantial number of radiocollars on herd cows. By locating all collared cows in both herds, we reduced any bias in aggregation behavior based on reproductive status. We compared differences in calf mortality rates between herds using a 1-tailed paired Student's *t* test.

We expected hunting to affect the sex ratios because bulls are harvested more frequently than cows. The Chisana herd was hunted until 1994, when harvest was closed. The Ibex herd was closed to hunting during all years of our study. In 1990, hunting of the Aishihik herd was stopped, and remained closed through our study. Hunting in the Wolf Lake herd remained open in all years. Inconsistent harvest rates could have biased comparisons of sex ratios, so we adjusted the sex ratios for the Chisana and Wolf Lake herds to remove the effect of harvest. We multiplied the number of bulls observed in each group by a factor equal to the ratio: (bulls counted + bulls harvested)/bulls counted (Appendix 2). We followed the same bootstrapping procedure described above to test for differences in adult sex ratio before and during wolf reduction. We compared sex ratios from the 3 pre-treatment years and the last 3 years of wolf reduction (1995 to 1997). We used 2-tail tests throughout in our comparisons of the adult sex ratios.

Estimating Adult Caribou Survival Rate:

Radiotelemetry data were collected each year to estimate range use, herd size, sex and age composition and adult survival rate. We captured and radio-collared 82 (69 F, 13 M) Aishihik caribou, 59 (54 F, 5 M) Wolf Lake caribou, and 79 cows from the Chisana herd. Only 5 Ibex caribou were radio-collared, so we could not estimate an adult survival rate. We captured Aishihik, Wolf Lake, and Ibex herd caribou from Bell 206B helicopters using a hand held net-gun (Barrett et al. 1982). We immobilized Chisana caribou from a Robertson R22 helicopter, using a combination of 3 mg/ml Wildnil (Wildlife Laboratories, Fort Collins, Colorado) and 100 mg/ml xylazine hydrochloride (Anased, Lloyd Laboratories, Shenandoah, Iowa) fired from a short range Cap-Chur pistol in 2-cc darts. Transmitters had a 36 to 48 month life expectancy (Telonics, Mesa, Arizona; Lotek, Aurora, Ontario) and motion-sensitive mortality switches. We captured mainly cow caribou between September and April to study reproduction and calf survival indices.

A total of 1,162 Aishihik, 839 Wolf Lake, and 640 Chisana radiotelemetry locations were recorded from fixed-wing aircraft during our study. Monitoring schedules were May or June, July, October, December and March for the Aishihik and Wolf Lake herds. We monitored Chisana caribou during May or June, September or October, and 1 or 2 times between November and March. The Kaplan-Meier survival estimator (Pollock et al. 1989) was used to calculate survival rates of radio-collared caribou each year: from March to February for Aishihik and Wolf Lake caribou, and September to August for Chisana caribou. We combined annual survival data into before or during treatment periods and used log-rank tests (Pollock et al. 1989) to compare rates between periods and herds.

We also used census interpolation methods to estimate adult survival rates for the Aishihik and Wolf Lake herds (Hatter and Bergerud 1991). We developed a computer model using population size, recruitment, and estimated harvest, and then adjusted adult survival in the model until the observed growth rate was replicated.

Estimating Caribou Pregnancy Rate, Forage Quality, Disease Prevalence, and Physical Condition:

Pregnancy rates, winter diets, physical condition and incidence of disease were studied to determine effects on caribou response. Pregnancy in wild ungulates can be reliably determined by progesterone concentration in the blood (Wood et al. 1986); Russell et al. (1998) found progesterone in caribou is a good indicator of pregnancy.

We captured cow caribou from all herds between 10 December and 3 April - 60 to 174 days after conception. We extracted, centrifuged, and then froze blood samples from a total of 216 cows. Progesterone analyses were carried out at the Central Laboratory for Veterinarians in Langley, British Columbia. A threshold value of 1.5 ng progesterone/mL serum was used to distinguish pregnant from non-pregnant cows (Russell et al. 1998). We also estimated annual pregnancy rates of the Chisana herd during late May 1993 to 1997 by determining the presence or absence of a calf, antlers, or distended udder (Whitten 1995). Bergerud (1980) reported a mean pregnancy rate of 82% for North American caribou herds; we assumed our study herds were food limited if pregnancy rates were below 82% in any year.

To estimate winter diet, we randomly collected fecal pellets in February or March on all herd ranges and compared the relative compositions of important food including: mosses, fruiticose and foliose lichens, horsetails, graminoids, deciduous shrubs, evergreen shrubs, and forbs. We collected 20 groups of 20 pellets for each herd then randomly selected 1 pellet from each group for fecal analysis (Sparks and Malechek

1968). Analyses were conducted by the Composition Laboratory at Colorado State University, Fort Collins, Colorado. Farnell et al. (1999) included the Aishihik, Chisana, and Wolf Lake herds in a serologic survey of 12 Yukon caribou herds carried out from 1988 to 1997. They tested for 8 diseases that could have affected caribou response: brucellosis, the bovine respiratory group of viruses (infectious bovine rhinotracheitis, bovine viral diarrhea, parainfluenza 3, respiratory syncytial virus) and the related diseases: bluetongue, epizootic hemorrhagic disease, and leptospirosis.

Kuzyk et al. (1999*a*) compared the body characteristics of 11 Yukon caribou herds (*n* = 382 cows >3 years old) based on alpine- versus forest-habitat selection in winter and on snow conditions. They sampled body size measurements (total length, shoulder height, chest height, hind foot length, chest girth) and body condition scores (Gerhart et al. 1996) from 101 Aishihik, 54 Chisana and 50 Wolf Lake caribou. Body condition scores are a subjective measure of body fatness, but they accurately reflect maternal condition, and scores are related to pregnancy rates (Gerhart et al. 1996). Spring and summer foraging conditions and food limitation on winter range can affect maternal condition, which has been correlated to fetal growth rate, calf body size, and timing of calving (Reimers et al. 1983, Skogland 1984).

Estimating Caribou Response to Deep Snow and Snow Melt Phenology:

We investigated 2 aspects of weather that could have affected caribou: 1) Deep snow could bury ground forage and impede the mobility of caribou in the winter, thus reducing condition and survival; and 2) The persistence of snow on the alpine calving areas could increase the predation rate on calves.

Snow depth is a critical factor influencing the condition and survival of caribou (Pruitt 1959). Deep snow (>100 cm) can elevate predation rates by wolves (Mech et al. 1998). Caribou herds tend to select areas of shallow snow to minimize energy cost during winter feeding (La Perriere and Lent 1977); caribou winter ranges in the Yukon tend to be in snow-shadow regions of mountain ranges (Farnell and McDonald 1989,1990; Russell et al. 1993).

Russell and Martell (1984) reported that mobility of solitary animals was impeded when snow depth was 50 to 60 cm and groups of caribou were impeded when depths were 80 to 90 cm. We used 55 cm as the minimum snow depth and 85 cm as the critical snow depth affecting condition and survival of caribou in late winter.

We obtained late winter snow depth measurements from Environment Canada snow stations in or near each caribou (and moose) study area (Fig. 1). Snow depth was measured at permanent snow pads on a monthly or twice-monthly schedule in late winter and spring.

Caribou calves suffer higher losses when they are born at lower, snow free elevations because they cannot rely on mottled snow cover for camouflage (Bergerud et al. 1984, Bergerud and Elliot 1986, Bergerud and Page 1987).

The last week of May is the peak of calving for woodland caribou in the Yukon (R. Farnell, Yukon Department of Renewable Resources, unpublished data). We used the total number of 'growing degree days' (GDD) in May as a proxy measure of snow melt before calving, based on temperatures from Environment Canada weather stations (Fig. 1). For any day the average temperature was 5°C or more, the GDD value is calculated as the average temperature minus 5. We examined the data to determine years when the May GDD were substantially lower than the long-term monthly average. Because data for the Wolf Lake area were incomplete, we calculated the daily average value for GDD.

Estimating Moose Abundance and Adult Survival Rate:

We used SRB aerial survey techniques (Gasaway et al. 1986) to estimate moose abundance and composition. We counted moose in 2 blocks of the Aishihik treatment area and in 2 control areas at the beginning and end of treatment (Table 1). We modified the technique of Gasaway et al. (1986) by substituting Bell 206B helicopters with 3 observers in place of fixed-wing aircraft with 1 observer. We used helicopters for all surveys except the Mayo 1998 survey when we used Piper PA-18 aircraft for the count and helicopters for estimating a sightability correction factor. Larsen and Ward (1995) described methods for aerially sexing adults and aging yearlings.

Tests for differences in moose abundance between SRB surveys followed methods of Gasaway et al. (1986). We used a 2-tailed Student's *t* test, setting alpha at 0.05. If no difference was detected, we used power analysis to assess the probability of detecting a significant change of the magnitude observed. When a significant change in population size was detected, we estimated the finite rate of population change. Mean annual survival rates of adult moose were estimated using census interpolation (Hatter and Bergerud 1991).

Estimating Moose Recruitment Rate and Adult Sex Ratio:

We estimated annual recruitment based on the proportion of 9-month-old calves counted in late winter (February and March) in the Aishihik and control moose areas (Mayo, Big Salmon, and Ladue; Table 1). We flew all moose recruitment surveys in a

Piper PA-18 or similar type aircraft at 90 to 100 meters above ground, at airspeeds from 125 to 160 km/hr. We classified moose as adult or 9-month-old calf. We could not differentiate sex of adults because most bulls had dropped their antlers by February. During recruitment surveys between 8% and 39% of the moose in each area were classified (Appendix 3).

The proportion of 9-month-old calves can be expressed as:

$$P_t = C_t / [C_t + (Y + A)_t]$$

Where:

P_t = proportion of 9-month-old calves in the recruitment survey
C_t = number of 9-month-old calves counted in the current year's recruitment survey
$(Y + A)_t$ = number of moose classified as adults (Yearlings + Adults) during the current survey.

By grouping yearlings (22 months old) and adults we further underestimated recruitment because yearling cows have a lower reproductive rate than do older cows (Schwartz and Hundertmark 1993). Nevertheless, we did not correct for yearlings, and we used the proportion of 9-month-old calves as our recruitment index to maintain the most conservative approach in comparing responses.

We compared moose recruitment in the Aishihik area before and during treatment, and between Aishihik and 3 control areas during treatment using the same bootstrapping procedure described for caribou recruitment analyses. For moose there were data for only 1 pre-treatment year (1993). Yates-corrected Chi-square tests were used to compare differences in adult sex ratios (bulls per 100 cows) at the beginning (1992 or 1993) and end of the treatment (1998) in each study area.

Estimating Moose Response to Snow Depth and Summer Growing Season:

Snow depth (Peterson 1977, Boertje et al. 1996) and quality of summer forage (Schwartz et al. 1988) can affect moose population dynamics. Deep snow can reduce the survival of adults and calves by impeding their ability to move and feed. The quality and length of the growing season affects the nutritional status of moose, and can affect recruitment and survival rates (Stewart et al. 1977). We examined both factors to determine effects on moose response.

Snow depths of 70 cm or greater impede movements of adult and calf moose (Coady 1974, Gasaway et al. 1992), and depths above 90 cm reduced survival of calves in interior Alaska (Boertje et al. 1996). We considered 70 cm as the minimum snow depth affecting moose, and 90 cm as the critical depth that would probably have a measurable effect on moose survival. We compared each year's maximum snow depth to these threshold levels.

Stewart et al. (1977) suggested a general correlation between moose recruitment and the length of the growing season. We determined whether changes in growing season length might have influenced moose population dynamics in our study areas. We compared the average growing season lengths before and during wolf reduction with changes in moose numbers.

We defined the growing season as extending from the first day a critical number of heat units had accumulated through to the first day when the daily minimum temperature was -5°C (Stewart et al. 1977). The timing of spring leaf flush is based on the growing degree days (Moss 1960), in conjunction with the phenological observations of Maini (1960). The number of heat units contributed by a given day was defined as: (maximum daily temperature - 12.2°C)/2, for any day maximum temperature exceeded 12.2°C. For each area, we calculated the change in the average growing season length from 1983 to 1992 (pre-treatment) to 1993 to 1998 (treatment). The change in average growing season length between the 2 periods was then ranked and compared with the rank change in moose numbers.

It was not possible to calculate growing season length for all years in each area because the appropriate temperature data were not always available. To ensure there was no bias in the years data were available, we also calculated average season lengths using only those years when data were available in all 3 areas. The reduction in number of years used did not affect the ranking of the results.

Finally, we identified unusually long or short growing seasons in each of the 3 areas by flagging any years when the length of the growing season deviated from the mean by more than 1 standard deviation. We then compared the number of extreme seasons in each area with the performance of the moose population. We determined whether shorter or longer than average growing seasons could have affected growth of the 3 moose populations.

Estimating Moose and Caribou Responses to Harvest:

Aishihik caribou hunting was first closed during 1990. Except for a small subsistence harvest by First Nations, moose hunting in the Aishihik treatment area was restricted in 1993, and closed from 1994 onward. Thus, caribou and moose responses could have been due to wolf or harvest treatments. We developed a simple population model to assess the relative importance of the reduction in harvest. In the moose model natural mortality rates were adjusted until the simulated growth matched the observed growth in the Aishihik South and Onion Creek moose count areas. Pre-treatment harvest estimates were then added to the model as an additional (additive) mortality factor to assess the effects on population growth. For the Aishihik caribou herd, we applied pre-treatment harvest estimates to assess how reducing harvest affected herd growth during treatment.

We estimated resident harvest from annual questionnaire responses (Kale 1982) and non-resident harvest from compulsory submissions (Yukon Department of Renewable Resources, unpublished data). We monitored harvest of Chisana caribou using harvest permit reports (Alaska Department of Fish and Game, unpublished data).

Before our study, harvest by First Nations people was monitored using household interviews (Quock and Jingfors 1989). Quock and Jingfors (1989) found that First Nations people were reluctant to report their harvest. Based on differences in reported harvest and community consumption needs (Quock and Jingfors 1989), we calculated harvest was consistently under reported by about 53%. Thus, to bound First Nation harvest we used the reported harvest as a minimum then doubled it.

Estimating Dall Sheep Abundance, Lamb Survival Rate, and Harvest:

Our design for testing sheep response (Table 2) followed Marcstrom et al. (1988). From 1983 to 1985, wolves were removed from the Rose Lake sheep range (Barichello et al. 1989). The Ruby Range mountains in the Aishihik area served as the control area. In 1993, we reversed the treatment areas. This approach allowed us to control variation in time by doing the experiment at the same time in 2 areas, and variation between areas by using each area for its own comparison through time (National Research Council 1997). Hayes et al. (1991) found wolves had recovered to about 90% of pre-reduction numbers in the Rose Lake area by 1988; we expect wolves were fully recovered by 1993.

We used helicopters to conduct total counts of sheep in June or July after lambing. We counted sheep in a 1,600 km^2 block in the Aishihik treatment area (Ruby Range) and in a 400 km^2 block in the Rose Lake area. Summer counts are most representative of population characteristics, based on strong seasonal range fidelity in Dall sheep (Hoefs and Cowan 1979). We classified sheep (after Geist 1971) as rams having half-, three-quarter- or full-curl horns; lambs; yearlings; or ewes. Whenever we could not confidently count yearlings, we lumped ewes, yearlings and the associated young rams as nursery sheep.

In both areas, licensed harvest was restricted to full curl rams. We estimated harvest rates from compulsory submission of horns for resident and non-resident hunters (Yukon Department of Renewable Resources, unpublished data); harvest by First Nation hunters was unknown.

We tested for changes in sheep population size by regressing adult population against time in treatment and control areas. We tested for the effect of wolf treatment on sheep recruitment by comparing lamb:nursery sheep ratios annually across treatment and control areas and by comparing the ratios across treatment and control periods for each area; in each case we used the Wilcoxon rank-sum test. We also tested for changes in age structure of adult males in the Ruby Range by examining the average age of hunter-killed rams before and during treatment using a Student's *t* test.

Results

Changes in Wolf Abundance:

Between February 1992 and January 1993, before we began aerial shooting, we detected a loss of 58 wolves in the Aishihik area. In addition to declining ungulate abundance in the area, illegal poisoning probably contributed to this decline. A big-game outfitter in the area was convicted of counseling his guides to place a lethal organochloride poison (Thimet; Phorate, Cyanide Canada) in the Aishihik area in 1992; Thimet-poisoned wolves were found near the Aishihik study area boundary in February 1993 (Carey et al. 1994).

From 1993 to 1997 we reduced March wolf density in the Aishihik area to between 1.5 and 2.8 wolves/1,000 km^2 (Table 5) – 69% to 83% less than the wolf density in 1992. Wolf numbers always increased by the next winter (λ = 1.5 to 1.8) largely through the recolonization of vacant territories by young adult pairs. Nevertheless, annual January density from 1994 to 1998 (2.6 to 4.1/1,000 km^2) remained 54% to 71% below pre-treatment density (Table 5, Fig. 3).

We killed 151 wolves by aerial hunting and ground snaring, and public trappers and hunters killed 26 (Table 5). The number of packs fell from 28 before treatment to 7 to 20 during treatment. Mean pack size declined from 5.6 before treatment to less than 4 wolves in treatment years. Males represented 32% to 58%, and females 42% to 69%, of wolves killed annually (Fig. 4); we found no differences in the annual proportions of males and females killed ($P = 0.38$). Adults comprised 54% to 79%, yearlings 0% to

18%, and pups 13% to 31% of annual wolf culls (Fig. 5). Density of wolves, mean pack size, and density of packs were all higher in the 3 control areas than in the Aishihik area during treatment, but lower than in Aishihik before treatment (Table 5, Fig. 3).

We also reduced the rate of increase of Aishihik wolves by surgically sterilizing adult wolves between 1994 and 1997. Spence et al. (1999) sterilized a total of 16 Aishihik wolves: 1 male in 1994, 3 females in 1996, 6 males and 4 females in 1997, and 2 females in 1998. There was 1 pair in 1994 and 1995 with sterilized members; 3 pairs by 1996; 3 pairs, 2 groups of 3 wolves, and 2 lone wolves by 1997; and 4 pairs and 2 groups of 4 wolves by 1998. Sterilization apparently stopped 15 of 16 potential breeding attempts. Only 1 pup was born among all treated packs after 1994.

Changes in Caribou Abundance:

The Aishihik herd stopped declining and increased in size during treatment, the Ibex herd increased, the Wolf Lake herd remained stable, and the Chisana herd continued to decline (Fig. 6). The Aishihik herd increased from 732 caribou in 1994 to 1,148 ± 6.5% (90% CI) in 1997 ($P < 0.001$), for an annual finite rate of increase of 1.15. The Wolf Lake herd was apparently stable at 1,249 ± 12% (90% CI) in 1993 and 1,491 ± 30% in 1998. The Chisana herd declined from 898 caribou in 1993 to 440 in 1998 - an annual finite rate of decline of 0.86. The Ibex herd increased from 150 animals in 1990 to 450 ± 22.8% (90% CI) in 1998 - an annual finite rate of increase of 1.14.

Caribou Calf Recruitment and Adult Sex Ratio:

Aishihik was the only herd that showed a significant increase in annual recruitment during the treatment period (Fig. 7). The mean ratio increased significantly from 15 calves per 100 cows (90% CI: 7.0 to 24.6) before treatment to 42 calves (90% CI: 38.0 to 45.8) during treatment ($P < 0.01$) (Fig. 8). Recruitment of Chisana caribou did not change but averaged 3.9 calves per 100 cows (90% CI: 0.04 to 8.8) before treatment, and 7.2 calves per 100 cows (90% CI: 3.8 to 11.2) during treatment ($P > 0.01$). The Ibex herd averaged 56.3 calves (90% CI: 50.1 to 63.8) before and 44.2 calves (90% CI: 36.0 to 51.7) during treatment ($P > 0.90$). There was no pre-treatment information for the Wolf Lake herd.

Before treatment, recruitment for the Aishihik herd was higher than for the Chisana herd, ($P < 0.05$, 2-tailed test) and less than for the Ibex herd ($P < 0.01$). During treatment Aishihik herd recruitment remained higher than for the Chisana herd ($P < 0.01$), and the Wolf Lake herd ($P < 0.01$), which averaged 26.3 calves per 100 cows (90% CI: 20.0 to 31.2). During treatment, Aishihik recruitment increased so that it was no longer different than for the Ibex herd ($P > 0.60$).

The Aishihik herd lost proportionately fewer calves between July and October during treatment (7% to 18%) compared to 2 years before wolves were reduced (34% to 41%; Appendix 4). Calf losses from July to October were lower for the Aishihik herd than for the Wolf Lake herd (17% to 60%) during all treatment years ($P<0.005$; Fig. 9).

The annual proportion of adult bulls in the Aishihik herd increased during the treatment period, whereas sex ratios in control herds did not show this trend (Fig. 10). The Aishihik adult sex ratio increased from 28.7 bulls per 100 cows (90% CI: 24.1 to 34.2) in the 3 years before treatment to an average of 51.7 bulls (90% CI: 45.7 to 58.3) during the last 3 years of treatment ($P < 0.01$). The Chisana herd averaged 35.9 bulls per 100 cows (90% CI: 31.1 to 40.6) before treatment, and 21.1 bulls (90% CI: 16.9 to 25.2) during treatment ($P > 0.30$). The Ibex herd averaged 59.2 bulls per 100 cows (90% CI: 41.0 to 78.6) before treatment, and 58.0 (90% CI: 49.9 to 77.2) during treatment ($P > 0.20$; Fig. 11).

Adult Caribou Survival Rate:

Before treatment, the survival rate of radio-collared adults in the Aishihik herd fell from 0.94 in 1991-1992 to 0.49 in 1992-1993. During treatment years, survival stabilized, averaging 0.89 ± 0.01 (SE) - similar to the control Wolf Lake herd average of 0.89 ± 0.04 (SE) (Table 6). The survival rate of adults in the Chisana herd did not differ before or during treatment ($P > 0.07$), averaging 0.80 ± 0.11(SE) for all years, no different than adult survival in the Aishihik herd before ($P > 0.90$) or during treatment ($P > 0.20$).

From census interpolation methods, adult survival in the Aishihik herd was 0.87 before treatment and 0.91 during treatment. Using the same methods, mean annual survival rate of Wolf Lake adults was 0.90 during treatment.

Caribou Pregnancy Rate, Forage Quality, Disease Prevalence, and Physical Condition:

Progesterone levels showed that 201 adult cows were pregnant (1.57 to 12.58 ng/mL) and 15 were not (0.09 to 0.97 ng/mL). Cows in the Aishihik herd had high pregnancy rates before (96% to 100%) and during treatment (88% to 100%; Table 7). During treatment, Aishihik mean annual pregnancy rate was 95% ± 2.93 (SE), the same as for the Wolf Lake herd (94% ± 4.09 (SE)).

Nine of the non-pregnant cows were from the Chisana herd. Because sample sizes were small for this herd, we combined both progesterone and June udder counts to provide better estimates of pregnancy rates. Estimated pregnancy rates were 50% in

1993, 86% in 1994, 93% to 95% in 1995 and 1996, and 82% in 1997. Thus, the pregnancy rate was low only for 1993 based on combined methods. The pregnancy rate was probably also low in 1992 when only 1 calf was seen among 1,142 caribou in October (C. Gardner, Alaska Department of Fish and Game, unpublished data).

Lichens were the preferred winter food of all herds, but there were differences in dietary composition (Appendix 5). Lichens constituted 84% ± 4 (SE) of the diets of Ibex caribou, 80% ± 12 (SE) of Aishihik caribou, 70% ± 7 (SE) of Wolf Lake caribou, and 53% ± 2 (SE) of Chisana caribou. The importance of other plant types varied. The frequencies of mosses were highest and lichens were lowest for Chisana caribou. However, in the 2 winters we studied Chisana food habits, the herd used forested lowland areas they had not previously used before, or since.

Farnell et al. (1999) conducted serological tests for 137 caribou from the Aishihik herd (1991 to 1996), 55 from the Chisana herd (1993 to 1995), and 59 from the Wolf Lake herd (1993 to 1995). They found evidence of epizootic hemorrhagic disease in 4 of 71 Aishihik caribou tested in 1991. Testing of Aishihik caribou from 1993 to 1996 found no positive titres. Farnell et al. (1999) found no evidence of disease among Chisana caribou and evidence of leptospirosis in only 1 of 28 animals tested in the Wolf Lake herd.

Kuzyk et al. (1999*a*) found a significant difference in shoulder height and no differences in other body measurements or body condition scores between alpine (including Aishihik and Chisana herds) and forest-wintering caribou (i.e., Wolf Lake herd). The Aishihik herd had higher body condition scores than the Chisana and Wolf Lake herds. The Chisana herd body condition scores ranked second from last among the 9 herds studied by Kuzyk et al. (1999*a*).

Caribou Response to Snow Depth and Snow Melt Phenology:

Snow depth on the Aishihik herd range never exceeded our upper threshold of 85 cm (Fig. 12). Depths reached or exceeded the threshold of 55 cm in 8 of 12 winters when the herd was in decline (1981 to 1993), and in 3 of 5 winters when the herd increased (1994 to 1998) – showing no trend in relation to caribou abundance.

Snow on the winter range of the Chisana herd slightly exceeded 55 cm in 3 years, and did not reach the lower threshold on the winter range of the Ibex herd in any year. Snow depths exceeded 85 cm only in the Wolf Lake herd range. The Wolf Lake herd increased from 1987 to 1993 (Table 3), when snow was near or above critical depths in 5 consecutive years (Fig. 12) - but the herd remained stable after 1993 when snow exceeded 85 cm in only 1 of 4 years. Thus, trends in control caribou herds could not be related to snow depth.

None of the 4 study herds experienced a trend in late snowmelt during our study (Fig. 13). Before treatment, the Aishihik and other herds experienced a marginally late snowmelt in 1992. Recruitment was low the next October in Aishihik, but it was also low in 1991 when the May GDD was above average. During treatment, snowmelt was early in 1993 and 1995 in all areas. Thus, recruitment or trends in herd sizes were not related to snow melt.

Changes in Moose Abundance:

During the treatment period, moose numbers stopped declining and increased in the treated Aishihik South ($P < 0.001$) and Onion Creek ($P < 0.001$) blocks (Appendix 6, Fig. 14). Moose numbers also increased in the Mayo area ($P = 0.003$), whereas the Big Salmon moose population remained stable ($P = 0.99$) (Appendix 6, Fig. 14). Mean finite rates of increase (λ) were 1.18 for Aishihik South, 1.16 for Onion Creek, and 1.11 for Mayo.

Moose Recruitment, Adult Sex Ratio and Adult Survival Rates:

Annual recruitment of moose in Aishihik increased and remained high during all treatment years. Recruitment in the Ladue area remained low, but it was widely variable in Mayo and Big Salmon (Fig. 15). Moose recruitment rates increased significantly in the Aishihik area during treatment (Fig. 16), increasing from 10.4% (90% CI: 5.6 to 15.5) in 1993 to average 18.8% (90% CI: 16.0 to 22.1) during treatment ($P < 0.05$). The Big Salmon area averaged 10.0% recruitment in 1993 (90% CI: 5.5 to 14.4) and 15.4% (90% CI: 11.3 to 19.9) during treatment ($0.05 < P <0.10$) The Ladue area averaged 7.4% (90% CI: 3.8 to 11.9) before and 7.2% (90% CI: 5.5 to 8.9) during treatment ($P > 0.30$). The Mayo area recruitment averaged 12.1% (90% CI: 8.5 to 16.7) before and 16.0% (90% CI: 11.6 to 20.5) during treatment ($P > 0.20$).

Pre-treatment recruitment in the Aishihik area (1993) was not different than in the Big Salmon ($P > 0.80$, 2-tailed test), Ladue ($P > 0.40$) or Mayo ($P > 0.60$) areas. During treatment, Aishihik showed higher recruitment than all control areas in 3 of 5 years (Fig. 15). Average recruitment during treatment was greater than in the Ladue area ($P < 0.01$), but it was not different than in the Big Salmon ($P > 0.60$) and Mayo areas ($P > 0.40$).

The moose sex ratio in the Aishihik South area was 60 bulls per 100 cows before treatment and 85 bulls per 100 cows in 1998 at the end of treatment, but the ratios were not different (*P* > 0.18). In the Onion Creek area the ratio increased from 49 to 97 bulls per 100 cows in the same period (*P* > 0.03). Sex ratios in Big Salmon were 68 bulls per 100 cows in 1993 and 70 bulls per 100 cows in 1998 (*P* > 0.75). Sex ratios in Mayo were 71 bulls per 100 cows in 1993 and 82 bulls per 100 cows in 1998 (*P* > 0.40). Based on census interpolation the mean annual survival rate of adult moose during treatment was 0.97 for Aishihik South and 0.98 for Onion Creek. In control areas adult survival was 0.99 for Mayo, and 0.85 for Big Salmon based on census interpolations from 1993 to 1998.

Moose Response to Snow Depth and Summer Growing Season:

In all moose study areas in all years, snow depths were less than 90 cm (Fig. 17). Before treatment (1977 to 1993) snow depth in Aishihik exceeded 70 cm only in 1991 and 1992. Snow depth did not exceed 70 cm in any year at Mayo and in only 1 year in the Big Salmon area. Thus, snow depth did not limit moose response in any year.

Table 8 ranks the magnitude of changes in growing season length and moose population size for each area. The rankings are not correlated and provide no evidence that variation in the length of the growing season was responsible for the relative differences in moose population performance.

Unusually short or long seasons also do not appear to have influenced the relative increase in moose numbers. The Aishihik area had the largest population increase and experienced 1 favorable and 1 unfavorable summer during wolf treatment (Table 8). Big Salmon had 1 unusually long season, but ranked third in moose population increase whereas Mayo, with 1 short season, ranked second in moose increase.

Moose and Caribou Responses to Harvest Reduction:

Annual harvest was estimated at 50 to 57 caribou for the Aishihik herd before treatment. If harvest remained the same during treatment, the annual finite rate of increase of the herd would have been 1.05 to 1.09, instead of 1.15. By 1998, herd size would have reached only 839 animals, 43% below the estimate of 1,471 animals that year. In 1990, harvest was 5% when the herd was in decline. Herd size did not increase in response to hunting closure between 1990 and 1993, when wolf reduction began.

Moose numbers in the Aishihik South area increased by 136% during treatment. Harvest simulations project that moose numbers would have increased by 94% to 69% if the pre-treatment harvest of moose had continued each year during wolf treatment. We estimated harvest was 6% to 8% before treatment when moose were declining.

In the Onion Creek block, moose numbers increased by 147% during treatment. If harvest of moose had continued during treatment, harvest would have reduced the rate of increase to 141%. The pre-treatment harvest rate in the Onion Creek block was about 3%.

Sheep Response:

None of the sheep populations, treated or control, changed significantly over time (Fig. 18). The annual licensed harvest was 3.3% in the Ruby Range and 1.7% in Rose Lake. Rams killed by hunters during treatment were significantly younger than during 5 years before treatment (Student's t test, $P = 0.02$).

Lamb:nursery sheep ratios differed between treatment and control areas in only 1 of 9 years (Table 9). In 1985, the treatment population showed a higher recruitment ratio than the control area. Lamb:nursery sheep ratios did not differ between treatment and control periods in either area (Fig. 19) (Ruby Range: Wilcoxon $Z = -1.73$, df = 1, $P = 0.08$; Rose Lake: $Z = 1.36$, df = 1, $P = 0.18$).

Discussion

Wolf Reduction:

Aishihik wolves were annually reduced from 69% to 83% below the 1992 pre-treatment level. During reduction, winter densities in Aishihik were less than in the 3 control wolf study areas. The annual rate of reduction was higher than the sustainable harvest of 30% to 50% estimated for wolves (Gasaway et al. 1983, Keith 1983, Peterson et al. 1984, Hayes et al. 1991). By each January, wolves were able to recover to only about 36% of the pre-treatment density. Thus, wolves were substantially reduced in all seasonal ranges of Aishihik ungulates during all treatment years.

We plotted our annual rates of increase against the percent of wolves left alive the previous winter (Fig. 20) and compared the results to 4 other wolf reduction studies (Gasaway et al. 1983, 1992; Hayes et al. 1991; R. Farnell, Yukon Department of Renewable Resources, unpublished data). We found a strong linear relation for the pooled data ($N = 27$, $r = -0.666$, $P < 0.001$), showing rates of increase were inversely related to the proportion of wolves remaining the previous winter. The X intercept indicates that wolf populations should remain stable when reductions are less than 30%, supporting Keith (1983) who used different methods to conclude harvest rates greater than 30% were unsustainable for wolves. The Y intercept of the line indicates regional wolf populations are capable of a maximum finite rate of increase of 2.8 when they are entirely removed from a large area.

Sterilization also reduced the recruitment of treated wolf packs. Assuming a potential litter size of 5.7 wolves (Hayes and Harestad 2000*b*), sterilization stopped 16 breeding events from producing a total of about 90 pups between 1994 and 1997. Mech et al. (1996) and Spence (1998) found wolf territoriality, pair bonding, and survival were not affected by surgical sterilization. Our study indicates sterilization is an effective tool for reducing wolf recruitment at the wolf pack and population level. Further research is required to determine how treated pairs in the Aishihik area behave and survive as the number of wolf packs and competition for prey resources increase during wolf recovery.

Caribou Response:

Aishihik Treatment Herd

During 5 years of wolf reduction calf survival in the Aishihik caribou herd increased from 15 calves before treatment to an average of 42 calves per 100 cows. This falls within the range of 40 to 50 calves per 100 cows in 3 other studies where wolves were reduced at similar intensities (Gasaway et al. 1983; Bergerud and Elliot 1998; R. Farnell, Yukon Department of Renewable Resources, unpublished data.) By comparing the rates of calf loss between the Aishihik and Wolf Lake herds from July to October, we found supporting evidence that reducing wolves increased calf survival rates during summer. Before July, when neonatal vulnerability is highest (Adams et al. 1995), calf survival in the 2 herds was similar (42 to 46 calves per 100 cows). After July wolves had the largest effect on calf survival in the Denali herd, Alaska (Adams et al. 1995). The untreated Wolf Lake herd lost almost 4 times as many calves during summer as did the Aishihik herd. This difference indicates that the Aishihik herd experienced lower rates of wolf predation from birth to October.

There was no evidence that survival of adult caribou in the Aishihik herd increased during wolf treatment. Before treatment, survival of radio-collared adults was highly variable for 2 years (0.52 to 0.94), making it difficult to assess changes. Survival during treatment was 0.89, no different than in the Wolf Lake control herd (0.90). Survival rates of 0.71 to 0.83 were reported for declining woodland caribou herds in Alberta and British Columbia (Fuller and Keith 1981, Edmonds 1988, Seip 1992, Stuart-Smith et al. 1997). Before treatment, our census interpolation model estimated Aishihik herd adult survival was 0.87. Using either method indicates that adult survival was within the range considered to be typical of caribou coexisting with undisturbed wolves (Bergerud 1980).

During treatment, the Aishihik herd annually increased at a rate of 1.15 (λ) similar to rates of 1.14 to 1.17 reported in 3 other wolf reduction studies (Farnell and McDonald 1988, Boertje et al. 1996, Bergerud and Elliot 1998). With adequate food and no predators, caribou are capable of increasing at a rate of 1.32 (Keith 1983). Although wolf predation is clearly important in all wolf reduction studies, other forces are removing 40 to 50 calves for every 100 cows by October, based on differences in pregnancy rates and calf recruitment. Data from this and other wolf reduction studies indicate that even when wolf numbers are substantially reduced, about half of the calves still die before October, adult survival does not exceed 0.90, and rates of increase remain at about half of the intrinsic potential.

Before treatment, the adult sex ratio in the Aishihik herd averaged 28.7 bulls per 100 cows, the lowest reported in the Yukon (R. Farnell, Yukon Department of Renewable Resources, unpublished data). The sex ratio increased each year to 51.7 bulls per 100 cows after we reduced wolves. In contrast, the sex ratio in the Chisana herd continued to decline after harvest was eliminated, falling to 21 bulls per 100 cows during the last 3 years of treatment. The decline in adult bulls was accompanied by chronically low calf recruitment, low or no harvest, a rapid decline in herd size, and a naturally-limited wolf population.

Our results support Bergerud and Elliot (1986), who hypothesized that as herd size declines and wolf predation rate increases, adult bull caribou are killed at proportionately higher rates than are cows. Bergerud (1980) speculated that high recruitment (>10%) adds young bulls into the herd, and that this is the primary mechanism that causes bull:cow ratios to increase. Recruitment in the Aishihik herd was high for the 5 years of wolf reduction, supporting Bergerud (1980). The adult sex ratio continued to decline in the Chisana herd when recruitment remained chronically low and harvest was closed.

Progesterone levels in our caribou study herds were similar to those in other studies (McEwan and Whitehead 1980, Seip 1992,Rettie and Messier 1998, Russell et al. 1998,). In all of our herds, pregnancy rates were similar to woodland caribou in British Columbia (94%; Seip 1992), Alberta (86%; Stuart-Smith et al. 1997), and Saskatchewan (94%; Rettie and Messier 1998). We had no evidence that pregnancy rates were negatively affected by physical condition of cows, except in the Chisana herd in 1992 and 1993. Likewise, the consistently high pregnancy rates that we observed suggests a low frequency of reproductive pauses for females as a response to low nutritional stress (Cameron 1994).

Winter diets of the Aishihik, Ibex and Wolf Lake herds were similar to diets of other caribou herds wintering on lichen range in taiga or in mountainous regions (Russell and Martell 1984, Boertje 1985, Russell et al. 1993). Body measurements and body condition scores of these 3 herds were not different than other Yukon herds (Kuzyk et al. 1999*a*), indicating that nutrition did not affect body reserves, physical growth or pregnancy rate.

Many studies have shown that poor summer nutrition and low body condition scores in October can cause a decline in pregnancy rates and affect herd dynamics (Dauphiné 1976, Thomas 1982, Skogland 1986, Messier et al. 1988, Crête and Hout 1993, Cameron 1994). Except for the Chisana herd, pregnancy rates and body condition scores were typical of caribou elsewhere.

Lenart (1997) found that warm and dry summer weather on the Chisana range between 1994 and 1995 decreased the quality and quantity of alpine summer forage. These conditions could have been the main factor contributing to the low body condition scores and pregnancy rates of Chisana caribou. Poor winter nutrition can also lower the birth mass of calves and delay birth (Skogland 1984, Couturier et al. 1990, Cameron et al. 1993), reducing calf survival (Espmark 1980, Adams et al. 1995). The winter diet of the Chisana herd showed the highest proportion of mosses and lowest proportion of lichen among our study herds. Mosses have low nutritional value and digestibility in contrast with lichens, which provide a highly digestible source of energy for caribou during winter (Russell and Martell 1984). Thus, we have evidence that winter food habits contributed to the low body condition scores for the Chisana herd.

We found no evidence that disease strongly limited any of our study herds. Brucellosis, a disease of caribou that can reduce reproduction, was not found and bovine respiratory viruses were at low prevalence. Epizootic hemorrhagic disease was present in the Aishihik herd but there was no evidence of exposure after 1991. These findings of low disease incidence are consistent with serological studies of other woodland caribou herds in the Yukon (Farnell et al. 1999) and Alaska (Zarnke 1992).

Haber and Walters (1980) speculated that movement of caribou among herds could explain observed changes in herd abundance. Extensive radiotracking data have discounted this as a factor in herd size changes (Thomas 1995). Radiotelemetry (Farnell et al. 1998) and genetic studies (Zittlau et al. 2000) have shown that Yukon woodland caribou herds are discrete at current densities. Historic and present-day distributions of barrenground caribou are known to periodically overlap with woodland caribou during winter (Zittlau et al. 2000). In all cases, radio-collared woodland caribou remained in their traditional range, and did not join the larger herds (Farnell and Russell 1984).

During our study, we monitored 82 radio-collared adults in the Aishihik herd, 25 in the Kluane herd, and 45 in the Klaza herd. A total of 2,022 locations were made. We recorded no exchange of radio-collared animals among the 3 adjacent herds. Likewise, there was no notable fluctuation in the size of adjacent herds as the Aishihik herd increased. The Kluane herd size was 180 to 200 animals from 1993 to 1997. The Klaza herd numbered 441 ± 2.9% (90% CI) in 1989 and 426 ± 17.9% (90% CI) in 1996 (R. Farnell, Yukon Department of Renewable Resources, unpublished data). We reject the idea that emigration contributed to the decline or increase in the Aishihik herd.

Control Herds

The study of control herds provides useful insights into the demography of woodland caribou by connecting patterns of recruitment and adult survival with herd growth. At the same time as the Aishihik herd was increasing, 3 control herds were all performing differently. The recruitment rate in the Ibex herd was high before the Aishihik treatment period, and it declined during treatment. Since 1983, recruitment in the Ibex herd has averaged more than 50 calves per 100 cows, the highest of any naturally-limited herd in the Yukon. Hayes et al. (1991) found wolves did not prey on Ibex caribou when the herd was small. Despite the high recruitment, this herd began to increase only after 1993 when First Nations hunters voluntarily suspended their harvest (O'Donoghue 1996, Farnell et al. 1998).

In contrast, the Chisana herd was declining when we began our study (Valkenburg et al. 1996), and was the most similar to the Aishihik herd in composition, recruitment and herd trend. Recruitment and adult survival remained low in all study years, and the ratio of adult bulls per 100 cows continued to decline despite hunting closures.

The Wolf Lake herd was apparently stable during our study, after showing an 11% annual growth between 1987 and 1992. During the Aishihik treatment period, the Wolf Lake herd averaged 26 calves per 100 cows and annual adult survival rate was 0.90, typical of stable caribou herds elsewhere (Bergerud 1980, Bergerud and Elliot 1998). Despite highly variable responses, no control herd showed the same trends as the Aishihik herd in increasing recruitment and adult sex ratios, nor did any control herd increase as rapidly as did the Aishihik herd.

Moose Response:

Aishihik Treatment Area

Without predators the intrinsic rate of increase of moose is between 1.15 and 1.49 (Keith 1983, Van Ballenberghe 1983, Messier 1994). Rates are lower in northern areas where bear and wolf predation combine to reduce recruitment rates (Ballard and Van Ballenberghe 1998). During wolf reduction, moose in the Aishihik area increased at an annual rate of 1.16 to 1.18, at the upper end of the of the range reported in other studies where wolves were intensively reduced (Larsen and Ward 1991,1995; Gasaway et al. 1992; Boertje et al. 1996; Bergerud and Elliot 1998). The rapid increase in moose numbers was due to strong responses in both recruitment and adult survival rates when wolves were reduced.

Recruitment nearly doubled from about 10% in 1993 to average 19% during wolf treatment, similar to increases reported in other studies where wolves were reduced to the same low levels (Gasaway et al. 1983, Larsen and Ward 1995, Bergerud and Elliot 1998). Where bears are important predators of moose calves, moose responses to wolf reduction were lowest (λ = 1.07, Larsen and Ward 1991; 1.04, Gasaway et al. 1992). Larsen et al. (1989) reported that brown bears caused 58% and wolves 25% of moose calf mortalities in the Coast Mountains, adjacent to our study area. Gasaway et al. (1992) found that brown bears caused 52% and wolves 12% to 15% of calf deaths. Ballard (1992) concluded that brown bears were an important cause of moose calf mortality when densities exceed 16 bears/1,000 km^2. We expected lower recruitment responses based on a density estimate of about 22 bears/1,000 km^2, and on results from 2 adjacent studies where brown bears were the most important predator of moose calves (Larsen et al. 1989, Gasaway et al. 1992).

Before wolf reduction, adult survival of moose was 0.80 to 0.82 before hunting (Ward and Larsen 1995). Survival increased to 0.97 to 0.98 during treatment – higher than the range of 0.90 to 0.95 in other areas where wolves were reduced to similar levels (Gasaway et al. 1983, 1992; Larsen et al. 1989; Ballard et al. 1991; Larsen and Ward 1995). Because adult survival has a profound effect on the trend of long-lived species (Eberhardt et al. 1982) the increase in adult survival of Aishihik moose during treatment also influenced the increase in moose numbers.

We had other evidence that adult survival increased during treatment. The ratio of adult bulls per 100 cows increased in both Aishihik South and Onion Creek count blocks, but not in control areas. Increases in bull:cow ratios also followed wolf reductions in the Finlayson area (Larsen and Ward 1995) and Unit 20E in Alaska (Gasaway et al. 1992)- but the effect of harvest was not estimated in either study. Reduction of harvest contributed to the higher sex ratio in Aishihik South, but probably had less of an effect in Onion Creek. Other wolf reduction studies did not measure differences in moose sex ratios before and during wolf reduction (Gasaway et al. 1983, Bergerud and Elliot 1998). Adult sex ratio can have a stronger effect on potential growth than does age distribution because a higher proportion of cows will accelerate the rate of increase (Van Ballenberghe 1983, Cederlund and Sand 1991). Conversely, if the sex ratio is strongly skewed to females wolf predation can have a stronger effect on the maternal component of a moose population, reducing the potential for increase.

We found no evidence that snow depth or summer weather affected moose response. Snow depth in late winter does not explain the decline in Aishihik moose during the 1980s, nor does it explain low recruitment rates in 1990 to 1992. Snow depth probably had little effect because depths never exceeded threshold levels in any area during our study. Even when snow is deep, responses of moose may not be immediate. In Alaska, snow depths reached 70 to 80 cm in 4 winters, but the survival of calves was low in only 1 of those winters (Gasaway et al. 1992). We conclude that during treatment, snow depths were favorable for moose (and caribou), reinforcing the positive effects of wolf reduction in Aishihik.

Other researchers have found evidence that growing season length can affect moose response (Stewart et al. 1977), but our study did not show this. Although average growing season length was longer in all areas during the treatment period, there was no relation between changes in season length and moose numbers. Unusually long or short growing seasons during particular years did not explain the larger increase in moose numbers in the Aishihik area.

It was possible that movement of moose could have affected moose responses. In Alberta, Rolley and Keith (1980) found ingress annually contributed 6% or more to the rate of increase of a moose population. We examined our moose data for the same possibility. Based on low surrounding densities, moose probably did not immigrate into the Aishihik area in substantial numbers. To the north, moose density was the lowest recorded in the Yukon (45 moose/1,000 km^2; Markel and Larsen 1988). To the south, the front ranges of the glaciated St. Elias Mountains support only a narrow strip of moose habitat. Densities to the east and west were between 120 and 170 moose/1,000 km^2 (R. Ward, Yukon Department of Renewable Resources, unpublished data); immigration into Aishihik from any direction was probably minimal.

Gasaway and Dubois (1985) suggested that fast-moving wildfires could temporarily force moose to abandon home ranges. We examined recent fire maps to see if large forest fires (>50 km^2 area) near the Aishihik area could have temporarily affected moose distribution and influenced our estimates. Fires burned one 85 km^2 area near the 3,400 km^2 Onion Creek count block in 1996 and no large fires burned near Aishihik South. Thus, fires probably did not affect moose distribution in 1998 in either Aishihik count area.

Moose Control Areas

Gasaway et al. (1983) detected moose migrations between their experimental and control areas, confounding responses. Our moose control areas were 70 to 150 km from the Aishihik area so it is unlikely control areas were affected by wolf reduction. In

Mayo, where moose numbers increased between 1993 and 1998, large fires burned a total of 980 km² near the survey area during the summer of 1998 - immediately preceding the population estimate (M. O'Donoghue, Yukon Department of Renewable Resources, unpublished data). The largest burn of 850 km² was along the entire southwestern border of the survey block. Although we have no direct evidence of moose moving from the newly burned areas into the count block, such migration may partially account for the population increase because the recruitment rates did not suggest an increasing population. Ingress from burned areas can also partly explain the unreasonably high survival rate of adults we calculated from census interpolation (0.99).

Harvest Effects on Caribou and Moose:

Most local people interviewed by Allen (1994) and Johnson (1994) believed that overhunting contributed to ungulate declines in the Aishihik area. We conclude that harvest rates of 5% to 8% were partly responsible for the declines in Aishihik caribou and moose before our study. Similar harvest rates contributed to a rapid decline in Alaska's Delta caribou herd during a period of adverse weather and increasing predation by wolves (Boertje et al. 1996). Gasaway et al. (1983) speculated that high harvest predisposes moose to increasingly depensatory wolf predation rates (i.e. wolves kill proportionally more as moose numbers decline). Gasaway et al. (1992; Fig. 17) estimated harvests of more than 5% are unsustainable for northern moose exposed to naturally-limited wolf and bear populations. We believe a similar situation existed in Aishihik, which explains the exceptionally low densities reached by moose and caribou before our study began.

Hunting closure was an additional treatment confounding our experimental design, especially the effect of wolf reductions on adult survival rate. The reduction of harvest nearly equaled the effect of wolf reduction on the rate of increase of Aishihik herd during treatment. However, harvest reduction alone could not have caused the Aishihik caribou to increase as rapidly as observed. When hunting was stopped from 1991 to 1993, the Aishihik herd continued to decline, mainly because recruitment rates remained low during those years.

Harvest reduction was also important in the increase in moose in the Aishihik South block, but not in the Onion Creek block. Aishihik South was accessible by road for most of the year and before our study was a favorite area for hunters. However, most of the wolf removal area, including Onion Creek, was remote and moose harvest rates were lower than in Aishihik South. Thus, wolf reduction was more important than harvest reduction to the increase in moose in most of the treatment area. However, both moose and caribou population responses would have been considerably lower during our study if harvest had not been reduced. Before wolf reduction, First Nation hunters killed cow moose and caribou throughout the year (Allen 1994, Johnson 1994). Reducing the hunting of cows increased the recruitment potential of both moose and caribou during wolf treatment.

Sheep Response:

Sheep population size and recruitment in the Ruby Range did not increase during treatment, nor were they different than the Rose Lake control area. We compared responses when the Ruby Range was used as our treatment, and when it was used as a control area to a previous wolf reduction in the Rose Lake area. We found no evidence that wolf reduction substantially increased sheep survival rates.

Bergerud and Elliot (1998) reported an increase in numbers and lamb survival rates of Stone's sheep (*O. d. stonei*) during a wolf reduction period. A review of their sheep data is less convincing (see their Table 8, page 1563). Total sheep numbers dropped during the wolf reduction period (1983 to 1985), and sheep numbers apparently increased when wolf numbers were recovering in their study area. The lack of adequate controls makes their arguments for sheep response to wolf reduction unconvincing.

In Alaska, Gasaway et al. (1983) found that there was no pattern in lamb survival related to wolf reduction. In the same area, Scotton (1998) radio-collared neonatal lambs and found 96% of mortality was due to predation including 43% to 60% by coyotes, 22% by golden eagles, and only 4% to 17% by wolves. Wolves increased 3-fold during the study, but he did not detect an increase in predation by wolves on lambs. In the Kluane area, Sumanik (1987) found wolves that relied on sheep had low densities, large home ranges, small pack sizes and low predation and consumption rates. He suggested that wolves that depended on sheep could not kill enough sheep to support themselves for long periods. Dall sheep represented only 12% of the diet of wolves in Denali (Mech et al. 1998) and 18% of the diet of wolves in the Coast Mountains, adjacent to Aishihik (Hayes et al. 1991). Although sheep could be important to the diet of some wolves, wolf predation does not appear to be a main factor limiting sheep in the Yukon and Alaska.

Wolves kill proportionately more old sheep (Murie 1944, Burles and Hoefs 1984, Sumanik 1987, Hayes et al. 1991, Mech et al. 1998), but population effects have not been determined. We examined the mean age of harvested rams in the Aishihik area before and during treatment. Ram ages were older before treatment; cohort effects probably play a more important role in determining age structure (Carey and Dehn 1998) than does wolf predation.

Local people identified bears, coyotes, golden eagles, lynx and wolverines as important predators of sheep in the Aishihik area (Johnson 1994). Hoefs and Cowan (1979) found coyotes were the most important predators of Dall sheep in nearby Kluane National Park. Wolverine, black and brown bears and lynx also live in the area and are known to prey on sheep (Hoefs and Cowan 1979). Golden eagles also prey on lambs (Nette et al. 1984, Scotton 1998) and eagles nest at high densities in the Ruby Range (Windsor 1979).

Lamb production in the Yukon shows considerable annual variability, ranging from 9 to 67 lambs per 100 nursery sheep during June or July (J. Carey, Yukon Department of Renewable Resources, unpublished data). Similar variability (8 to 81 lambs per 100 ewes) has also been reported in Alaska (Nichols 1978). Much of this variation has been linked to stochastic weather events (Hoefs 1984, Barichello and Carey 1988, Heimer and Watson 1986). The decline in sheep numbers in the Ruby Range between the 2 treatment periods can be related to several years of poor lamb production in the 1980s (Carey and Dehn 1998).

We had no evidence that adverse weather affected the sheep response during our study. We examined various weather variables assessed for moose and caribou in the Aishihik area and could not detect adverse conditions in any year. The overall production of 28 lambs per 100 nursery sheep in July (range 24 to 32) seen in the treatment area was close to the long term average of 30 lambs:100 nursery sheep measured throughout the Yukon since 1973 (J. Carey, Yukon Department of Renewable Resources, unpublished data).

During our study, annual sheep harvest rates were kept below 3%, after local people recommended voluntary restrictions in the area. Harvest of mature rams could have reduced growth of the sheep population in our treatment area, but reported harvest rates during treatment were below the 4.4% average recruitment of rams entering the mature category (full curl) (Hoefs and Cowan 1979). Low harvest of mature rams has not been shown to have an effect on sheep population size or productivity in Alaska (Gasaway et al. 1983, Murphy et al. 1990).

Test of Hypotheses and Predictions:

In Table 10 we summarize our quantitative predictions for ungulate responses (Hayes 1992) and evaluate how much support we have for each prediction. Predictions of increased caribou recruitment and herd size were supported (P1, P2, P3, P4). We had weak support for prediction P5 because the Ibex herd increased in the absence of wolf reduction, whereas the Wolf Lake herd remained stable and the Chisana herd declined. The Ibex herd showed high but declining recruitment through all years of our study;

herd size only began to increase when First Nations harvest was suspended. We had the weakest support for predictions P6 and P7. Adult survival in Aishihik herd increased compared to only 1 of 2 pre-treatment years, and mean annual survival rate of Aishihik adults during treatment was no different than of adults in the Wolf Lake herd.

We conclude that there is strong support for Caribou H1: (Wolf reduction caused calf survival rates to increase in the Aishihik herd); support for Caribou H2: (Wolf reduction caused the Aishihik herd to increase); and no support for Caribou H3: (Wolf reduction caused adult survival rates to increase in the Aishihik herd).

For moose, 3 of our 6 predictions were supported (P1, P3, P5). Responses in the rate of increase of Aishihik moose (P3) and adult survival rate (P5) exceeded our expectations when wolves were reduced. Aishihik moose were the only group to show a significant increase in recruitment during treatment (P1).

We found partial support for moose predictions P4 and P6. Moose numbers also increased in the Mayo control area in the absence of wolf reduction, and annual adult survival was slightly higher in Mayo than in the Aishihik area. In Big Salmon area, moose numbers did not change and adult survival was lower than in Aishihik.

We found strong support for Moose H1: (Wolf reduction caused moose recruitment to increase in the Aishihik area); weak support for Moose H2: (Wolf reduction caused moose densities to increase in the Aishihik area); and weak support for Moose H3: (Wolf reduction caused survival rates of adult moose to increase in the Aishihik area).

We found no evidence to support our Dall sheep H: (Wolf reduction caused adult Dall sheep numbers and lamb recruitment rates to increase). Adult sheep population size and lamb recruitment rates were not related to changes in wolf abundance.

The strongest evidence for the wolf predation hypotheses was the before and after treatment Aishihik results. The Aishihik moose and caribou populations increased with treatment, whereas most control moose populations and caribou herds continued as before. Our conclusions are tempered by evidence that some of the control populations (i.e., Ibex caribou herd, Mayo moose) increased without wolf reduction. The strength of the conclusions from our Aishihik experiment is also confounded by reduction of both wolves and harvest at the same time. Harvest reduction played a substantial role in caribou and moose population responses, but it did not add to the strong increases in recruitment rates of both species during treatment.

For caribou, we found no evidence that pregnancy rates, winter food habits, disease, physical condition, snow depth, or snow melt influenced responses. For moose, we found no evidence that snow depth or summer growing season could explain observed responses. Environmental conditions were generally positive for ungulate survival during the treatment period, enhancing the positive effects of reduced predation.

Wolf-Ungulate Models:

The dynamics of multiple predator-prey systems depend on how each species of predator singularly interacts with each prey species, and how changes in the abundance of 1 species affects other species in the system. Several conceptual models have been presented to explain the dynamics of wolf-ungulate systems (e.g., Boutin 1992; Seip 1992; Messier 1994, 1995; Valkenburg et al. 1996), but none adequately integrate moose and caribou population dynamics. In the next section we discuss how wolves singularly interact with moose and caribou. We then discuss how changes in either prey species could affect Yukon predator-prey relations as a whole.

Ballard and Van Ballenberghe (1997) summarized 4 predator-moose models: recurrent fluctuations, single low density stable-state, 2-stable-state (predator-pit), and stable limit cycle. Each model credits predation with a strong role in limiting moose populations. Of the 4 models, the single low density stable-state and the 2-stable-state models provide for the regulation of moose populations through density-dependent processes. In each model, wolf predation acts to hold moose within a narrow range of densities (influenced by other ecological conditions at the time) by causing moose to decline when densities increase above the equilibrium range. When moose fall below the range, predation rates eventually decrease allowing moose numbers to increase again and eventually stabilize. Ballard and Van Ballenberghe (1997) concluded that there was evidence for the recurrent fluctuations model in simple wolf-moose systems (e.g. Isle Royale, Michigan), but there was more evidence for the single stable-state model in multiple predator-prey systems in North America.

Adding a second predator should increase total predation losses, unless predator kill rates are compensatory. There is growing evidence that the combined predation by bears and wolves, and periodic severe winters maintain moose at a narrow range of low density (Van Ballenberghe 1987, Gasaway et al. 1992, Messier 1994, Hayes and Harestad 2000*a*). Whether wolves 'regulate' moose or not remains a point of debate among ecologists (Messier and Crete 1985, Boutin 1992, Gasaway et al. 1992, Messier 1994, Hayes and Harestad 2000*a*). Messier (1994) presented a model showing that density-dependent predation by wolves regulated moose density from 200 to 400 moose/1,000 km^2. Hayes and Harestad (2000*a*) added kill rate data for the Yukon to the model of Messier, showing wolves should maintain moose in the Yukon somewhere below 120 moose/1,000 km^2.

Valkenburg et al. (1996) proposed a caribou model where adverse weather interacts with predation and nutrition to limit interior Alaska caribou herds over a wide range of densities. A combination of adverse weather and high wolf predation rates have caused caribou declines in interior Alaska (Boertje et al. 1996, Valkenburg et al. 1996, Mech et al. 1998), but we have not seen such effects after 2 decades of caribou studies in the Yukon (R. Farnell, Yukon Department of Renewable Resources, unpublished data).

Bergerud (1980, 1992) reported that when wolves reached densities of 6.5/1,000 km^2 they should regulate caribou to low abundance (<60 caribou / 1,000 km^2). Yukon data do not support the regulation model: there are a number of Yukon caribou herds at higher density where wolf densities exceed 6.5/1000 km^2 (Farnell et al. 1998). Yukon woodland caribou live in complex multiple predator-prey systems where moose are the primary prey of wolves (Hayes et al. 1991, 2000). Wolf numerical response is linked to the high biomass values of moose (Fuller 1989, Messier 1994, Bergerud and Elliot 1998, Hayes and Harestad 2000*a*) –wolf-caribou regressions that discount effects of moose density are too simplistic. In his review of wolf-caribou relations, Thomas (1995) concluded that where sympatric moose are common wolves exceed 5 to 8 wolves/1,000 km^2, keeping woodland caribou herds at low abundance for long periods. In the Yukon, wolf density averages 8.7 wolves/1,000 km^2 (range 3.6 to 18.8 wolves) based on 18 wolf surveys since 1983 (A. Baer, Yukon Department of Renewable Resources, unpublished data). These densities indicate that wolves could strongly limit Yukon woodland caribou herds.

Valkenburg et al. (1996) found little evidence for density-dependent food limitation in interior Alaskan caribou, and we found no evidence of it in our study. Pregnancy rates, winter food habits, disease (Farnell et. al 1999) and body condition scores (Kuzyk et al. 1999*a*) indicate that all Yukon herds were in good physical condition. In the Yukon and other northern areas, caribou densities are relatively low compared to potential food supply. Wolf predation can apparently hold caribou at densities well below levels where density-dependent forage limitation could be important (Seip 1992).

How wolf predation interacts with sympatric moose and caribou populations is poorly understood (see Messier 1995). Holt (1977:201-202) states, 'The introduction of a second prey species increases the density of the predator, the original prey suffers heavier levels of predation because of the increased density of predators, and it equilibrates at a lower density.' Seip (1991) and Messier (1995) proposed similar models where the presence of moose increases wolf density, and woodland caribou suffer increasingly depensatory predation. Both models implied predation by wolves could cause caribou extinction when numerical response of wolves is insensitive to declining caribou biomass. However, caribou herd extinctions caused by predator switching have not been documented.

Bear predation is apparently anti-regulatory (Ballard and Van Ballenberghe 1997), and it has a substantial effect in reducing the already low density of moose caused by wolf predation (Messier 1994, Hayes and Harestad 2000*a*). Thus, bears can determine the range of densities within which moose populations naturally fluctuate (Gasaway et al. 1992, Messier 1994). Bears can also indirectly limit caribou and other prey by removing a high proportion of the moose calves that wolves could otherwise kill, displacing more wolf predation onto alternate prey.

We hypothesize that wolves increase their predation on caribou when moose fall below some low density threshold level, with various caribou population outcomes that depend on a combination of wolf numerical and functional responses, and caribou behavior (Fig. 21). In our model, wolf predation is depensatory on both prey species until moose decline to 120 moose/1,000 km^2, the density at which the moose rate of increase should equal the predation rate by wolves on moose (Hayes and Harestad 2000*a*). Below this density, predation by wolves on caribou could respond 3 different ways. One, wolves could strongly switch from moose to caribou (i.e., a Type III functional response curve when moose are at low abundance; Fig. 21). If the wolf numerical response has a long lag period, the outcome is eventual extinction of the caribou herd (Curve 1, Fig. 21). Two, a caribou herd that is heading for extinction could find refuge from wolf predation by reducing its range size after a decline (Bergerud et al. 1983), minimizing exposure to the fewest number of wolf packs. By becoming rare, caribou could avoid further predation by wolves and eventually increase to some unstable higher density (Curve 2, Fig. 21). Three, a combination of adverse weather and wolf predation could initiate a recurrent decline at any caribou density. If wolves show a weak switching response to caribou, predation could act to maintain low caribou density for long periods, while moose are also maintained at low density (Curve 3, Fig. 21).

Determining the nature of the wolf-moose-caribou systems in the Yukon requires studying predation rates when moose are at densities below 200 moose / 1000 km^2. At higher densities, predation rate by wolves on moose has already reached an asymptote, kill rates are density-invariate (Hayes and Harestad 2000*a*), and wolves show a low switching response to caribou prey (Hayes et al. 2000).

The Yukon predator-prey system we describe is relatively new in the evolutionary context of the recent Holocene. Current scientific studies in Alaska and Yukon (Gasaway et. al 1992, Hayes and Harestad 2000*a*) support the hypothesis that wolves maintain moose at low abundance. However, until the mid-1800s moose were rare or absent from large parts of Alaska and northern Canada, including the Yukon (Peterson 1955, Kelsall 1972, Coady 1980, Yesner 1989). Caribou were abundant in the southern

Yukon in the recent Holocene (Kuzyk et al. 1999*b*). Their numbers have declined in recent times (Cruikshank 1985) as forest replaced tundra in Alaska and Yukon (Yesner 1989). First Nations people in the southwestern Yukon relied primarily on caribou into the early 20th century when moose were not common (Allen 1994). Clearly, our current moose-caribou models are based on short-term scientific data spanning less than a few decades. Such models do not reflect a long-term dynamic in wolf-prey relations that is continually evolving in response to environmental change. Ecological systems are in a natural and constant state of disequilibrium, and observations and expectations of stability are inconsistent with evolutionary theory (Yesner 1989, Pielou 1991).

Management Implications

Sustainable Harvest Rates on Moose and Caribou:

Gasaway et al. (1992) determined that harvest rates over 5% are probably unsustainable in Alaska and the Yukon where bears and wolves are naturally limited. In our Yukon wolf-moose-caribou model, small levels of overharvest can act in a depensatory fashion, causing greater declines than would occur without harvest (Hayes and Harestad 2000*a*). During periods of low to moderate recruitment, Aishihik moose declined when harvest was 6% to 8%, and caribou declined when harvest was 6% to 10%. We recommend that harvest of moose and caribou should be conservatively set at 0% to 5%, favoring lower values when recruitment is consistently below 30 calves per 100 cows and sex ratios are highly skewed to cows.

People can directly cause ungulate declines in 2 ways: losses by hunting and losses by habitat alienation. Declines can be enhanced or diminished by natural population fluctuations. The cumulative degradation of a population is often the result of anthropogenic processes, whereas recurring fluctuations are often the result of natural ecological and environmental processes.

Wildlife managers need to separate the impacts of human actions from natural variations in caribou and moose abundance. When natural and negative human actions combine, the ungulate population decline will assume an insidious 'ratchet'-like character: the population increases and decreases with the periodicity (if there is any) of the natural recurrent fluctuation in a progressively downward fashion (Anderson 2000).

For woodland caribou herds declining in a 'ratchet'-like pattern the threatened stage is entered after negative human actions have acted over a long term, finally depressing the population to a critically low level at which point the natural fluctuation can drive it in a depensatory spiral toward extinction. We believe these conditions were present in both Aishihik moose and caribou at the onset of our study. In our Yukon wolf-moose-caribou model, 'ratchet' effects of harvest could result in extinction of caribou in all 3 caribou response curves.

The differing dynamics of our caribou study herds reinforces the principle of managing woodland caribou on an individual herd basis (Yukon Department of Renewable Resources 1996). What is a sustainable harvest for 1 caribou (or moose) population may be too high for another, depending on ecological conditions. Harvest rates should be dependent on a range of factors influencing recruitment, survival, ingress and egress – and 'ratcheting' caribou to lower than natural levels of abundance should be avoided. Managers needs to more accurately predict the effects of harvest and other human-related activities that affect habitat condition, predator abundance, population age and sex structure, physical condition, and pregnancy rate of ungulates.

Options for Managing Predation:

The decision to reduce predators to increase ungulates for people is a socioeconomic and ethical choice (National Research Council 1997) and beyond the scope of our monograph. For example, Gasaway et al. (1992), Boertje et al. (1996) and Bergerud and Elliot (1986, 1998) argued that areas with low ungulate abundance have low biological and human values. In contrast, Hummel (1995) and Gilbert (1995) argued that naturally-limited systems are more publicly acceptable to urban people than intensively managed ones. Nonetheless, the expected biological outcomes of wolf management choices are relevant to decision-makers.

A decision to not manage wolf predation in the Yukon and Alaska will probably result in moose and wolves remaining at low density for long periods (Gasaway et al. 1992, Bergerud and Elliot 1998, Hayes and Harestad 2000*a*). However, we are not suggesting that all moose populations will be held at a constant state of low abundance, especially if there is favorable habitat. We believe moose and caribou can increase in parts of the Yukon without wolf reduction but there is no evidence of a 2-stable-state system existing for moose. Even the highest natural densities in the Yukon do not exceed 400 moose/1,000 km^2- well below the density moose are capable of reaching in Alaska and the Yukon without predators (Gasaway et al. 1992).

Rapid increases in moose and caribou were reported after 4 or more years of wolf reduction in Unit 20A in Alaska (Gasaway et al. 1983), the Finlayson area of the Yukon (Farnell and McDonald 1988, Larsen and Ward 1995), and in northern British Columbia (Bergerud and Elliot 1998). However, the long-term trend of these populations is uncertain. Although equivocal, we believe that the evidence to date supports the single-state model, and that these populations should return to their previous low abundance once wolf reduction has ended.

In the future, we believe government-sponsored lethal wolf control will be rare. There is substantial public opposition to aircraft-assisted wolf reductions in Alaska (Gasaway et al. 1992, Boertje et al. 1995), and we experienced opposition to our program from conservation groups in the Yukon and other parts of Canada. Gasaway et al. (1992) proposed 6 alternatives to aircraft-assisted wolf reductions: 1) diversionary feeding of predators on or near calving areas; 2) temporary relocation of bears away from calving areas; 3) increasing alternate prey numbers to reduce predation; 4) reducing birth rates of predators; 5) public trapping and hunting of predators; and 6) habitat enhancement. Boertje et al. (1995) evaluated most of these options for reducing predation on moose in Alaska. We present arguments in support of options 4, 5, and 6 as being useful in the Yukon.

Reducing birth rates of predators

Bergerud and Elliot (1998) and Spence (1998) argued that reducing predation where it was most beneficial to calf survival produced the greatest effect on ungulate populations. Spence (1998) showed surgical sterilization of breeding adult wolves was effective in maintaining small packs (2 to 4 wolves) in the Aishihik area. Her spatial modeling also implied that wolf sterilization on caribou summer range could allow the Aishihik caribou herd to continue increasing. In our study, sterilization was an important factor limiting wolf recruitment in the last 2 years of wolf treatment. To determine its long-term effectiveness, we are continuing to study behavioral responses of sterilized wolves as wolves recover into the Aishihik area, and we are monitoring responses of ungulates in treated and untreated wolf pack territories.

Surgical sterilization is one of a number of non-lethal methods now being applied on the summer range of the Fortymile caribou herd. In 1998, a combination of trapping, sterilization, and movement of live wolves to other areas was followed by sharp increases in calf recruitment and herd size (Boertje 1999). We recommend research be designed to experimentally test responses of moose and caribou recruitment to future fertility-control treatments. Despite the potential benefits of fertility control, some First Nations people are opposed to it for cultural reasons. These concerns should be resolved before initiating such programs.

Public Trapping and Hunting

There is broader support for public trapping and hunting of predators in Alaska (Boertje et al. 1995) and the Yukon (Yukon Wolf Planning Team 1992) than for other methods of reducing predation. In Alaska, public hunting and trapping of wolves effectively limits wolf populations near populated areas (Gasaway et al. 1992, Boertje et al. 1996). In the Yukon, wolf harvest was <4% per year, and wolves are not limited by hunting and trapping in any area (Hayes and Gunson 1995). Recent attempts to initiate community-based wolf trapping programs in the Yukon have had limited success, largely because the economic returns to wolf trappers are low, and concession holders show little interest in wolves. If harvest of wolves is to be useful in the long-term, incentives besides wolf fur values need to be offered to trappers, and the rights of trapping concession holders need to be changed to allow others to trap wolves in their areas.

Habitat Manipulation

Prescribed burning of moose range has not been attempted in the Yukon but a moose population increased dramatically in the Kenai area of Alaska after wildfires (Schwartz and Franzmann 1989). Moose densities in the Teslin burn area were among the highest recorded in the Yukon (Yukon Department of Renewable Resources, unpublished data). Thompson and Stewart (1997) reviewed moose habitat management and concluded that little is known about the effect of habitat management on moose populations at the landscape level. They recommended long-term experiments include replicated treatments to test responses of moose to habitat manipulations. Given the limited alternatives to increasing moose numbers through management of predation, habitat manipulation approaches should be considered.

The long-term suppression of wildfires in the Yukon is being reconsidered in areas where there is a low threat to human structures. In these areas, fires should be allowed to naturally burn mature forests, or areas should be deliberately burned to provide the seral communities preferred by many species. Wildfires could also benefit caribou by providing a mosaic of cover on winter ranges and the opening of the canopy could increase productivity of old, less productive lichen stands (Klein 1982).

Indications of Ungulate Population Trends

The propensity of a wildlife population to change is reflected in the internal processes of recruitment, mortality, ingress and egress. Current SRB methods for estimating moose and caribou populations are usually bounded by wide confidence intervals, making it difficult to determine short-term trend (Gasaway and Dubois 1987, Farnell and Gauthier 1988). Evaluation of the risks of management actions is dependent on how quickly the effect on abundance can be detected. In most instances, variances around SRB estimates are wide enough that changes in the order of 30% to 40% are required to detect significant changes in population size (W. Gasaway unpublished report to Yukon Department of Renewable Resources). Changes of this magnitude frequently take 5 years or more to detect, as we saw in our study.

Local people reported low calf numbers of both moose and caribou in the Aishihik area (Allen 1994, Johnson 1994), and their belief that both species were declining in the area was accurate. We recommend annual recruitment be used as a key measure of population trend because it acts as a complex integrator of population responses and environmental factors (McCullough 1979). Population trends should be verified with ongoing contact with local people, and by periodic monitoring of populations. For low-density northern ungulates, recruitment rates of 20 to 30 calves per 100 cows are sufficient to compensate for adult natural mortality and stabilize densities (Bergerud and Elliot 1998; R. Farnell, Yukon Department of Renewable Resources, unpublished data; R. Ward, Yukon Department of Renewable Resources, unpublished data). Caribou recruitment rates reported here were consistent with these ratios. Chisana caribou herd declined when mean annual ratios averaged 7 calves per 100 cows. The Aishihik herd declined more slowly at 15 calves per 100 cows, the Wolf Lake herd was stable at 26 calves, the Aishihik herd increased at 42 calves, and the Ibex herd increased at 44 calves for every 100 cows.

Adult sex ratios should be monitored regularly because of the large effect they have on population recruitment and potential rates of increase (Van Ballenberghe 1983). The reversing trends in sex ratio for the Aishihik and Chisana herds suggest that adult sex ratio is not independent of recruitment (Bergerud and Elliot 1986). Moose showed a similar relationship between recruitment and sex ratio. If selective hunting of bulls is not causing a biased sex ratio, then a sex ratio skewed to cows should be an early warning to managers of possible chronic low recruitment rates, and a higher risk of a population in decline. Moose and caribou managers should regularly model sex ratio, recruitment indices, and estimates of population size to assess the relative risks of harvest and habitat management decisions.

An understanding of the effects of habitat and adverse weather may be essential to determine the causes of fluctuations in the sizes of caribou herds. It is difficult to reliably measure annual variation in weather and estimate range condition relative to the needs of caribou, and then infer these effects on population dynamics. We chose to directly study caribou physiology to assess the relative importance of other potential limiting factors. Although these indices of population performance are not as quantitative as estimates of population dynamics, they offer useful insight into other potential factors limiting reproduction and survival.

Wildlife Conservation in the Yukon:

The Yukon Umbrella Final Agreement (Canada Dept. of Indian Affairs and Northern Development, 1993) entrenches co-management of wildlife between the Yukon and 14 First Nation governments throughout the territory. Local Renewable Resources Councils advise both governments on regional management issues. We found our scientific data on moose, caribou and sheep populations matched what local people observed during our study. After making working partnerships with local First Nations and other advisory groups, we found support and understanding of the project was increased with local participation in field studies and regular meetings to exchange ideas.

Most Yukon people favor sustainable use of wildlife, and there is agreement that the consumptive interests of people should be balanced with the needs of predators (Yukon Wolf Planning Team, 1992). In many places, the subsistence demands for wild food exceeds the natural supply. Wildlife managers and conservation groups must understand wolf-moose-caribou systems in the Yukon, and recognize that there is only a limited share of wildlife populations available for people to harvest. Where people choose to increase their share, the net result will be a reduction in the amount for predators and possible declines in prey populations.

We believe that woodland caribou become increasingly vulnerable to the depensatory effects of wolf predation when moose are in decline, and that the ratchet effects of overharvest can lead to local extirpation of caribou. Although we have little evidence of weather affecting caribou dynamics, adverse weather could initiate declines independent of the status of sympatric moose populations. We recommend that management decisions about regional moose and caribou populations not be made independently, and that a more systematic approach be taken to researching, managing and conserving both species, along with natural predators.

Human developments can directly contribute to wildlife declines by restricting range use or by providing new access to areas where harvest was previously light. Governments, boards, and councils must recognize the complexity of factors affecting moose and woodland caribou populations and design effective decision-making processes that address the spatial and habitat requirements of wildlife populations.

In place of broadly reducing wolf numbers to increase depressed prey populations, wildlife managers should be managing proactively to avoid such declines (Yukon Wolf Planning Team 1992). The challenge will be to find a publicly acceptable approach without compromising predator populations.

Regardless of the methods used, intensive management of wolf-prey systems will be unacceptable to some segments of society (Hummel 1995). On the other hand, wildlife managers are under increasing pressure to provide a reasonable share of wildlife for human consumption. Wildlife conservation in the Yukon will require the integration of both sustainable use and preservation models to satisfy broad public values.

In the Yukon, there are ways to balance these conflicting values. One option is to use the Yukon Protected Areas Strategy (Yukon Department of Renewable Resources 1998) to secure areas where large mammal systems would be managed for natural change and predators could not be manipulated to benefit people's use of ungulates. In other areas, some reduction of predation using socially acceptable methods could be considered to allow people a larger share of wildlife than is naturally available.

Adaptive Management and Predator-Prey Experiments:

Given constraints imposed by ecological, social, and monetary limits, we designed our experiment to test the effects of wolf predation through a hypothetico-deductive method.

The ideal wolf-prey experiment would consist of at least 2 ungulate prey units treated with wolf reduction, randomly interspersed among 2 or more untreated control units. Controlled and replicated field experiments can be carried out on a small scale, but on the scale of large mammal systems, it is often impractical (Sinclair 1991). Our large-scale experiment was not ideal because:

1) We were limited to treating 1 area with wolf reduction (Yukon Wolf Planning Team 1992), so we had no replication of treatment to estimate random error.
2) The assignment of the treatment area was not random but chosen by public concern, increasing the risk of systematic bias.
3) Without replication we had no interspersion, increasing the risk of bias and stochastic effects (Hurlbert 1984).
4) We were required to eliminate hunting of moose and caribou as part of our research design based on ethical guidelines (Yukon Wolf Planning Team 1992), adding a second treatment effect.

The problem of a non-random single treatment is shared with other large-scale wolf experiments (Gasaway et al. 1983, 1992; Farnell and McDonald 1988). A single treatment area is a fundamental problem because, for ethical reasons, the public will not add a second large-scale wolf reduction for strictly research purposes (Yukon Wolf Planning Team 1992). Outcomes of single treatment area experiments cannot generalize to other areas, and results must wait for future opportunities to repeat the observations (Sinclair 1991).

Replication can be achieved by treating several smaller areas rather than 1 large area, or the treatment area can be large enough to affect several systems that could constitute replicates (Sinclair 1991). We could not alter several smaller areas because the minimum treatment area included the annual range of the Aishihik caribou herd. We could not test for variability in moose or sheep responses in the treatment area because we could not determine whether populations were separate or subsamples - and the problem of pseudoreplication and lack of interspersion remained.

Smaller scale experiments could be designed to examine wolf-prey systems (Yukon Wolf Planning Team 1992, Boertje et al. 1995). Smaller replicated experiments could be designed at the level of watershed, wolf pack territory, or important seasonal range of an ungulate population (Spence 1998). Smaller experiments could also better serve the community interests in conserving locally important wildlife populations, by incorporating proper experimental design with traditional approaches to predator management.

Hunting closures added a confounding treatment to our experiment (National Research Council 1997) and elsewhere (Gasaway et al. 1983, Farnell and McDonald 1988). The Yukon public will not accept the reduction of wolves when hunting remains (Yukon Wolf Planning Team 1992). Including both treatment effects into experimental designs is inevitable. We assumed wolf predation and hunting were additive (the effects of both sum), then we modeled the relative effects of each treatment on changes in ungulate densities. In this way, we were able to separate to effects of the treatments.

A standard assumption when modeling population dynamics is that most animals are equal, and that the average responses of animals are reflected in a numerical change at the population level. However, simply measuring changes in the abundance of prey does not reflect possible internal dynamics of change. Age distribution (Page 1989), proportion of adult cows (Van Ballenberghe 1987), physical condition (Peterson 1977, Mech et. al. 1998), and calf mass at birth (Adams et al. 1995) can all have strong density-independent effects on ungulate population trends. Ideally, these factors should be examined as part of an experimental design.

Wolf-caribou-moose relations will only be exposed over a long time. No single model will prevail (Thomas 1995, Ballard and Van Ballenberghe 1997) and we should not be surprised when the system dynamics change (Pielou 1991). To fully understand what ultimately controls a species' density, we could examine the entire community in which the species exists (Holt 1977, Thomas 1995). Although this may be desirable, the ability to study multiple factors is rarely possible, especially in large mammal systems (Sinclair 1991). We join Walters and Holling (1990), Sinclair (1991), and Boutin (1992), and encourage other agencies to test the assumptions of management actions through the testing of hypotheses that expose the nature of important limiting factors on wildlife populations.

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Table 1. Experiment design schedules for estimating population parameters of wolves, caribou, moose, and sheep in treated and control areas over the duration of the study.

	Pre-treatment						Treatment		
	1990	1991	1992	1993	1994	1995	1996	1997	1998
Wolf Study Area									
Aishihik			PE	• /PE	• /PE	• /PE	• /PE	• /PE	PE
Wolf Lake					PE				
Mayo						PE			
Tatchun Hills							PE		
Caribou Herd									
Aishihik	C	C/TC/R	C/R	• /C/R	• /C/TC/R	• /C/R	• /C/R	• /C/PE/R	C/R
Wolf Lake				C/PE/R	C/R	C/R	C/R	C/R	C/PE/R
Chisana	C/R	C/R	C/TC/R	C/R	C/R	C/R	C/R	C/PE/R	C/R
Ibex	C/TC	C	C	C	C	C	C	C	C/PE

Table 1. (continued) Experiment design schedules for estimating population parameters of wolves, caribou, moose, and sheep in treated and control areas over the duration of the study.

	Pre-treatment						Treatment		
	1990	1991	1992	1993	1994	1995	1996	1997	1998
Moose Study Area									
Aishihik	C	C	C	• /C/PE	• /C	• /C	• /C	• /C	• /C/PE
Big Salmon				C/PE	C	C	C	C	C/PE
Mayo				C/PE	C	C	C	C	C/PE
Ladue				C	C	C	C	C	C

• = wolf reduction
C = sex and age composition count
TC = total count (includes composition)
PE = population estimate
R = radio collar relocation surveys

Table 2. Experimental design for Dall sheep population size and lamb recruitment rate.

Area	1982	1983	1984	1985	1986	1993	1994	1995	1996	1997
Rose Lake	TC	●TC	●TC	●TC		TC	TC	TC	TC	TC
Ruby Range	TC	TC	TC	TC	TC	●TC	●TC	●TC	●TC	●TC

● wolf reduction
TC is a total count, including composition

Table 3. Characteristics of caribou herds in Aishihik and 3 control areas before wolf treatment began in March 1993.

	Aishihik[a]			Wolf Lake[a]		Ibex[b]		Chisana[c]	
	Oct	Mar	Mar	Mar	Mar	Oct	Oct	Oct	Oct
	1981	1991	1993	1987	1993	1987	1992	1987	1992
Annual range size (km^2)		7,345	7,345	9,663	9,663	3,923	3,923	4,000	4,000
Estimated herd size (90% CI)	1,500	785	732	664±20%	1,249±12%	112	126	1800	1270
Caribou density (per 1,000 km^2)	204	107	100	69	129	28	32	450	318
Annual population change (r)		-0.06	-0.02		0.11		0.02		- 0.07
Bulls per 100 cows		19	35	29	48	41	76	39	31
Calves per 100 cows		21	7	27	13	48	53	28	<1

[a] All data for Aishihik and Wolf Lake herds from Farnell et al. (1996).

[b] Data for Ibex herd from R. Farnell (Yukon Fish and Wildlife Branch, unpublished data).

[c] Data for Chisana herd from C. Gardiner (Alaska Department of Fish and Game, unpublished data).

Table 4. Characteristics of moose populations in Aishihik and 2 control areas before wolf treatment began in March 1993. All moose data are from surveys conducted in November (Ward and Larsen 1994).

	Moose areas in Aishihik treatment				Untreated moose areas		
	Aishihik South Block			Onion Creek Block	Big Salmon	Mayo	
	1981	1990	1992	1992	1993	1988	1993
Survey area (km^2)	1,965	1,965	1,965	3,397	2,700	3,029	3,049
Estimated number ± (90% CI)	322±8%	253±19%	118±16%	416±18%	527±22%	315±22%	361±14%
Moose density (per 1000 km^2)	166	129	64	122	195	104	118
Annual population change (r)		-0.05	-0.24				NSC[1]
Bulls per 100 cows	67	42	61	49	71	58	95
Yearlings per 100 cows	45	26	15	12	17	46	25
Calves per 100 cows (Oct)	24	56	11	21	50	67	52

[1] no significant change; $P>0.20$

Table 5. Abundance of wolves in the Aishihik treatment area and 3 control study areas, 1992-1998.

								Wolf mortalities					
Area (km^2)	Period	No. wolves	No. packs	Pack density (No. packs/ 1,000 km^2)	Mean pack size (±SE)	Density (wolves/ 1,000 km^2)	Survey coverage rate (km^2/hr)	Yukon Fish and Wildlife	Natural Mortality	Public	Total	% reduction from 1992 population	Rate of increase
Aishihik (20,000)	Feb 1992	178[a]	28	1.4	5.6±0.6	8.9	205						
	Jan 1993	120	26	1.3	4.2±0.4	6.0					58	33	0.67
Wolf treatment began Feb 1993													
	Mar 1993	55	11	0.6	3.8±0.5	2.8	72	54	1	10	65	69	
	Jan 1994	81	20	1.1	3.7±0.4	4.1						54	1.5
	Mar 1994	44	12 (1)[b]	0.6	3.1±0.3	2.2	100	32	4	1	37	77	
	Jan 1995	75	18	0.9	3.8±0.6	3.8						58	1.6
	Mar 1995	38	11	0.6	2.7±0.2	1.9	95	36		1	37	79	
	Jan 1996	52	12	0.6	3.9±0.6	2.6						71	1.5

Table 5 (Continued). Abundance of wolves in the Aishihik treatment area and 3 control study areas, 1992-1998.

								Wolf mortalities					
Area (km^2)	Period	No. wolves	No. packs	Pack density (No. packs/ 1,000 km^2)	Mean pack size (±SE)	Density (wolves/ 1,000 km^2)	Survey coverage rate (km^2/hr)	Yukon Fish and Wildlife	Natural Mortality	Public	Total	% reduction from 1992 population	Rate of increase
	Mar 1996	30	7 (3) [b]	0.4	3.4±0.7	1.5	102	17		5	22	83	
	Jan 1997	55	13	0.7	3.8±0.8	2.8						69	1.7
	Mar 1997	33	9 (6) [b]	0.5	2.8±0.7	1.7	100	12	1	9	22	81	
Wolf treatment ended Apr 1997													
	Jan 1998	58	14	0.7	3.8±0.5	2.9						67	1.8
	Mar 1998	52	14	0.7	3.4±0.4	2.6	222			6	6	71	
Control Study Areas													
Mayo (15,680)	Mar 1995	96-107	15	1.0	5.8±0.8	6.1–6.8	224						
Wolf Lake (6,750)	Mar 1994	45-52	8	1.2	5.1±0.7	6.7-7.7	157						
Tatchun (10,050)	Mar 1996	45-52	9	0.9	4.6±0.4	4.5-5.1	223						

[a] Total pre-treatment wolf population in February 1992 was the sum of the 1992 count area (15,000 km^2;125 pack wolves and 13 lone wolves) plus the number counted in the extension area (5,000 km^2) in 1993 before treatment began (37 pack wolves and 3 lone wolves) =178 wolves (Carey et al. 1994).

[b] (n) No. of packs with 1 or more wolves

Table 6. Kaplan-Meier survival rates for adult caribou in the Aishihik, Wolf Lake and Chisana herds, 1991-1997.

Area	Period	Year	No. at risk	No. deaths	Annual survival	No. censored	No. added	Variance	Upper 95% confidence bound	Lower 95% confidence bound
a) Aishihik herd	Before treatment	1991	17	1	0.941	0	11	0.003	0.833	1.050
		1992	27	13	0.518	0	15	0.005	0.383	0.654
	Treatment	1993	29	3	0.896	0	9	0.003	0.792	1.002
		1994	35	4	0.885	4	8	0.003	0.787	0.985
		1995	35	5	0.857	1	21	0.003	0.750	0.964
		1996	50	3	0.940	4	0	0.001	0.876	1.004
		1997	43	4	0.906	4	0	0.002	0.824	0.990
		Total	236	33		13				
b) Wolf Lake herd		1993	29	1	0.965	0	0	0.001	0.900	1.031
		1994	28	4	0.857	0	7	0.004	0.737	0.977
		1995	31	8	0.741	0	23	0.005	0.609	0.875
		1996	46	1	0.978	0	0	0.000	0.937	1.020
		1997	45	3	0.933	4	0	0.001	0.863	1.004
		Total	179	17		4	30			

Table 6 (Continued). Kaplan-Meier survival rates for adult caribou in the Aishihik, Wolf Lake and Chisana herds, 1991-1997.

Area	Period	Year	No. at risk	No. deaths	Annual survival	No. censored	No. added	Variance	Upper 95% confidence bound	Lower 95% confidence bound
c) Chisana herd	Before treatment	1989-1990	23	8	0.652	15	15	0.006	0.495	0.809
		1990-1991	25	4	0.840	12	12	0.005	0.708	0.972
		1991-1992	24	8	0.667	5	5	0.006	0.513	0.821
		1992-1993	23	2	0.913	15	15	0.003	0.803	1.023
	During treatment	1993-1994	19	2	0.895	0	0	0.004	0.764	1.025
		1994-1995	18	5	0.722	2	2	0.008	0.546	0.898
		1995-1996	17	4	0.765	7	7	0.008	0.588	0.941
		1996-1997	16	1	0.938	5	5	0.003	0.823	1.052
		Total	165	34		22	61			

Table 7. Percent pregnancy in the Aishihik and 3 control caribou herds. Sample sizes are in parentheses, 1991-1996

	Year					
Herd	1991	1992	1993	1994	1995	1996
Aishihik	100 (6)	96 (50)	93 (14)	88 (8)	100 (11)	100 (22)
Ibex					100 (4)	
Chisana			25 (4)	78 (26)	100 (19)	
Wolf Lake			95 (21)		86 (7)	100 (23)

Table 8. Comparison of growing season length with moose population change.

Moose population	Average season length in days, 1983-1992$^{(*)}$	Average season length (days) 1993-1998$^{(*)}$	Change in growing season length (days)	No. of short seasons 1993-1998	No. of long seasons 1993-1998	Rank change in season length	Rank increase in population
Big Salmon	110$^{(9)}$	125$^{(6)}$	+15	0	1	1	3
Aishihik	102$^{(8)}$	114$^{(5)}$	+12	1	1	2	1
Mayo	111$^{(9)}$	114$^{(5)}$	+3	1	0	3	2

(*) = number in brackets represents number of years for which data available.

Table 9. Results of Wilcoxon Z-value tests for differences in lamb recruitment between treatment and control areas 1982-1985 and 1993-1997.

		Wilcoxon Z values	df	P
Rose Lake (T) vs. Ruby Range (C)	1982	0.57	1	0.57
	1983	0.78	1	0.44
	1984	-0.11	1	0.91
	1985	2.52	1	0.01
Ruby Range (T) vs. Rose Lake (C)	1993	1.16	1	0.25
	1994	-1.32	1	0.19
	1995	1.11	1	0.26
	1996	-1.57	1	0.16
	1997	-1.59	1	0.11

(T = treatment area, C = control area)

Table 10. Predictions about wolf and ungulate responses (Hayes 1992) and levels of support from our study.

Prediction	Level of Support
Caribou	
P1) Calf recruitment in Aishihik caribou will increase to more than 30-35 calves per 100 cows after wolf treatment.	++
P2) The proportion of calves in the control herds will not increase.	++
P3) Aishihik caribou will increase at a rate of 1.15 annually after treatment.	++
P4) Herd size will double after 5 years.	++
P5) Control herds will not increase.	+ (2 of 3 herds)
P6) Survival rates of radio-collared adults in the Aishihik herd will increase to 0.90-0.95 during wolf treatment.	+ (close to lower end)
P7) Adult survival in the control herds will be lower than for the Aishihik herd.	-
Sheep	
	-
P1) The number of adult sheep will increase in treatment area, but not in control area.	-
The lamb to nursery sheep ratio will increase in treatment area, but not in control area	
Moose	
P1) The proportion of moose short-yearlings in the Aishihik area in late winter will increase to 13%-20% during wolf treatment.	++
P2) The proportion of short-yearlings in control areas will not increase.	+
P3) Aishihik moose densities will increase at a finite annual rate of 1.08-1.12 after wolf treatment.	++ (exceeded)
P4) Moose densities in control areas will not increase.	+
P5) Mean annual adult survival rate will increase to 0.96 in the Aishihik area.	++ (exceeded)
P6) Adult survival will be higher in Aishihik compared to 2 control areas.	+

- Prediction not supported.
+ Weak support for prediction
++ Strong support for prediction

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Fig. 12. Maximum snow depth by year on winter ranges of the treated Aishihik herd and 3 control caribou herds. Horizontal lines show critical depths for caribou.

Fig. 13. Growing degree days in May for the treated Aishihik herd and 3 control caribou herds.

Fig. 14. Estimate change in moose numbers in the Aishihik South and Onion Creek census areas (treated), and the Mayo and Big Salmon census areas (controls) before (1992-93) and at the end of wolf treatment (1998) in the Aishihik area.

Fig. 15. Annual proportions of moose calves in late winter in the Aishihik treatment area and 3 moose control areas. Data for Aishihik 1992 was based on 87 adults and 7 short yearlings seen during wolf surveys, February and March (A. Baer, Yukon Fish and Wildlife Branch, unpublished data).

Fig. 16. Differences in the proportion of calf moose during late winter in the Aishihik treatment area and 3 control areas before (1993), and during treatment in Aishihik (1994-98). Vertical lines show bias-corrected 90% confidence intervals from resampling 2,000 times.

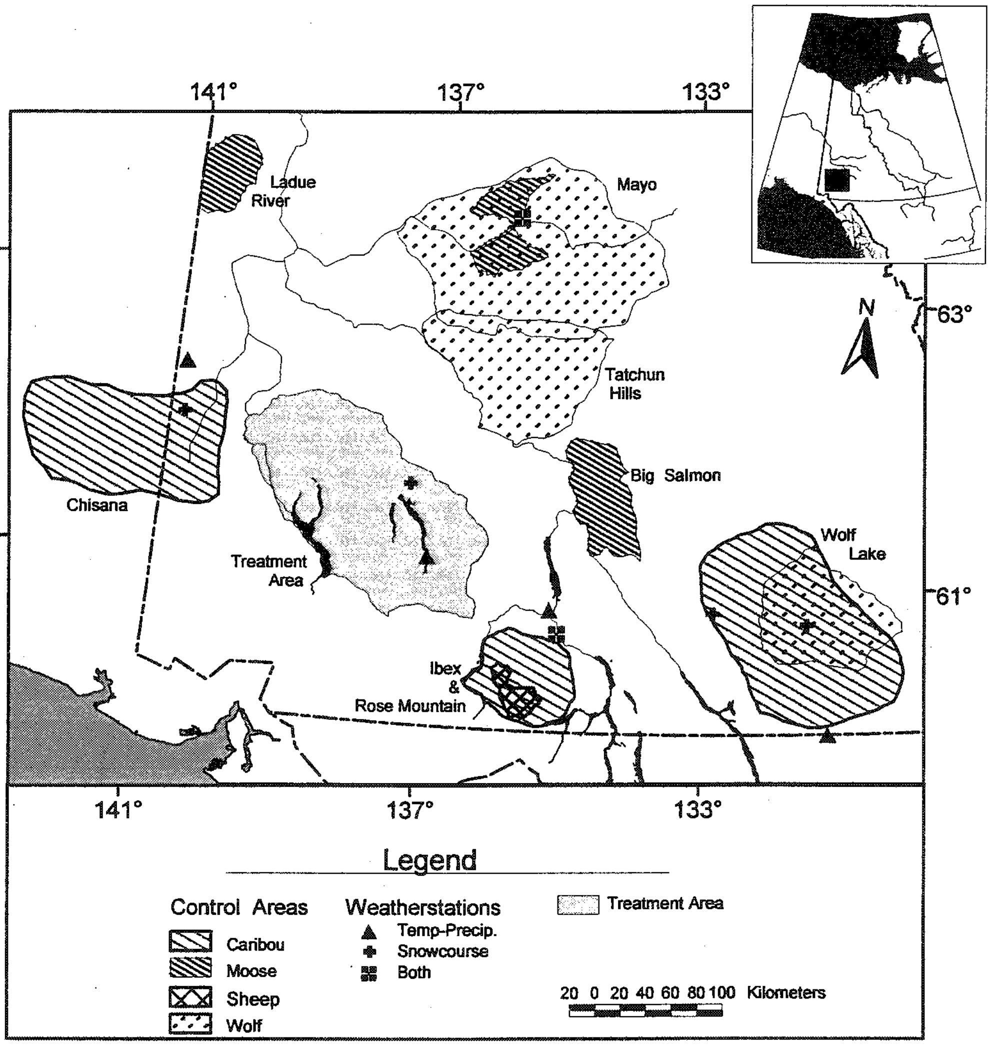
Fig. 17. Maximum snow depth by year for all moose study areas. Horizontal lines show critical snow depths for moose.

Fig. 18. Total number of adult sheep counted in Ruby Range and Rose Lake, 1983-85 and 1993-97. All regressions of sheep numbers by year ($y = a + bx$) were not significant, Ruby Range 1983-85 (control, $P=0.72$), Ruby Range 1993-97 (treatment, $P=0.42$), Rose Lake 1983-85 (treatment, $P=0.72$), Rose Lake 1993-97 (control, $P=0.79$).

Fig. 19. Ratios of lambs/100 nursery sheep in Ruby Range (control) and Rose Lake (treatment) areas, 1982-87; and in Ruby Range (treatment) and Rose Lake (control) areas, 1993-97.

Fig. 20. Annual rate of increase of wolves and reduction levels in our study and 4 other studies (Game Management Unit 20A, Gasaway et al. 1983; Game Management Unit 20E, Gasaway et al. 1992; Coast Mountains, Hayes et al. 1992, Finlayson, R. Farnell unpublished data).

Fig. 21. Conceptual wolf-moose-caribou model for the Yukon. Curve for wolf predation rate on low density moose from Hayes and Harestad (2000b). M_s is stable low density equilibrium of 70 to 120 moose/1,000 km^2 (Hayes and Harestad 2000b). Three curves for wolf predation rate on woodland caribou are inversely density dependent (see Messier 1995). All 3 equilibrium points at lower caribou density are unstable. Three equilibrium points at high density are stable. Curve 1 implies eventual extinction of caribou due to depensatory predation rate. Curve 2 implies long-term stability, and Curve 3 implies a recurrent fluctuation. Growth rate of prey without predation declines due to competition for food resources.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Big Salmon
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Wolf Lake
Ibex & Rose Mountain
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133°
Legend
Control Areas
Caribou
Moose
Sheep
Wolf
Weatherstations
Temp-Precip.
Snowcourse
Both
Treatment Area
20 0 20 40 60 80 100 Kilometers

Figure 1

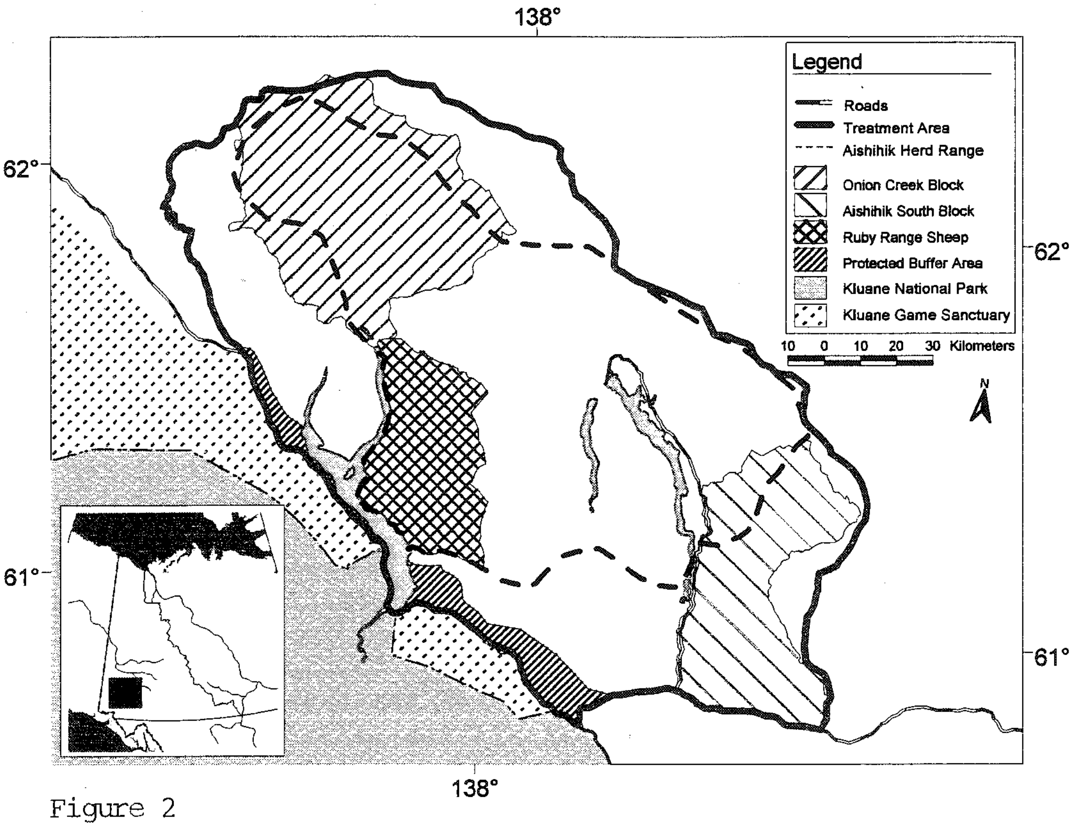
138°
62°
61°
62°
61°
138°
Legend
Roads
Treatment Area
Aishihik Herd Range
Onion Creek Block
Aishihik South Block
Ruby Range Sheep
Protected Buffer Area
Kluane National Park
Kluane Game Sanctuary
10 0 10 20 30 Kilometers
N

Figure 2

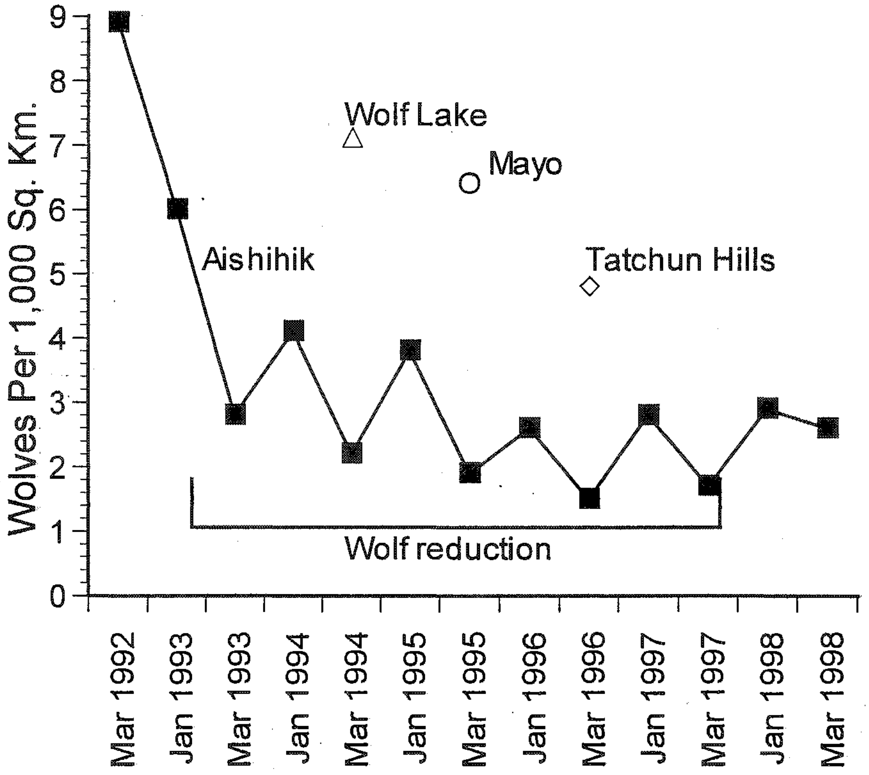
Wolves Per 1,000 Sq. Km.
0
1
2
3
4
5
6
7
8
9
Wolf Lake
Mayo
Aishihik
Tatchun Hills
Wolf reduction
Mar 1992
Jan 1993
Mar 1993
Jan 1994
Mar 1994
Jan 1995
Mar 1995
Jan 1996
Mar 1996
Jan 1997
Mar 1997
Jan 1998
Mar 1998

Figure 3

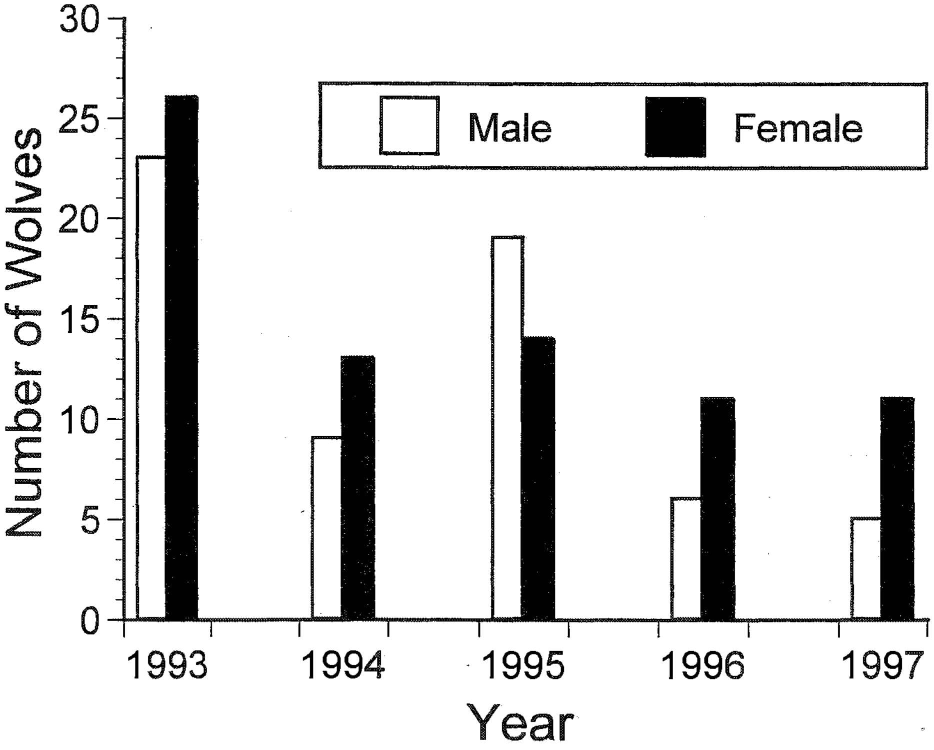
30
25
20
15
10
5
0
Number of Wolves
Male
Female
1993
1994
1995
1996
1997
Year

Figure 4

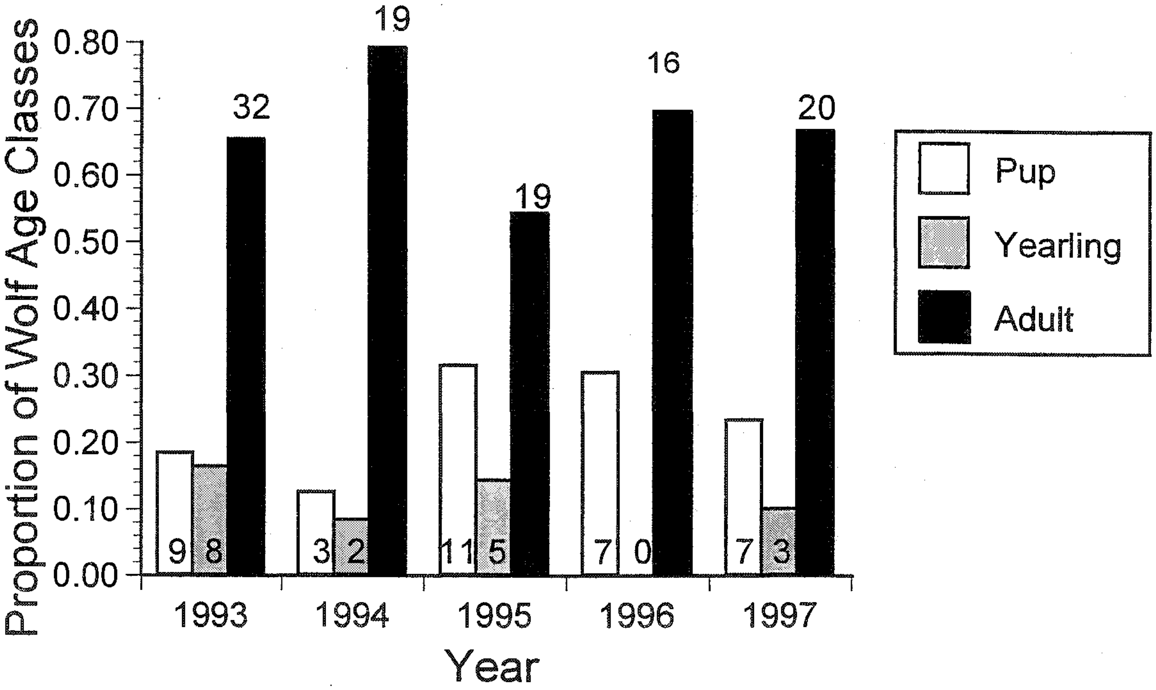
Proportion of Wolf Age Classes
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
32
19
19
16
20
9
8
3
2
11
5
7
0
7
3
1993
1994
1995
1996
1997
Year
Pup
Yearling
Adult

Figure 5

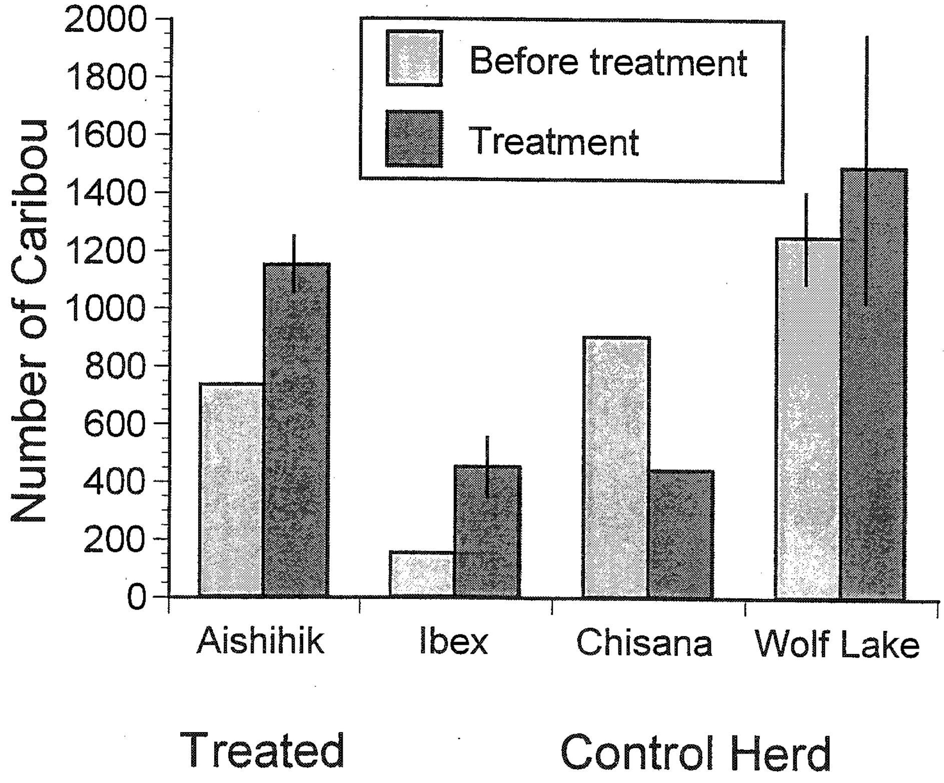
Number of Caribou
2000
1800
1600
1400
1200
1000
800
600
400
200
0
Before treatment
Treatment
Aishihik
Ibex
Chisana
Wolf Lake
Treated
Control Herd

Figure 6

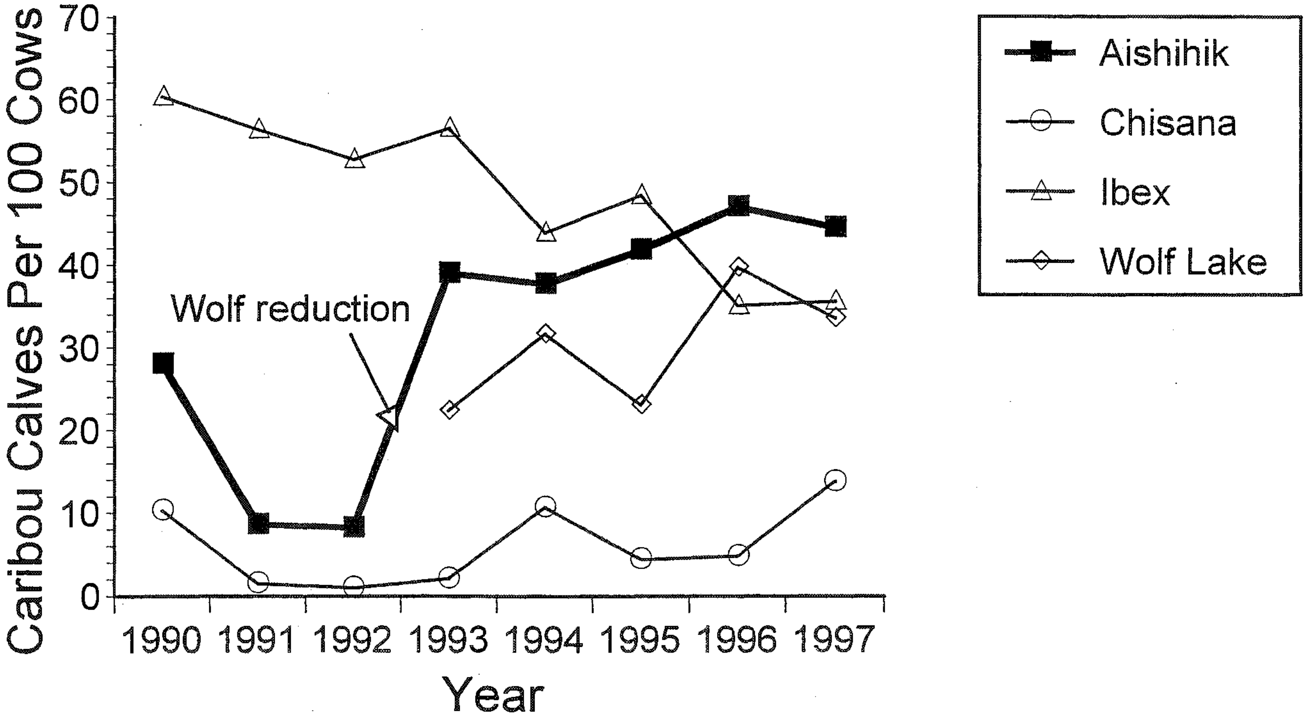
Caribou Calves Per 100 Cows
70
60
50
40
30
20
10
0
1990
1991
1992
1993
1994
1995
1996
1997
Year
Wolf reduction
Aishihik
Chisana
Ibex
Wolf Lake

Figure 7

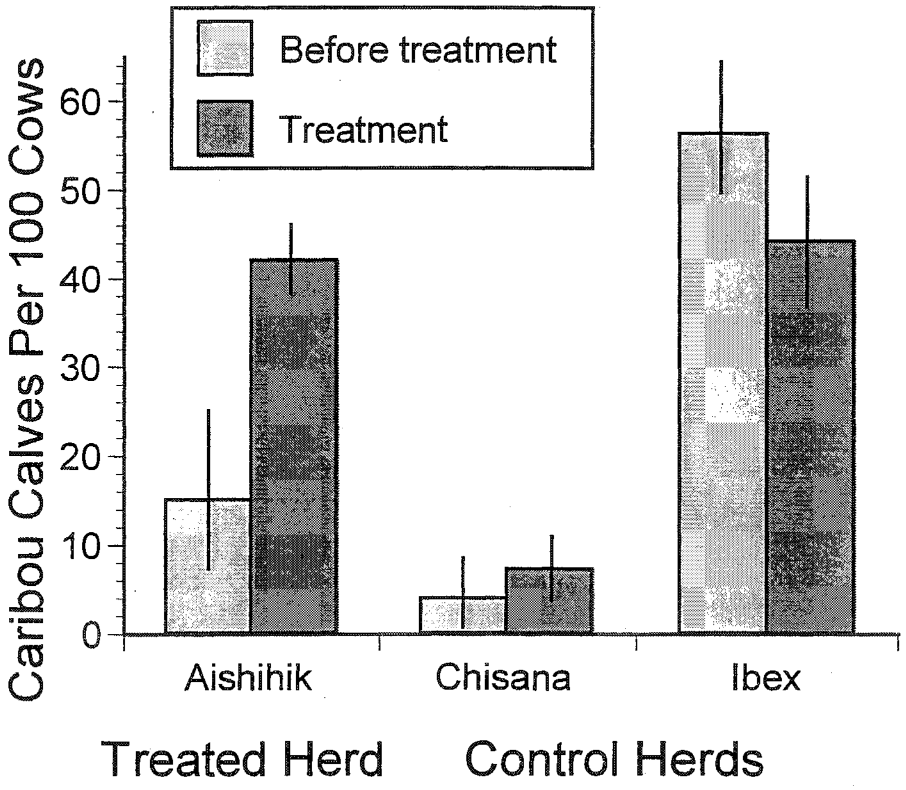
Before treatment
Treatment
Caribou Calves Per 100 Cows
0
10
20
30
40
50
60
Aishihik
Chisana
Ibex
Treated Herd
Control Herds

Figure 8

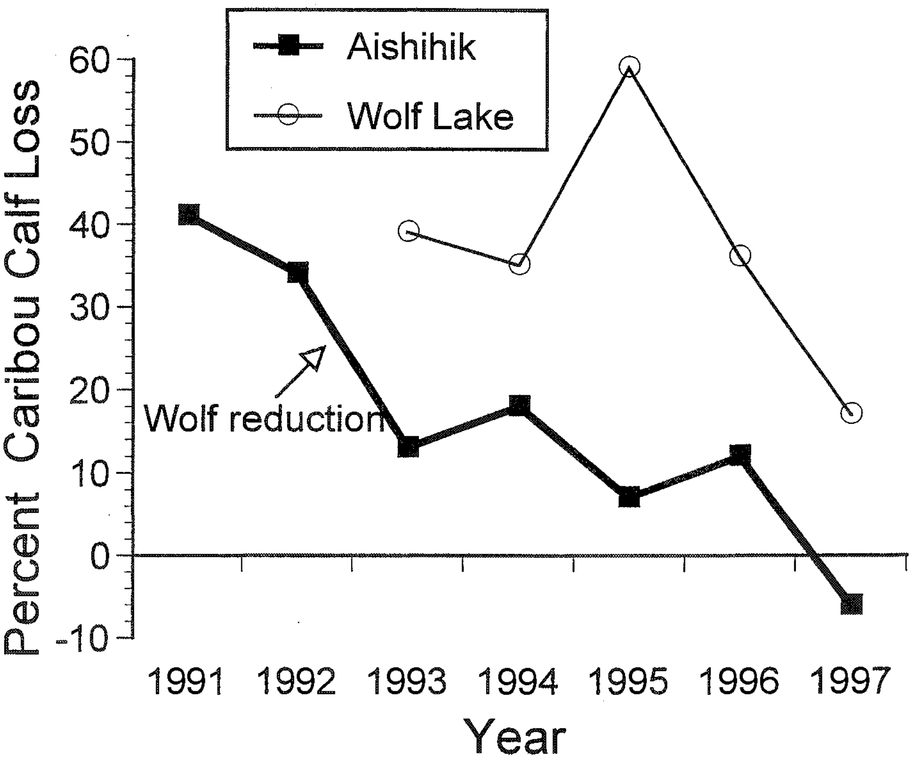
Aishihik
Wolf Lake
Percent Caribou Calf Loss
60
50
40
30
20
10
0
-10
Wolf reduction
1991
1992
1993
1994
1995
1996
1997
Year

Figure 9

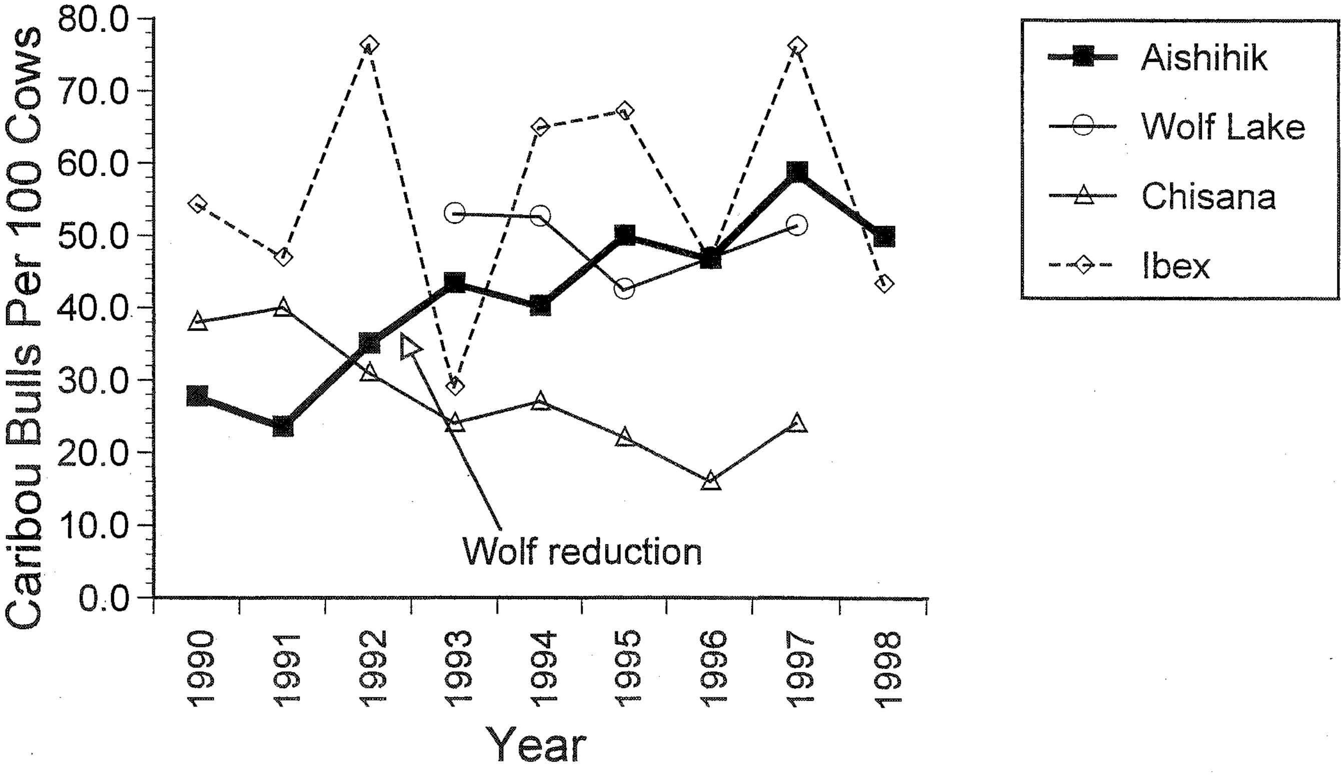
Caribou Bulls Per 100 Cows
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
1990
1991
1992
1993
1994
1995
1996
1997
1998
Year
Wolf reduction
Aishihik
Wolf Lake
Chisana
Ibex

Figure 10

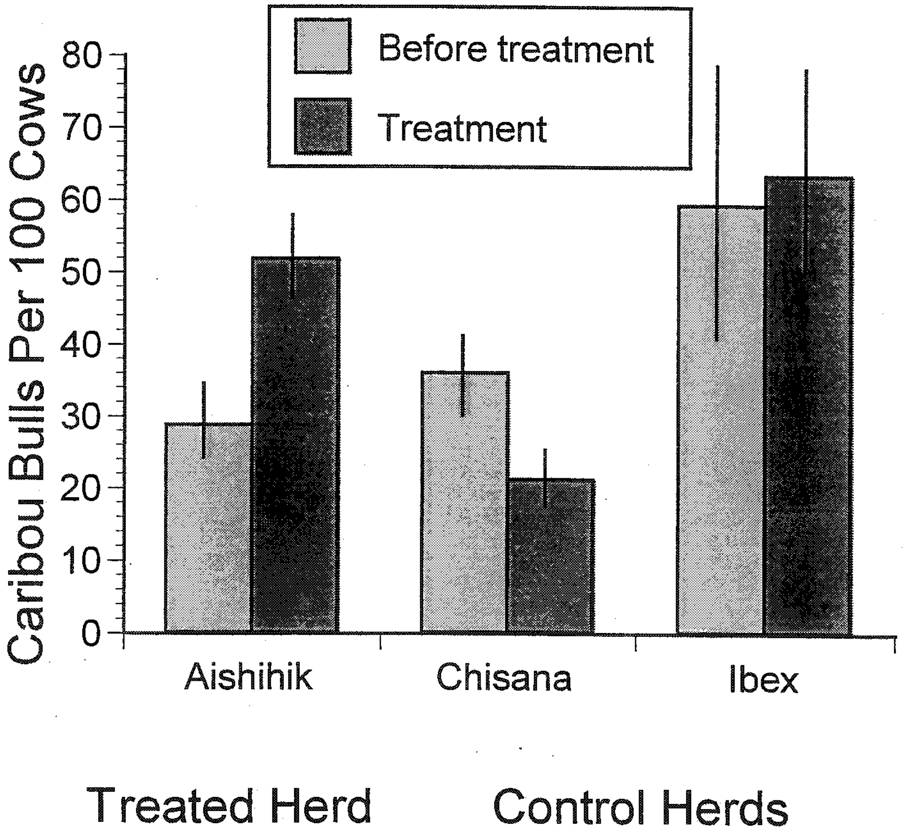
Before treatment
Treatment
Caribou Bulls Per 100 Cows
0
10
20
30
40
50
60
70
80
Aishihik
Chisana
Ibex
Treated Herd
Control Herds

Figure 11

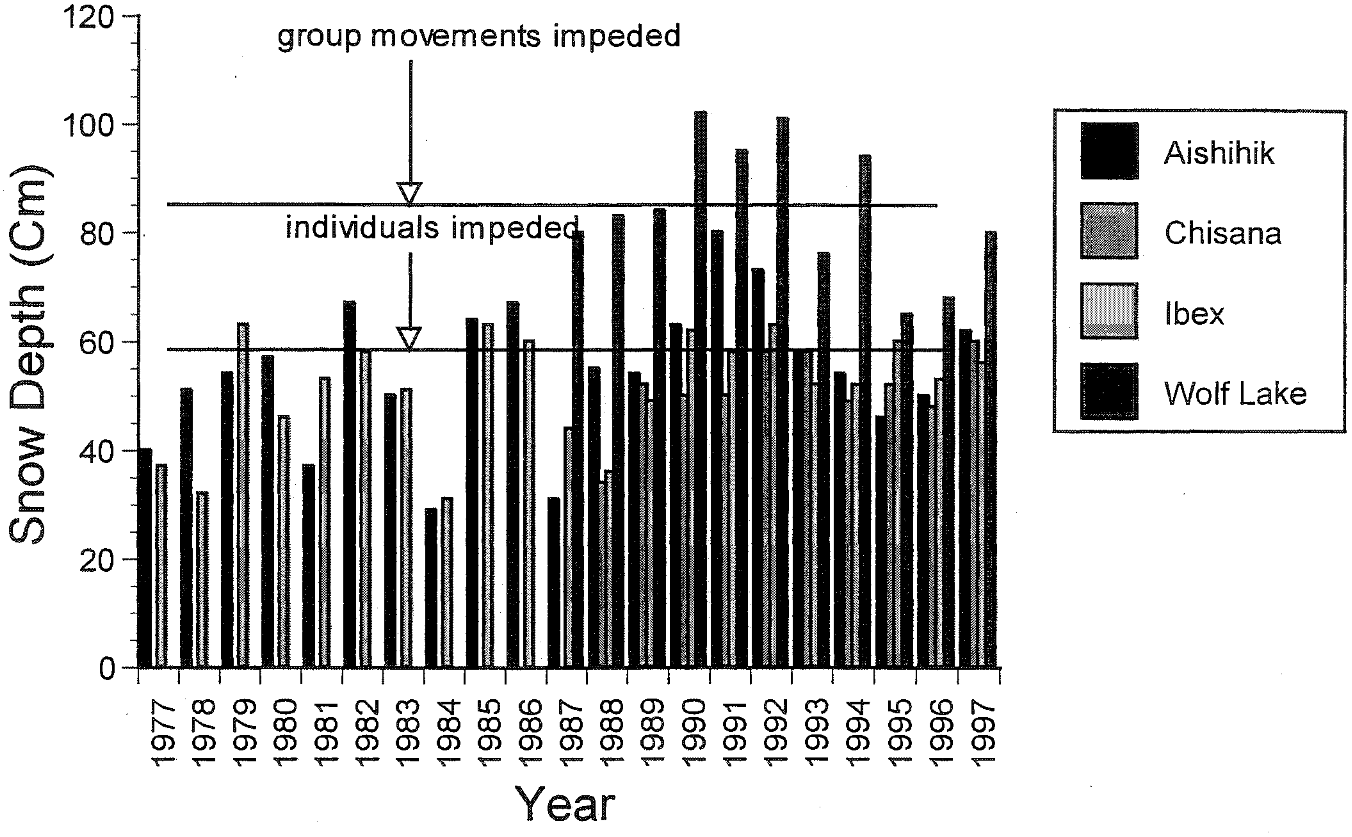
Snow Depth (Cm)
0
20
40
60
80
100
120
group movements impeded
individuals impeded
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
Year
Aishihik
Chisana
Ibex
Wolf Lake

Figure 12

Aishihik herd)

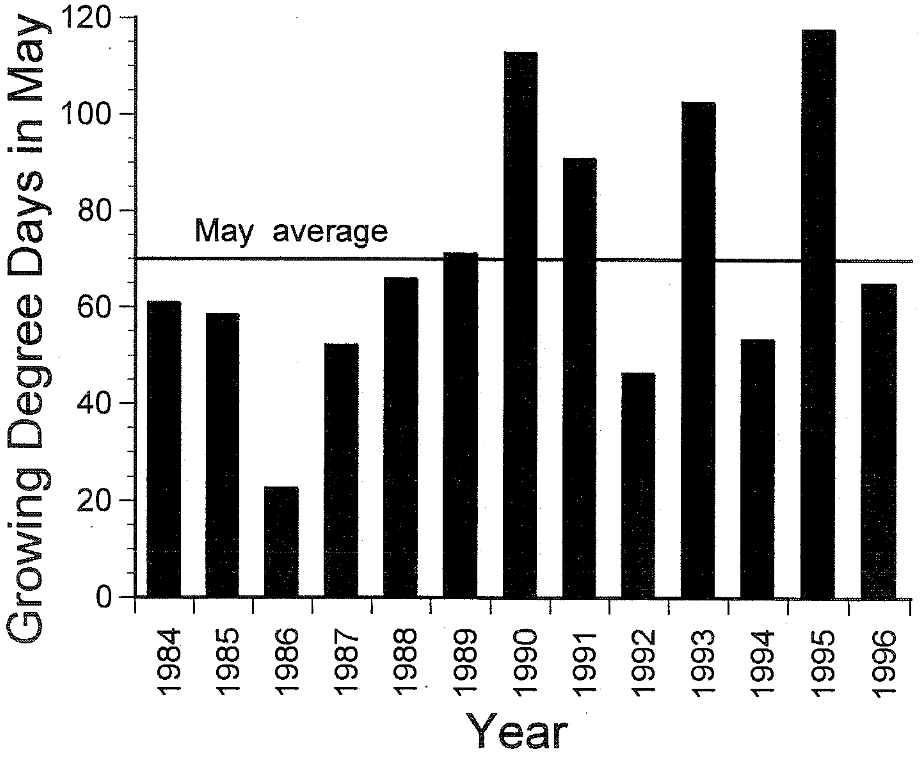

Figure 13

Chisana herd)

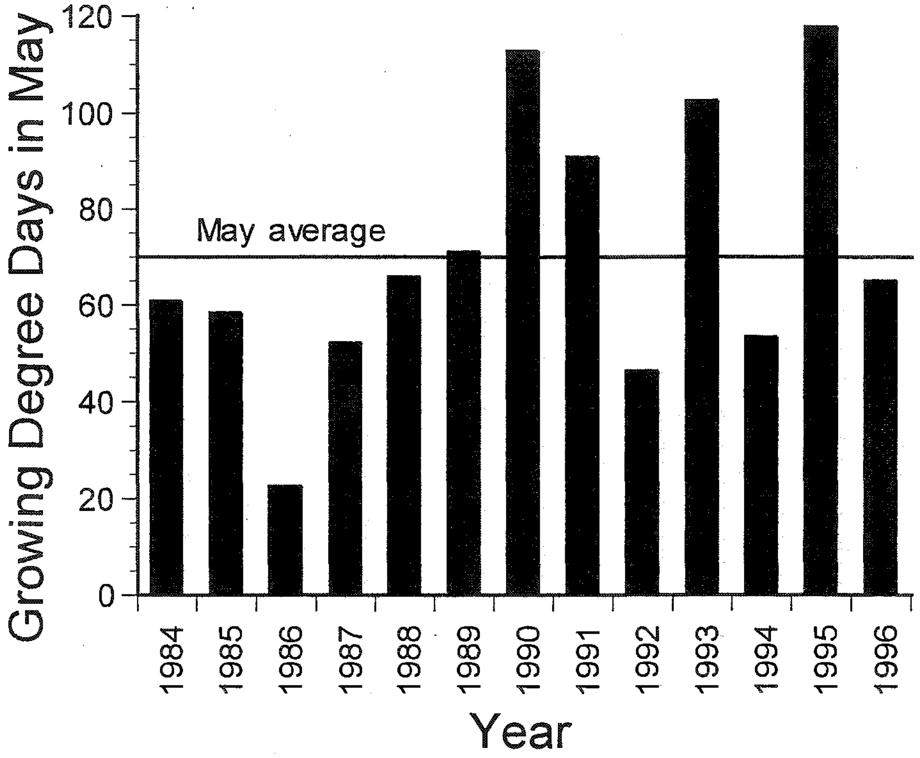

Figure 13

Ibex herd)

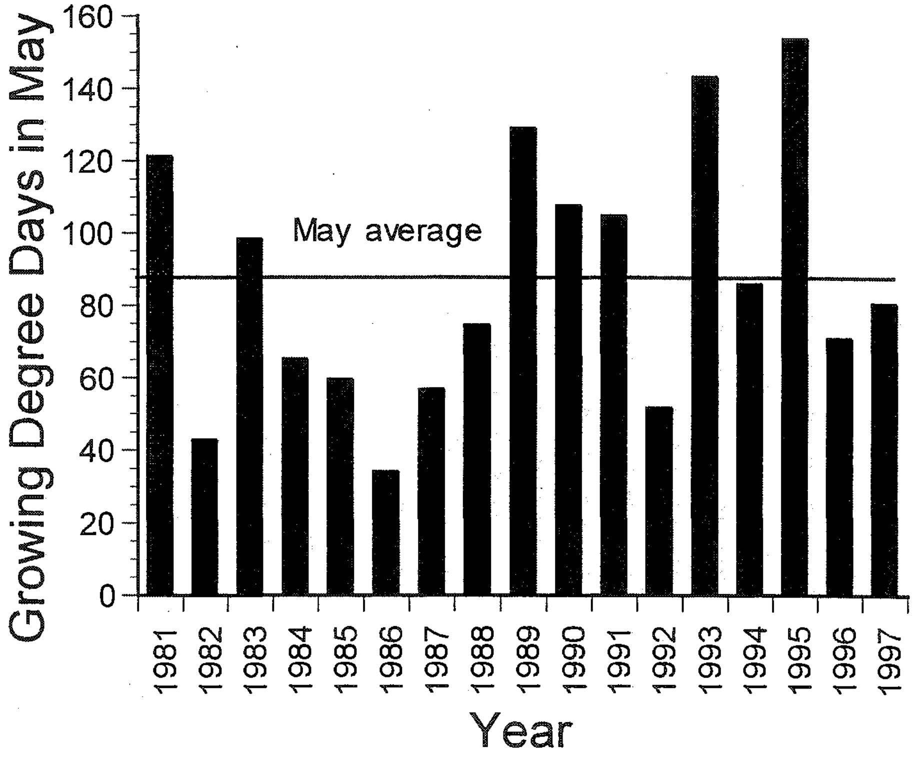

Figure 13

Wolf Lake herd)

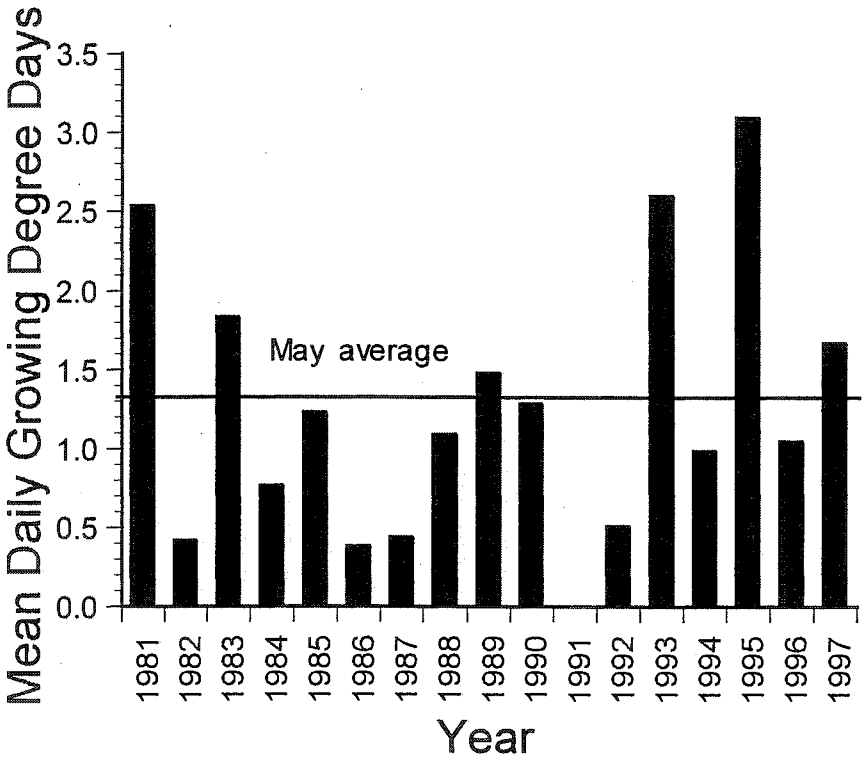

Figure 13

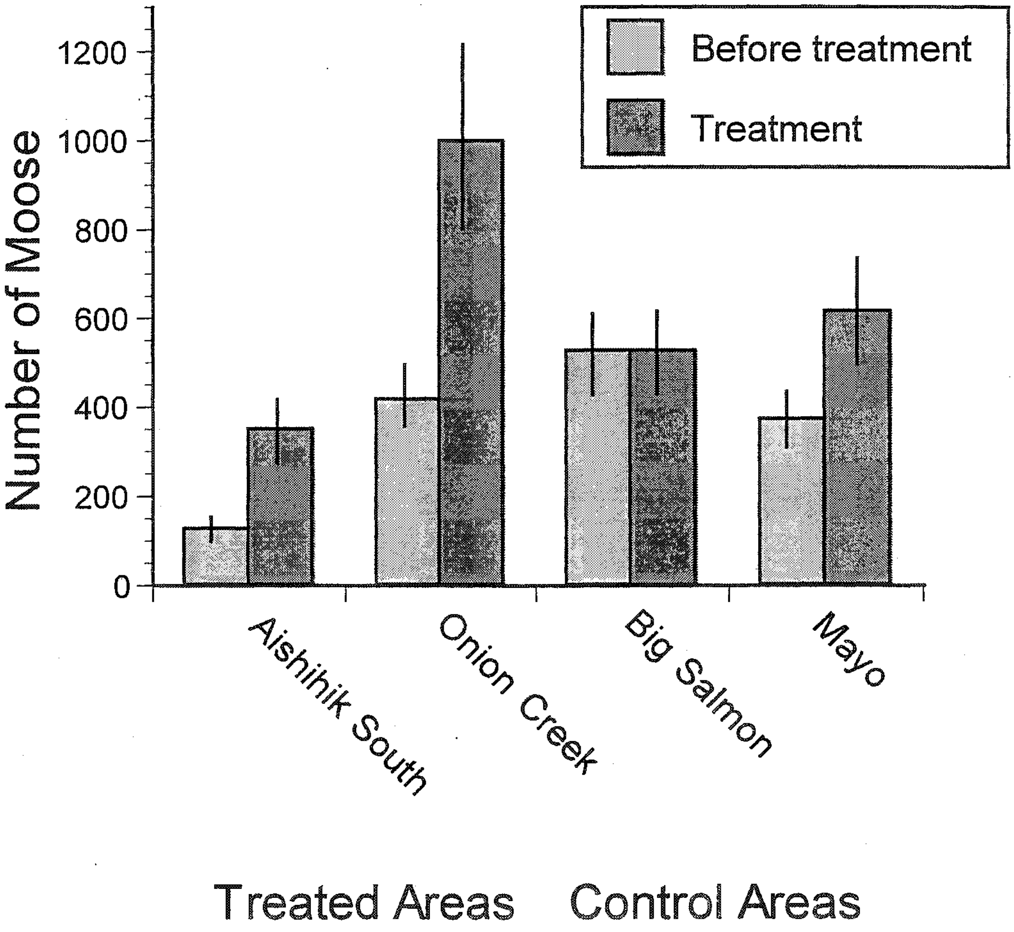
Number of Moose
0
200
400
600
800
1000
1200
Before treatment
Treatment
Aishihik South
Onion Creek
Big Salmon
Mayo
Treated Areas
Control Areas

Figure 14

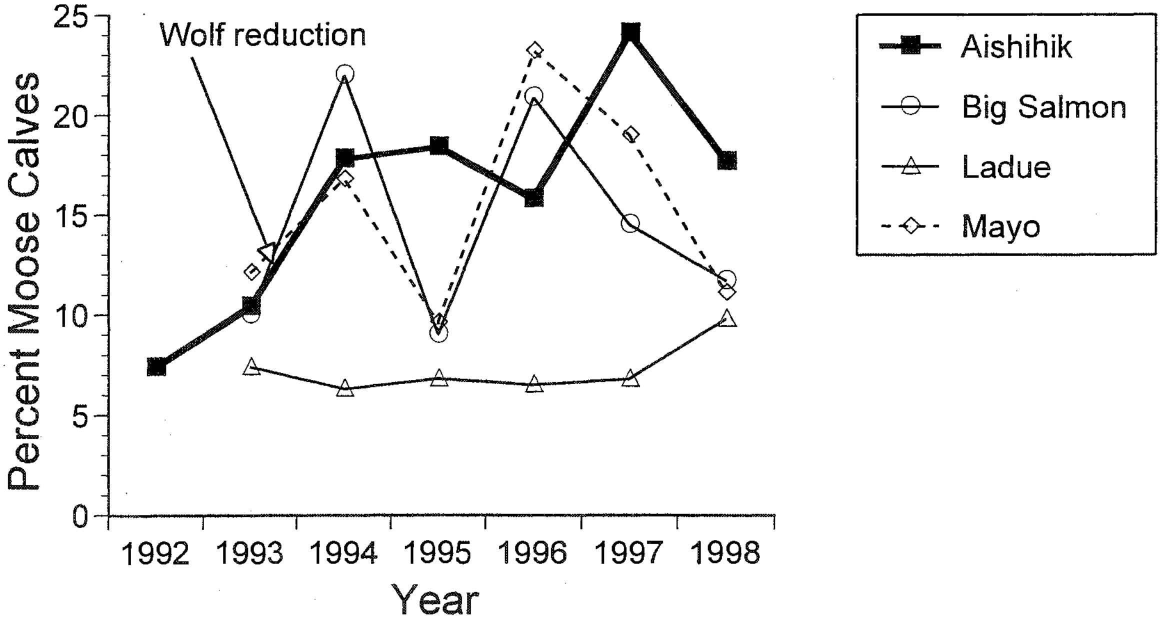
Wolf reduction
Percent Moose Calves
0
5
10
15
20
25
1992
1993
1994
1995
1996
1997
1998
Year
Aishihik
Big Salmon
Ladue
Mayo

Figure 15

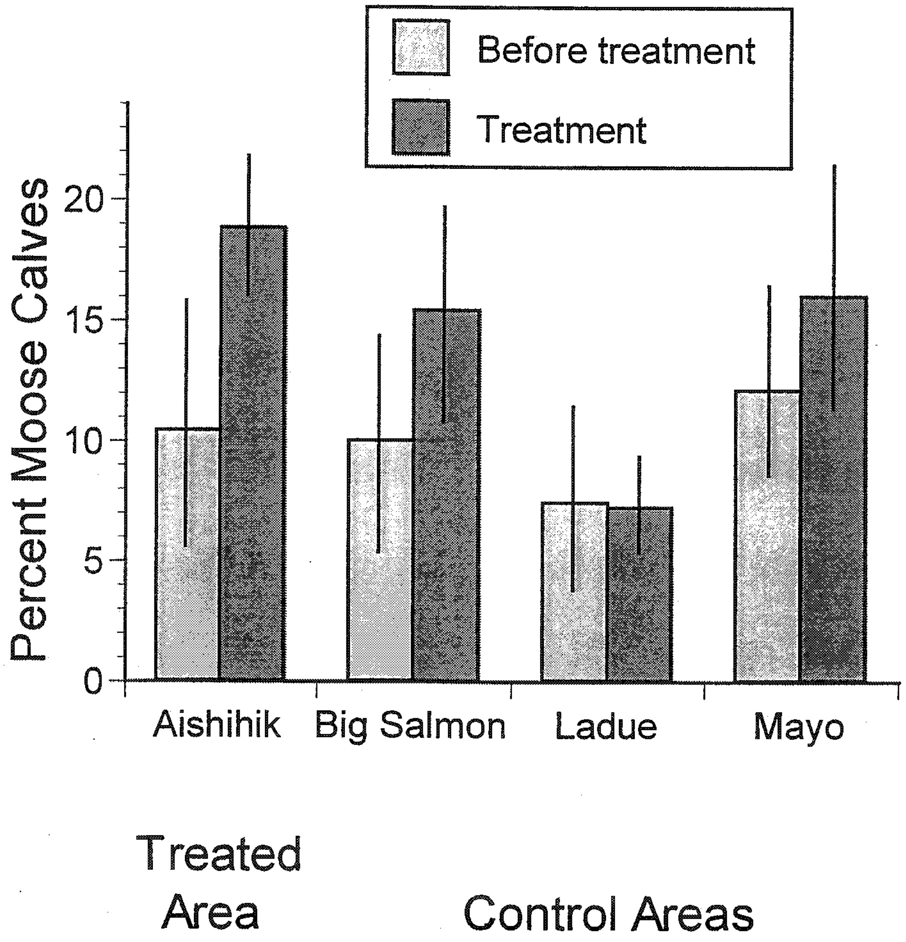
Before treatment
Treatment
Percent Moose Calves
0
5
10
15
20
Aishihik
Big Salmon
Ladue
Mayo
Treated Area
Control Areas

Figure 16

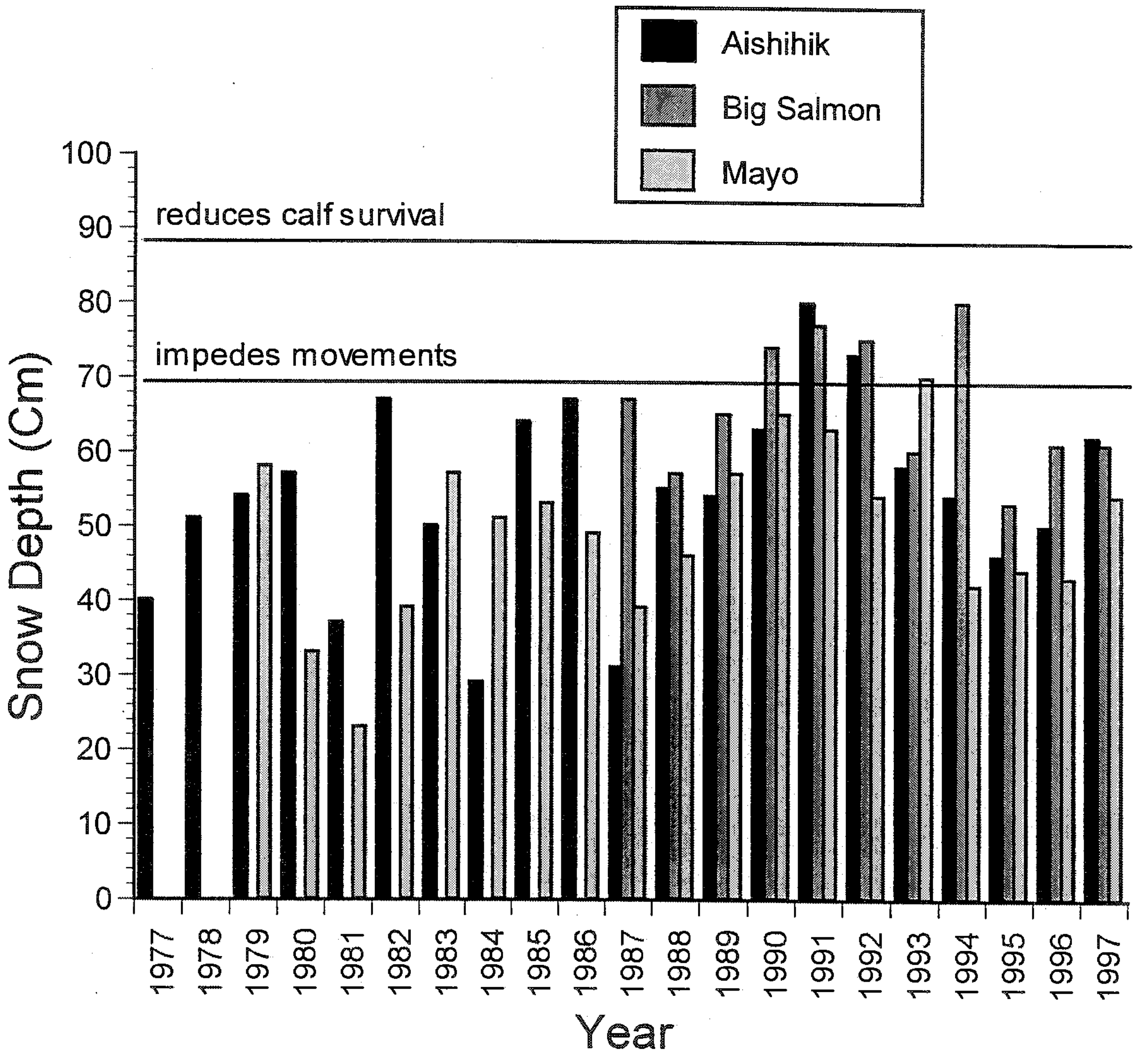
Aishihik
Big Salmon
Mayo
Snow Depth (Cm)
100
90
80
70
60
50
40
30
20
10
0
reduces calf survival
impedes movements
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
Year

Figure 17

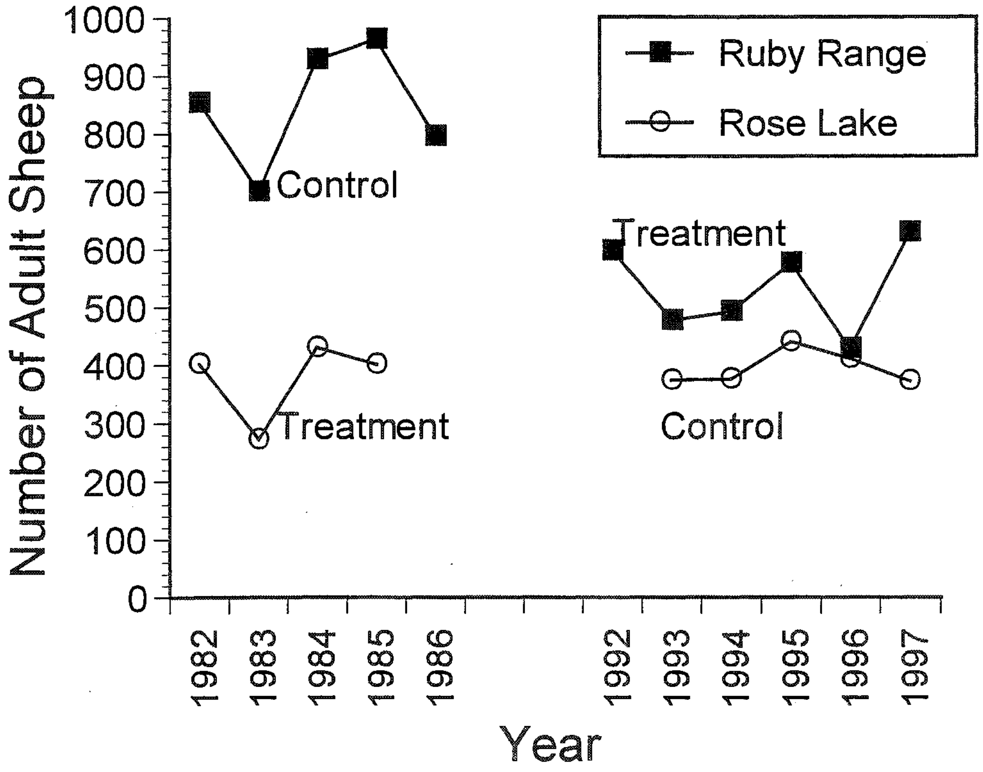
Number of Adult Sheep
1000
900
800
700
600
500
400
300
200
100
0
Ruby Range
Rose Lake
Control
Treatment
Treatment
Control
1982
1983
1984
1985
1986
1992
1993
1994
1995
1996
1997
Year

Figure 18

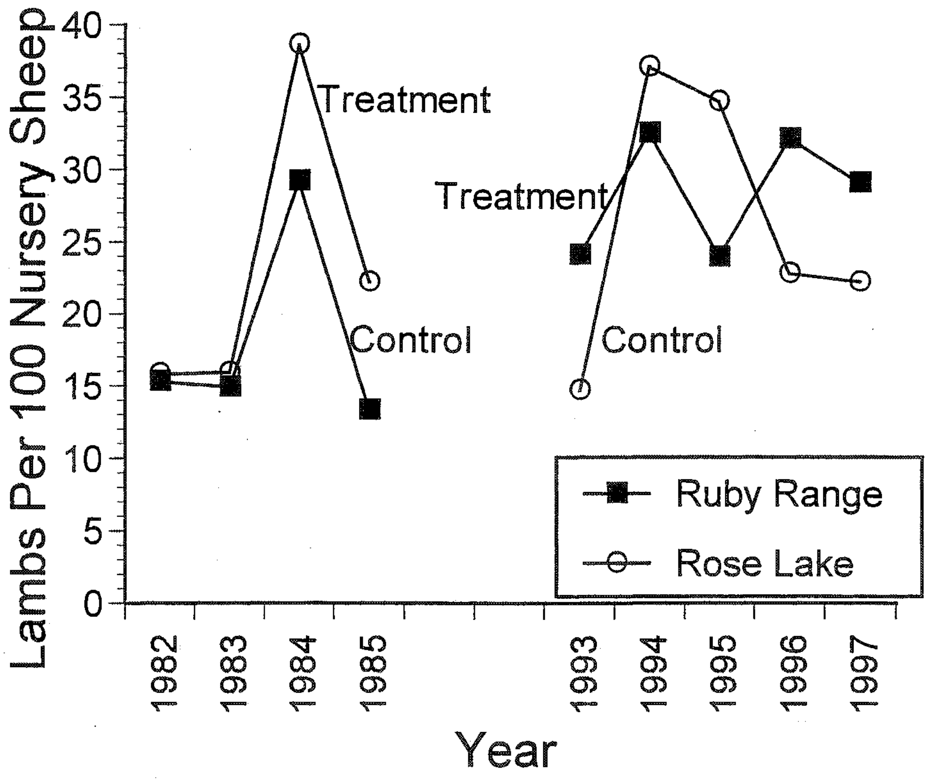
Lambs Per 100 Nursery Sheep
0
5
10
15
20
25
30
35
40
Treatment
Control
Treatment
Control
Ruby Range
Rose Lake
1982
1983
1984
1985
1993
1994
1995
1996
1997
Year

Figure 19

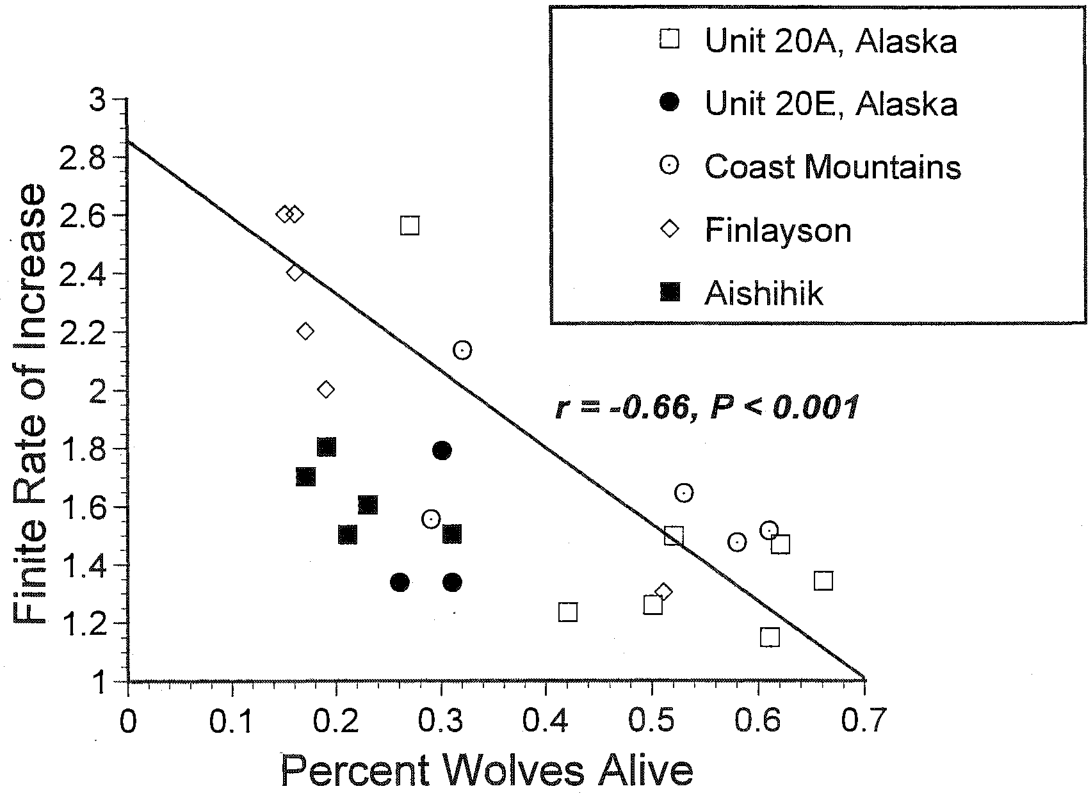
□ Unit 20A, Alaska
● Unit 20E, Alaska
⊙ Coast Mountains
◇ Finlayson
■ Aishihik
r = -0.66, P < 0.001
Finite Rate of Increase
Percent Wolves Alive
3
2.8
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7

Figure 20

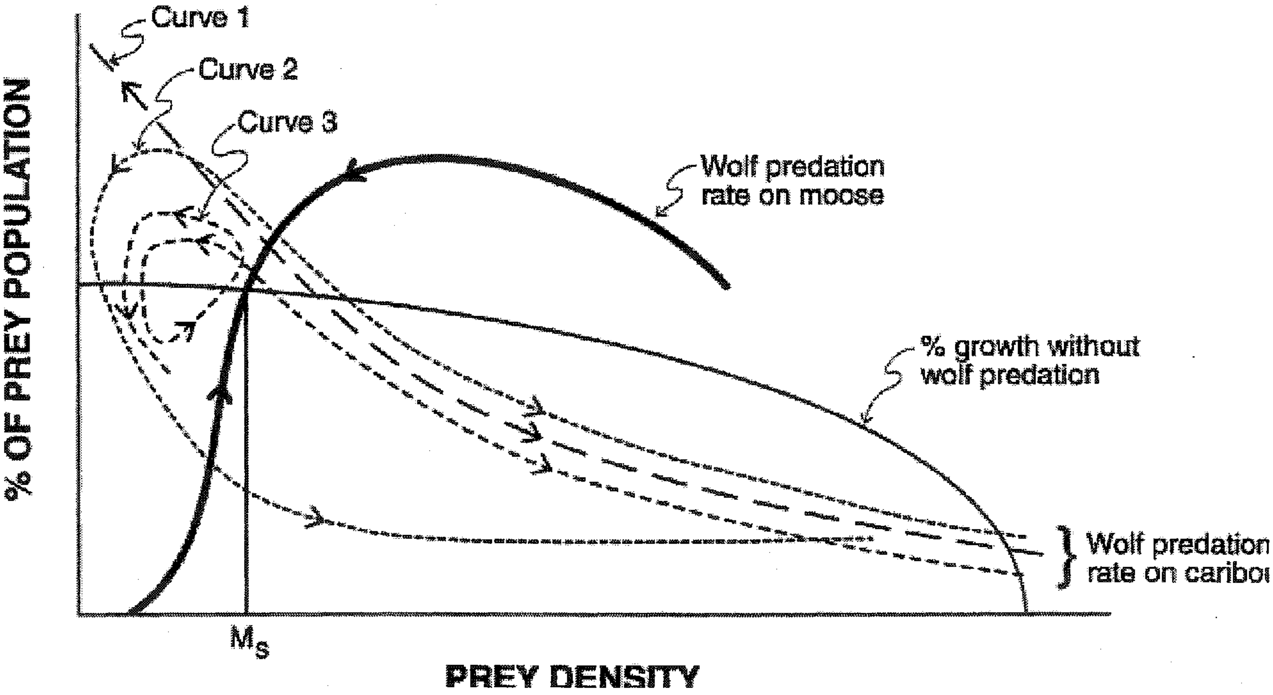
Curve 1
Curve 2
Curve 3
Wolf predation rate on moose
% OF PREY POPULATION
% growth without wolf predation
Wolf predation rate on caribo
M$_S$
PREY DENSITY

Figure 21

Appendix 1. Estimated proportion of each caribou herd observed during October composition surveys.

	1990	1991	1992	1993	1994	1995	1996	1997	Average
Aishihik	0.82	0.97	0.88	0.84	0.76	0.53	0.49	0.75	0.76
Chisana	1.00	1.00	1.00	0.68	0.68	0.68	0.47	0.65	0.77
Ibex	0.75	0.33	0.63	0.58	0.60	0.70	0.53	0.28	0.55
Wolf Lake				0.50	0.51	0.42	0.61	0.57	0.52
Average	0.86	0.77	0.84	0.65	0.64	0.58	0.52	0.56	

Appendix 3. Estimated proportion of moose sampled during late winter recruitment surveys (n = total number of animals observed, N = estimated population size at the last census, and n/N = estimated fraction of each population sampled).

	Aishihik	Big Salmon	Ladue	Mayo	Sum	Overall n/N
1993						
n	106	100	108	124	438	0.12
N	1,309	928	339	1,063	3,639	
n/N	0.08	0.11	0.32	0.12		
1994						
n	152	100	112	101	465	0.12
N	1,518	928	339	1,176	3,961	
n/N	0.10	0.11	0.33	0.09		
1995						
n	185	133	133	114	565	0.13
1996						
n	177	187	108	164	639	0.13
N	2,043	928	339	1,438	4,748	
n/N	0.09	0.20	0.32	0.11		
1997						
n	195	117	118	179	609	0.12
N	2,370	928	339	1,591	5,228	

Appendix 4. Aishihik and Wolf Lake recruitment indices (calves per 100 cows) in July and October, 1991-97.

	Aishihik			Wolf Lake		
Year	July	October	% Loss	July	October	% Loss
1991	0.15	0.09	40.8			
1992	0.11	0.07	34.0			
1993	0.45	0.39	12.8	0.37	0.22	38.9
1994	0.46	0.38	18.0	0.47	0.31	35.0
1995	0.45	0.42	7.1	0.39	0.16	59.8
1996	0.53	0.47	11.9	0.47	0.30	36.4
1997	0.42	0.44	-6.1	0.40	0.34	17.0

Appendix 6. Changes in moose numbers in 2 Aishihik census areas and 2 control areas during our study.

	Pre-treatment			1998					
	Year of census	Population estimate	90% confidence interval	Population estimate	90% confidence interval	Exponential increase	Finite rate of increase		
						r±10% CI	λmin	λ	λmax
Aishihik	1992	126	±25.9%	349	±18.1%	0.170 ± 0.048	1.13	1.18	1.24
Onion Creek	1992	416	±17.9%	999	±20.9%	0.146 ± 0.045	1.11	1.16	1.21
Big Salmon	1993	527	±17.5%	526	±17.9%	0.000 ± 0.047	0.95	1.00	1.05
Mayo	1993	372	±17.4%	615	±19.1%	0.100 ± 0.048	1.05	1.11	1.16