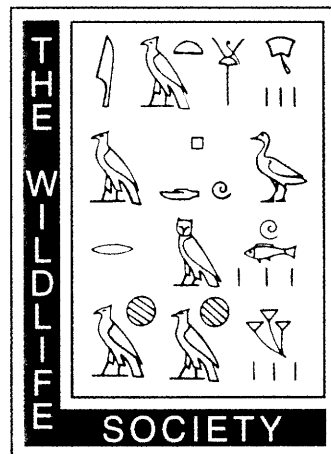


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EXPERIMENTAL REDUCTION OF WOLVES IN THE YUKON: UNGULATE RESPONSES AND MANAGEMENT IMPLICATIONS

by

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FRONTISPIECE. A cow caribou leading her calf across a frozen river is now a more common sight in the southwest Yukon. This calf is one of many new recruits into the Aishihik caribou herd.

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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 10 contemporary controls including 3 caribou herds and 3 moose, 1 Dall sheep, and 3 wolf populations. We tested the hypothesis that wolf predation was the main factor limiting recruitment, adult survival, and population size for the 3 ungulates. Caribou productivity, winter forage quality, disease prevalence, snow depth, snowmelt phenology, harvest, and migration were also assessed. For moose, we also examined harvest, snow depth, and spring and summer growing seasons. Treated moose and caribou populations showed the greatest differences in changes in rates of increase during wolf treatment compared to controls, supporting the wolf predation hypothesis. We found evidence that wolf predation strongly limited recruitment of caribou and moose, and survival of adult moose. We found no evidence that adult survival of caribou improved when wolf numbers were reduced, nor did we find evidence that Dall sheep recruitment or adult numbers responded to lower wolf numbers. Wolf predation and human hunting were probably the main causes of caribou and moose declines before our study. The combination of reduced hunting and lowered predation by wolves was the primary factor causing the increase in the treated Aishihik caribou herd. Lowered predation by wolves, especially upon adult moose, 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 maximum harvest rates should be set conservatively at 2% for caribou and 5% for moose. We recommend that managers use habitat enhancement and public wolf trapping to sustain higher ungulate densities and avoid the need for reactive broad-scale wolf control. We found that wolf fertility control was effective in reducing the rate

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of increase of wolves and that it was more publicly acceptable than lethal control. We evaluate large-scale wolf-prey experiments as an adaptive management approach.

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Key words: *Alces alces*, *Canis lupus*, Dall sheep, experimental design, gray wolf, moose, *Ovis dalli*, predator-prey relations, *Rangifer tarandus*, adaptive management, woodland caribou, fertility control, Yukon.

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INTRODUCTION

There is compelling evidence that predation by wolves is a primary force limiting moose and caribou 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, Jingsfors 1988, Hayes et al. 1991, Hayes and Harestad 2000a). 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 (Messier 1994, Hayes and Harestad 2000a).

One way to study predation is to "treat" or reduce its effect on a prey population and monitor other "control" populations where predation is not altered, and look for differences in responses (Gasaway et al. 1983, 1992). In most previous wolf reduction

studies, treated populations were not monitored after wolf reduction ended, control populations were often not adequately monitored during treatments and evidence for prey response was often based on before–after effects in reduction areas (National Research Council 1997). Due to weak experimental designs, most of these studies were not able to expose the relative effects of wolf predation compared to other factors, including effects of reduced harvest and mild winters (National Research Council 1997).

In the Aishihik (Eh-zhee-ak) area of the southwest Yukon, local people first became concerned about declining numbers of caribou, moose, and Dall sheep during the 1980s when subsistence and sport harvest success began to fall sharply (Hayes 1992, Allen 1994, Johnson 1994). By 1990, R. Farnell (Yukon Department of Environment, unpublished data) reported 50% declines in the Aishihik and neighboring Kluane caribou herd compared to earlier studies (Larsen 1981, Gauthier and Theberge 1985). Moose declined by more than 60% between 1980 and 1992 (Larsen and Ward 1995). Dall sheep numbers had also decreased in the area (J. Carey, Yukon Department of Environment, unpublished data). Wolves were first counted in the Aishihik area in 1992 when Hayes (1992) estimated a ratio of 65–72 ungulate biomass units per wolf, lower than any value reported in the literature (see Fuller 1989). Local people believed that both predation and overhunting were responsible for the declines in caribou and moose numbers (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 initiated a citizens' team to develop a plan for the conservation and management of 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 shaped our study in 2 important ways: (1) by limiting wolf reduction to 1 treatment area in the Yukon at any one time and (2) by requiring that there be no hunting in a wolf control

area. Our experimental design was based on a public workshop that involved academic ecologists, other biologists, and members of the public (Government of Yukon 1992). The study design included a series of quantitative predictions about ungulate responses to reduced wolf numbers in a treatment area and several control areas (Hayes 1992). The study was large, spanning 7 of the 23 Yukon ecoregions. The Aishihik treatment area alone was 20,000 km² (the size of the Yellowstone ecosystem); control areas totaled nearly 70,000 km². We anticipated that some control areas would experience different ecological forces due to the scale of the study. We assessed other possible explanations for ungulate responses. We also examined management implications of our research, and the benefits and limitations of adaptive approaches to wolf–prey studies.

Hypothesis and Experimental Design

Our hypothesis was that after controlling for other factors that could influence prey responses, a strong reduction in wolf numbers would cause increased recruitment, adult survival rates, and numbers of caribou, moose, and sheep. We expected differences in the rates of increase among treated and control groups before and during wolf reduction to provide the key evidence that reduced predation would cause the responses in ungulate populations. The notation of Campbell and Stanley (1966) was modified to represent our experimental designs for each species (Tables 1 and 2).

Our experimental design separated as many factors as possible that could affect study populations (Walters and Holling 1990). In 5 consecutive years wolf numbers in the Aishihik area were reduced and numbers compared to 3 control areas. We studied the effects of winter food habits and productivity on caribou response, and snowmelt phenology, snow depth, and changes in harvest rates on caribou and moose responses. We also studied the effect of spring and summer weather on moose response.

STUDY AREAS

Our study areas included the Aishihik wolf treatment area and 10 control areas (Fig. 1). Population trends in control areas did not

Table 1. Experiment design schedules for estimating population parameters of wolves, caribou, and moose in treated and control areas over the duration of the study in the Yukon, 1990–1998.

Study and control areas	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
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

Key: • = wolf reduction; •* = wolves had recovered slightly in 1998 but remained well below pre-treatment density; C = sex and age composition count; TC = total count (includes composition); PE = population estimate; R = radio collar relocation surveys.

influence our selection and we expected ecological conditions would vary due to the large scale of the study (Tables 3 and 4). Our criteria for selecting control areas were:

1. Recent wolf reduction programs (Farnell and McDonald 1988, Larsen et al. 1989) could not have affected wolf or prey numbers in any area.
2. Woodland caribou herds had to number fewer than 1,500 animals and we had to be able to annually sample about 30% of each herd for changes in 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 to be ecologically different from those in the rest of the territory, based on behavior and habitat use. Of the 4 potential control herds in the southwest Yukon ecotype, the Ibex and Chisana caribou herds were the only ones that were not affected by wolf reduction. We added the Wolf

3. Lake caribou herd as a control because it bordered the southwest Yukon ecotype and had little human activity in its range.
4. Moose densities in control areas had to be less than 200 moose/1,000 km². We chose 3 control areas that were far enough away (i.e., 100–150 km) to ensure that they were not affected by our wolf treatment.
5. The Dall sheep control area should follow the experimental design of Marcstrom et al. (1988) to allow us to include data from a previous wolf–sheep experiment where control areas and areas treated with wolf reduction were reversed from our study (Barichello et al. 1989).

Aishihik Wolf Treatment Area

Physiography, Climate, and Vegetation.—The 20,000-km² Aishihik wolf treatment area (Fig. 2) lies mainly within the Ruby Ranges ecoregion (Ecological Stratification Working Group 1995). The climate is characterized by short, cool summers and long, cold winters. Winter temperature inversions are common, giving milder temperatures at

Table 2. Experimental design schedule for estimating Dall sheep population parameters in 2 areas of the Yukon, 1982–1986 and 1993–1997.

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

Key: • = wolf reduction; TC is a total count, including composition.

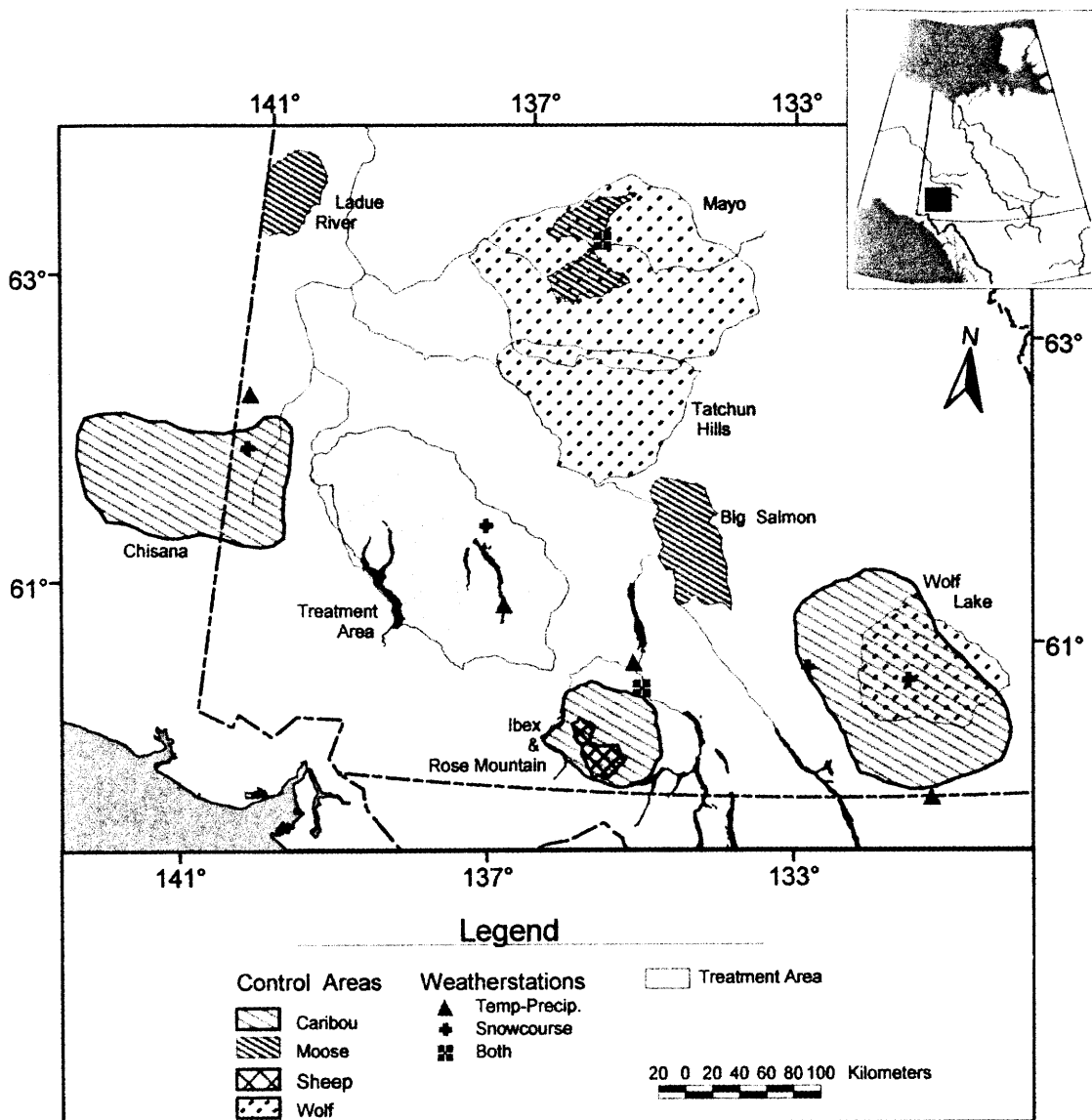


Figure 1. Location of Aishihik wolf treatment area, and caribou herds, moose, sheep, and wolf areas in the Yukon and Alaska used as experimental controls in our study, 1993–1998.

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 low, ranging from 250 to 300 mm. The terrain consists of rugged mountains rising to 2,300 m above sea level (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 caribou composition and numbers, wolf numbers, and moose recruitment each winter throughout the entire Aishihik wolf treatment area. We monitored changes in moose abundance in the Aishihik South (2,000 km²) and Onion Creek (3,400 km²) count blocks (Fig. 2). Each year we monitored Dall sheep recruitment and

Table 3. Population data for caribou herds in Aishihik and 3 control areas in the Yukon, 1981–1998.

Area	Estimated herd size (90% CI)	Caribou		
		density (per 1,000 km ²)	Calves per 100 cows	Bulls per 100 cows
Aishihik (16,100 km²)^a				
Oct 1981	1,500 ^b	9.3		
Oct 1990			29	28
Mar/Oct 1991	785	4.8	9	24
Oct 1992			7	35
Mar 1993	732	4.5		
Oct 1993			39	43
Oct 1994			38	40
Oct 1995			42	50
Oct 1996			47	47
Mar 1997	1,148±6.5%	7.1		
Oct 1997			45	59
Oct 1998	1561 ^c		33	50
Wolf Lake (20,000 km²)				
Mar 1987	664±20% ^b	3.3	27	29
Mar 1993	1,249±12%	6.2		
Oct 1993			22	53
Oct 1994			31	53
Oct 1995			16	42
Oct 1996			30	47
Oct 1997			34	51
Mar 1998	1,491±30%	7.4		
Ibex (2,000 km²)^b				
Oct 1990	155	7.8	60	54
Oct 1991			56	47
Oct 1992			53	76
Oct 1993			57	29
Oct 1994			44	65
Oct 1995			50	67
Oct 1996			35	47
Oct 1997			36	76
Mar 1998	450±24%	22.7		
Chisana (13,200 km²)^d				
Oct 1987	1,800	13.6	33	39
Oct 1990			11	36
Oct 1991			1.3	40
Oct 1992	1,270	9.6	<1	31
Oct 1993	869		2	24
Oct 1994			11	27
Oct 1995			4	21
Oct 1996			4.8	16
Oct 1997			14	24
Oct 1998	493	3.7	4	19

^a Range size determined from minimum convex polygons from radio telemetry studies (R. Farnell, Yukon Fish and Wildlife Branch, unpublished data).

^b R. Farnell (Yukon Fish and Wildlife Branch, unpublished data).

^c Population estimate derived from computer modeling simulation.

^d Data for Chisana herd from C. Gardner (Alaska Department of Fish and Game, unpublished data).

total adult numbers in the 1,600-km² Ruby Range study area (Fig. 2). In addition to moose, caribou, and Dall sheep, the Aishihik area included introduced herds of fewer

Table 4. Characteristics of moose populations in Aishihik and 2 control areas in the Yukon.

Areas	Estimated number ±(90% CI)	Moose Calves			
		density (per 1,000 km ²)	per 100 cows (Oct)	Yearlings per 100 cows	Bulls per 100 cows
Moose areas in Aishihik treatment blocks					
Aishihik South					
1981 ^a	332±10%	168	24	37	69
1990	247±32%	125	58	40	43
1992	126±29%	64	11	15	61
1998	349±18%	173	51	30	85
Onion Creek					
1992	416±18%	122	21	12	49
1998	999±21%	294	18	22	67
Untreated moose areas					
Big Salmon					
1993	527±17%	195	50	17	71
1998	526±18%	195	49	41	68
Mayo					
1988 ^a	315±22%	104	72	54	65
1993	372±17%	122	51	18	82
1998	615±19%	200	58	37	70

^a No sightability correction factor incorporated.

than 50 elk (*Cervus elaphus*) and 400–500 wood bison (*Bison bison*) (R. Hayes, Yukon Department of Environment, unpublished data). We found no predation by wolves on bison during our study. Brown bear (*Ursus arctos*) density was estimated at 22 bears/1,000 km² for the treatment area (Yukon Department of Environment, unpublished data). In adjacent Kluane National Park, where bear habitat is better, density was 40 bears/1,000 km² (Pearson 1975, McCann 2001). Black bears (*U. americanus*) were present in the treatment area but uncommon in the mountains.

Lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) were both abundant until 1990, but by 1992 both predator populations crashed (O'Donoghue et al. 1997) after snowshoe hares (*Lepus americanus*) declined (Boutin et al. 1995). Wolverines (*Gulo gulo*) were also present at unknown densities. Golden eagles (*Aquila chrysaetos*) nested at high densities in the region (Windsor 1979) and they are known to kill neonatal sheep (Hoefs and Cowan 1979) and caribou (Whitten et al. 1992).

Control Study Areas

Control study areas were located throughout southern and central Yukon (Fig. 1). Wolves, brown bears and black bears were

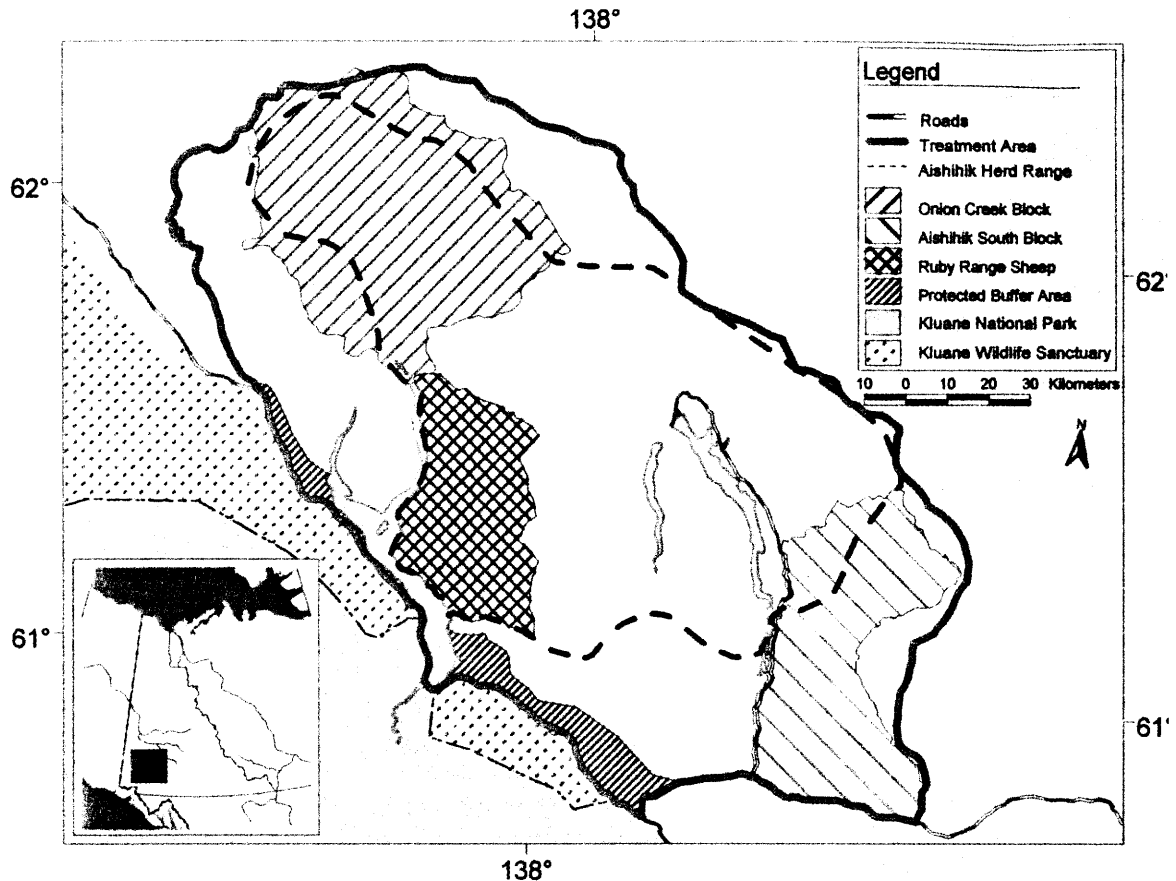


Figure 2. Moose, caribou, and Dall sheep study areas in the Aishihik area, Yukon, 1993–1998.

present in all study areas, but densities were not known in most areas. Three control areas were located in the Pelly Mountain ecoregion including the Wolf Lake caribou herd (9,700 km²) and wolf population (6,800 km²) and the Big Salmon moose study area (2,700 km²). Sheep were also present. Wolves were counted in the Wolf Lake area in 1994, when there was a density of 6.9 wolves/1,000 km² (A. Baer, Yukon Department of Environment, unpublished data). The Pelly Mountains ecoregion has annual temperatures similar to the Aishihik area but receives twice the precipitation (500–1,000 mm). The ecoregion is generally mountainous with elevations over 1,500 m asl. The alpine community consists of dwarf willow and birch, ericaceous shrubs, and lichens. Mesic lowland forests are dominated by lodgepole pine (*Pinus contorta*).

The Rose Lake Dall sheep area (800 km²) and the Ibex caribou herd (4,000 km²) were located in the Yukon Southern Lakes ecoregion. Moose are also found in this ecore-

gion. Larsen and Markel (1989) estimated a density of 16 brown bears/1,000 km² in this ecoregion. Hayes et al. (1991) estimated a density of 10.8 wolves/1,000 km² in 1988. Most of the area is dominated by alpine vegetation, as in the Pelly Mountains and Ruby Range ecoregions. Precipitation and temperature are similar to the Aishihik area.

Wolves (15,700 km²) and moose (3,000 km²) were monitored in the Mayo area, a part of the Yukon Plateau–North ecoregion. A density of 5.3 wolves/1,000 km² was found in the Mayo moose area in 1995 (A. Baer, Yukon Department of Environment, unpublished data). Two small woodland caribou herds and a few isolated sheep populations were present within the wolf study area. This ecoregion is mountainous with broad U-shaped valleys containing white spruce forests up to 1,500 m asl. The Mayo area receives 300–600 mm precipitation per year. Winters are generally colder than Aishihik with a mean temperature of –20°C.

The 13,000-km² Chisana study area lies in

the St. Elias Mountains ecoregion where we annually monitored the Chisana caribou herd. Moose were also present. Wolf density was 5.6/1,000 km² in this area in 1989 (A. Baer, Yukon Department of Environment, unpublished data). This area is highest of all study areas with glaciated mountains surrounded by permanent ice and snowfields. At the lower elevations, mean temperatures are warmer in winter than in the Aishihik area. Precipitation is similar and permafrost here 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 km²) in the Yukon Plateau–Central ecoregion. Moose, caribou and scattered groups of sheep were present. 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. The Tatchun Hills area has 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 km²) was in the Klondike Plateau ecoregion. There were no sheep here. The Fortymile caribou herd sometimes wintered in this control area (C. Gardner, Alaska Department of Fish and Game, unpublished data). Gasaway et al. (1992) used part of this same area as a control for their wolf–prey experiment. Brown bear density was estimated at 16 bears/1,000 km² near the Ladue area (Gasaway et al. 1992). Temperatures and precipitation are similar to the Aishihik area, except winters are slightly colder, averaging –23°C. Spruce forests occupy lower slopes and valley bottoms. Open black and white spruce, aspen, and lodgepole pine are found 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 annual wolf numbers in the Aishihik area by aerial counts January–March 1992–1998, following methods of Hayes and Harestad (2000b). We used both radiotelemetry and aerial snow-tracking methods to count wolves in all years. Each of the 3 control wolf survey areas was counted once during our study using aerial snow-tracking methods (Stephenson 1978; Table 1).

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 leghold traps. Surgical sterilization was also used between 1994 and 1997 to limit reproduction in up to 6 wolf groups each year (Spence et al. 1999). Aerial killing of wolves and the use of nonlethal methods followed ethical treatment recommendations set out in the Yukon Wolf Conservation and Management Plan (Yukon Wolf Planning Team 1992). Carcasses of all killed wolves were retrieved for study and the pelts of all animals were recovered and sold.

To help prevent Kluane National Park wolves from being killed we established a 920-km² buffer area between the Kluane Wildlife Sanctuary and the Aishihik study area (Fig. 2). The fate of boundary wolf packs was set by an agreement between Canadian Parks Service and the Yukon Government (Carey et al. 1994).

Estimating Changes in Caribou Herd Size and Rates of Increase

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 chose methods based on the herd's ecological type (Farnell et al. 1996). To estimate the size of alpine-wintering herds we used a total count in March 1994 for the Aishihik caribou herd and in

October 1990 for the Ibex caribou herd. We tried to count the Aishihik caribou herd in March 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 subtracting the number of calves seen in 1994 and assuming 10% annual adult mortality (see Results). We used a total count to estimate Chisana caribou herd size in October 1992, 1993, and 1998 because almost all animals in this small herd were observable. We used locations of radiocolored caribou and other searches from fixed-wing aircraft to establish boundaries of total count areas. Two crews in helicopters then counted all caribou within the bounded areas.

We used SRB methods in March 1993 and 1998 to estimate the size of the Wolf Lake caribou herd, a forest-wintering herd that was more difficult to count than the alpine-wintering herds (Farnell et al. 1996). As the study progressed we used SRB methods to estimate the Aishihik caribou herd in 1997, and the Ibex caribou herd in 1998 when count conditions were favorable. Based on observed levels of recruitment and mortality, we used the 1997 count to estimate the population size of the Aishihik herd in 1998. We compared herd size estimates for the Aishihik, Wolf Lake, and Chisana herds (1993 and 1998), and the Ibex herd (1990 and 1998). Mean rates of annual increase, adult survival, and recruitment were estimated after methods of Hatter and Bergerud (1991). Because we used total counts to estimate the Aishihik and Ibex herds before treatment, we determined whether those estimates were within the 90% confidence interval of SRB counts at the end of treatment for the Aishihik caribou herd in 1997, and for the Ibex caribou herd in 1998. We compared the Wolf Lake SRB estimates using a 1-tailed Student's *t* test with the pooled variance from the 1993 and 1998 estimates.

We estimated differences in the annual rate of change (λ) of the Aishihik caribou herd before (1991–1993) and during wolf treatment (1993–1998). We then compared its performance to differences in the rates of increase of the Wolf Lake caribou herd

between 1987–1993 (before) and 1993–1998 (during Aishihik treatment); and the Chisana herd between 1987–1993 and 1993–1998. Key evidence for the wolf predation hypothesis was whether the change in the rate of increase of the Aishihik caribou herd differed substantially from 3 control herds.

Estimating Caribou Calf Recruitment and Adult Sex Ratio

Each October we sampled 28–100% of the caribou in each herd to determine calf recruitment (calves per 100 cows) and adult sex ratio (bulls per 100 cows). We used telemetry 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 (1990–1992) and 5 years during wolf treatment (1993–1997; Table 1). There were pre-treatment data available for the Wolf Lake caribou herd in 1987.

Each annual ratio of calves per 100 cows was averaged over years before and during wolf treatment and the 90% confidence interval was calculated using a bootstrap procedure (Manley 1997). We also used bootstrapping to estimate the differences in the ratio of calves per 100 cows before and during wolf treatment, and among Aishihik and control herds. 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. The pre-treatment and treatment ratios were then averaged and their difference calculated. These 3 numbers formed the output of 1 resampling cycle. We repeated the procedure 2,000 times and used the resulting distributions to estimate the bias-corrected confidence intervals and to compare the difference of the ratios to 0 (i.e., no difference before and during wolf treatment). We used 1-tailed probability to compare recruitment before and during treatment because we expected the Aishihik ratio to be higher after wolves were reduced. We used 2-tailed probability to compare recruitment because

we had no reason to expect that the treated Aishihik herd would have higher recruitment than all control herds.

We compared the net loss of calves between the Aishihik and Wolf Lake caribou herds from July to October in all treatment years. July surveys followed the same methods as October composition surveys. We chose to compare the Wolf Lake caribou herd because it was our best example of a naturally limited herd, and there were a substantial number of radio collars on herd cows. By locating a large number of collared cows in both herds, we reduced any possible 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 (Davis et al. 1988, Adams et al. 1995).

We expected harvest by people could influence the sex ratios because bulls are taken more frequently than cows. The Chisana caribou herd was hunted under a bull-only bag limit until 1994 when harvest was closed. The Ibex caribou herd was closed to hunting in all years of our study but subsistence hunting by First Nations hunters continued until 1993 when their hunting was voluntarily stopped (O'Donoghue 1996). In 1990 hunting of the Aishihik caribou herd was stopped and remained closed through our study. This allowed us to estimate the effect of harvest reduction alone between 1990 and 1993. Hunting of the Wolf Lake caribou herd remained open in all years but harvest was light. Inconsistent harvest rates could have biased comparisons of sex ratios so we adjusted ratios for the Wolf Lake caribou herd to account for the possible effect of harvest. We multiplied the number of bulls seen in each group by a factor equal to the ratio: (bulls counted + bulls harvested)/bulls counted. We followed the same bootstrapping procedure described above to test for differences in the 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 (1995–1997). We used 2-tailed tests for all comparisons of the adult sex ratios.

Estimating Adult Caribou Survival Rate

Telemetry data were collected each year to estimate caribou range use, herd size, sex

and age composition, and adult survival rate. We captured and radiocollared 81 (69 F, 12 M) Aishihik caribou, 59 (54 F, 5 M) Wolf Lake caribou, 5 Ibex caribou, and 84 cows from the Chisana herd. Aishihik, Wolf Lake, and Ibex herd caribou were captured from Bell 206B helicopters using a hand-held net-gun (Barrett et al. 1982). Chisana caribou were immobilized from a Robertson R22 helicopter using a combination of 3 mg/ml Carfentanil citrate (Wildnil, Wildlife Pharmaceuticals, Fort Collins, Colorado) and 100 mg/ml xylazine hydrochloride (Anased, Lloyd Laboratories, Shenandoah, Iowa) in 2-cc darts fired from a pistol. Transmitters had a 36–48 month life expectancy and motion-sensitive mortality switches (Telonics, Mesa, Arizona; Lotek, Aurora, Ontario). We captured cow caribou between September and April to study reproduction and calf survival.

We recorded 1,162 Aishihik, 839 Wolf Lake, and 640 Chisana telemetry locations from fixed-wing aircraft. Monitoring schedules were May–June, July, October, December, and March for the Aishihik and Wolf Lake caribou herds. The Chisana caribou herd was monitored in May–June, September–October, and 1 or 2 times between November and March. We used the Kaplan–Meier survival estimator (Pollock et al. 1989) to calculate survival rates of radiocollared caribou each year. Survival periods were March–February for the Aishihik and Wolf Lake caribou herds. We used the period September–August for the Chisana caribou herd because of different monitoring schedules. Log-rank tests were used to compare rates among periods and among herds (Pollock et al. 1989).

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

Estimating Caribou Pregnancy Rate and Forage Quality

Pregnancy rates and winter diets were studied to estimate effects on caribou

response. We captured 216 cow caribou from all herds between 10 December and 3 April (60–174 days after conception). Blood was extracted, centrifuged, and then frozen for progesterone analysis (Central Laboratory for Veterinarians, Langley, British Columbia). Blood progesterone is a good indicator of caribou pregnancy (Wood et al. 1986, Russell et al. 1998); the threshold value of 1.5 ng progesterone/mL serum was used to separate pregnant from nonpregnant cows (Russell et al. 1998). We also estimated annual pregnancy rates of Chisana cows in late May 1993–1997 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 a herd was reproductively limited if pregnancy rate was below 82% in any year.

On each herd range we collected 20 groups of 20 fecal pellets in February or March and then randomly selected 1 pellet from each group for fecal analysis (Sparks and Malechek 1968; Composition Laboratory at Colorado State University, Fort Collins, Colorado). We compared the relative composition of important foods including mosses, fruticose and foliose lichens, horsetails, graminoids, deciduous shrubs, evergreen shrubs, and forbs.

Estimating Caribou Response to Deep Snow and Snow Melt Phenology

We investigated 2 aspects of weather that could have affected caribou. First, deep snow could bury preferred ground-lichen forage and impede the mobility of caribou in the winter reducing physical condition and survival. Second, the persistence of snow on the alpine calving areas could increase the predation rate on calves. Caribou calve at higher elevations to space away from predators; this strategy is most effective when there is a camouflage mosaic of open ground mixed among snowfields (Bergerud et al. 1984, Bergerud and Elliot 1986, Bergerud and Page 1987).

Snow depth can also affect the condition and survival of caribou (Pruitt 1959). Russell and Martell (1984) reported that mobility of solitary animals was impeded

when snow depth was greater than 50–60 cm, and groups were impeded when depths were 80–90 cm. Deep snow (>100 cm) can also cause increased predation rates by wolves on caribou in Alaska (Mech et al. 1998). 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 basis in late winter and spring.

The last week of May is the peak of calving for woodland caribou in the Yukon (R. Farnell, Yukon Department of Environment, unpublished data). We used the total number of “growing degree days” (GDD) in May as a proxy measure of snowmelt 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 was 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 Changes in Moose Abundance, Adult Survival Rate, and the Rates of Increase

We used SRB aerial survey techniques (Gasaway et al. 1986) to estimate moose abundance and composition. We counted moose in 2 blocks (Aishihik South and Onion Creek) of the Aishihik area in November 1992 and in 2 control areas (Mayo and Big Salmon) in November 1993. We repeated counts in the 4 areas in 1998, 1 year after wolf reduction ended (Table 1). We used Bell 206B helicopters with 3 observers for all counts except for Mayo in 1998 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 sexing adults and aging yearlings from the air.

Population estimates for surveys conducted after 1988 were corrected for sightability of moose. When calculations and statistical tests involved population estimates for which there were no sightability correction factors, uncorrected estimates were used in the comparisons.

Tests for differences in moose abundance 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 change in population size was detected we estimated the finite rate of change (λ). Mean annual natural mortality rates (i.e., not caused by humans) of adult moose were estimated using census interpolation methods (Hatter and Bergerud 1991).

We estimated differences in the finite rate of change of moose in the Aishihik South count area before (1990–1992) and during wolf treatment (1992–1998) using the same methods as for caribou. We then compared it to differences in the rate of increase of Mayo moose between 1988–1993 (before) and 1993–1998 (during Aishihik treatment). There were no pre-treatment data for the Onion Creek treatment area and the Big Salmon control area. Key evidence for the wolf predation hypothesis was whether the change in the rate of increase of moose in the treated Aishihik South area differed substantially from the Mayo control area.

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 or 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 90–200 meters above ground. We classified moose as adults of unknown sex or 9-month-old calves, based on differences in size and behavior. The sex of adults could not be determined because most bulls drop their antlers by February. Each year we classified 8–39% of the moose in each area.

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, and $(Y + A)_t$ = number of moose classified as adults (Yearlings + Adults) in the current survey.

By grouping yearlings (22 months old) and adults we underestimated recruitment rate as a proportion of adults because yearling cows have a lower reproductive rate than do older cows (Schwartz and Hundertmark 1993). We compared moose recruitment in the Aishihik area before and during treatment, and among 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). We expected that both harvest reduction and wolf reduction could increase the number of bulls per 100 cows in Aishihik South and Onion Creek. To isolate the effect, if any, of wolf reduction, we reduced the number of bulls actually counted by the number that would have been killed if harvest had remained at the pre-treatment level. Yates-corrected chi-square tests were used to compare differences in adjusted adult sex ratios at the beginning (1993) and end (1998) of the wolf treatment 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 reduces the survival of adults and calves by impeding their abilities to move and feed. The quality and length of the growing season affects the nutritional status of moose, in turn affecting recruitment and survival rates (Stewart et al. 1977). We used simple linear regression analysis to look for relationships between annual recruitment rates and season length, May and June GDD (see caribou methods section for calculation procedures), and maximum snow accumulation in the year preceding and following birth.

We used threshold values reported in the literature to identify years when maximum snow accumulations were likely to affect recruitment. 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 reduce 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 examined each year's maximum snow depth and looked for trends in moose recruitment.

We examined whether changes in growing season length could have influenced moose population dynamics in our study areas. Stewart et al. (1977) identified a general correlation between moose recruitment and the length of the growing season. We followed their definition of growing season as the period from the first day a critical number of heat units (41.67) had accumulated through to the first day when the daily minimum temperature was -5°C . The number of heat units contributed was defined as: (maximum daily temperature $- 12.2^{\circ}\text{C}$) / 2, for any day temperature exceeded 12.2°C . For each area, we calculated the change in the average growing season length from 1983–1992 (pre-treatment) to 1993–1998 (treatment). The change in average growing season length between the 2 periods was then ranked and compared with the rank change in moose numbers and to recruitment rates.

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 that there was no bias in the years data were available, we also calculated average season lengths using 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 year when the length of the growing season deviated from the mean by more than 1 standard deviation. We determined whether shorter- or longer-than-average growing seasons could have affected responses of the 3 moose populations.

Estimating the Role of Changes in Harvest, Recruitment, and Adult Survival in Moose and Caribou Responses

Caribou and moose responses could have been because of wolf reduction, harvest

reduction, or a combination of these factors. Aishihik caribou hunting was first closed in 1990. Except for a small subsistence harvest by First Nations people, moose hunting in the Aishihik area was restricted in 1993 and closed from 1994 onward. Hunting regulations and harvest patterns in our control areas remained unchanged during treatment. We developed a simple model to assess the effect of the reduction in harvest. For both moose and caribou in the treatment area, natural mortality rates were adjusted until the simulated growth matched the observed population growth. Harvest estimates from before the wolf treatment period were then added to the model to assess harvest effects on population rates of increase.

We estimated resident harvest from annual questionnaire responses (Kale 1982) and nonresident harvest from compulsory submissions (Yukon Department of Environment, unpublished data). Before our study, harvest by First Nations people was monitored using household interviews. Quock and Jingfors (1989) found that harvest was consistently under-reported by about 50%. We bounded our estimate of First Nations harvest using the reported harvest as a minimum then doubled it for a maximum. We also used this model to assess the relative importance of changes in adult survival and recruitment in producing the overall response in Aishihik South and Onion Creek moose populations. We set the model parameter values to mimic the observed moose population decline before the start of treatment. In a stepwise fashion, we then reset harvest, recruitment, and adult survival to the values estimated during treatment while leaving the other parameters at pre-treatment levels. The population change was recorded for each iteration.

Estimating Dall Sheep Abundance, Lamb Survival Rate, and Harvest

Our design for testing Dall sheep response (Table 2) followed Marcstrom et al. (1988). From 1983 to 1985 wolves were reduced in the Rose Lake area (Barichello et al. 1989). The Ruby Range mountains in the Aishihik area served as the control area for this earlier wolf–sheep experiment. In 1993, we reversed treatment areas. This allowed us

to control temporal variation by doing the experiment at the same time in 2 areas, and to control variation between areas by using each area for its own comparison through time. Hayes et al. (1991) found that wolves had recovered to 90% of pre-reduction numbers in the Rose Lake area by 1988.

We used helicopters to conduct total counts of Dall sheep in June or July when counts are most representative of population characteristics due to the strong seasonal range fidelity in Dall sheep (Hoefs and Cowan 1979). Sheep were counted in a 1,600-km² block in the Aishihik area (Ruby Range) and in a 400-km² block in the Rose Lake area. We classified Dall sheep as rams having half-, three-quarter-, or full-curl horns; lambs of the year; yearlings; or ewes (after Geist 1971). Whenever we could not confidently count yearlings, we grouped ewes, yearlings, and the associated young rams as "nursery sheep."

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

We tested for changes in Dall sheep numbers by regressing adult population against time in treatment and control areas. We tested for effects 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. For both comparisons we used the Wilcoxon rank-sum test.

RESULTS

Changes in Wolf Abundance

From 1993 to 1997 we reduced March wolf density in the Aishihik area 69–83% below the 1992 pre-treatment density (Table 5). The number of wolf packs fell from 28 in 1992 to 7–20 packs during the reduction period winters. Mean pack size declined from 5.6 wolves before treatment to <4 wolves during treatment. We found no difference in the annual proportion of males and females killed ($P = 0.38$). Adults comprised 54–79% of annual culls, yearlings

0–18%, and pups 13–31%. Wolf density, wolf pack density, and mean pack size were all higher in the 3 control areas than in the Aishihik area during treatment. Before treatment, Aishihik wolf density was higher than Mayo and Tatchun, but similar to Wolf Lake (Table 5).

A big-game outfitter was convicted in 1994 of counseling guides to place poison (Thimet; Phorate, Cyanide Canada) in the central Aishihik area. No poisoned wolves were found but 4 packs in this area declined from a total of 38 wolves in 1992 to only 2 packs totaling 8 wolves in 1993. Poisoned wolves and avian scavengers were found at the southern border of the Aishihik area in February 1993 (Carey et al. 1994).

Changes in Caribou Abundance and Population Trends

Between 1990 and 1992 all harvest of Aishihik caribou was stopped but herd size continued to decline (Table 3). When wolves were reduced in 1993 the Aishihik caribou herd stopped declining ($\lambda = 0.98$) then rapidly increased ($\lambda = 1.15$), a cumulative difference of 0.17 points in the finite rate of increase. The Ibex herd increased from 1990 to 1998 ($\lambda = 1.14$). Because there was no 1993 population estimate we were unable to compare pre- and post-treatment rates of change. The Wolf Lake caribou herd stopped increasing and became stable for a difference of -0.11 points (pre-treatment $\lambda = 1.11$, treatment $\lambda = 1.00$); the Chisana caribou herd declined more rapidly for a difference of -0.04 during treatment compared to before (pre-treatment $\lambda = 0.93$, treatment $\lambda = 0.89$) (Table 3).

Caribou Calf Recruitment and Adult Sex Ratio

The Aishihik caribou herd was the only herd that showed a sustained increase in annual recruitment during treatment. The mean ratio increased from 15 calves per 100 cows (90% CI: 7.0–24.6) before treatment to 42 calves per 100 cows (90% CI: 38.0–45.8) during treatment ($P < 0.01$) (Table 3). Recruitment of Chisana was low in all years, averaging 3.9 calves per 100 cows (90% CI: 0.04–8.8) before treatment and 7.2 calves (90% CI: 3.8–11.2) during treatment ($P > 0.10$). The Ibex caribou herd averaged 56.3 calves (90% CI: 50.1–63.8)

Table 5. Characteristics of wolf populations in the Aishihik area and 3 control study areas in the Yukon, 1992–1998. Wolf treatment began February 1993 and ended April 1997.

	Aishihik treatment area (20,000 km ²)												Control study areas			
	1992 Feb	1993 Jan	1993 Mar	1994 Jan	1994 Mar	1994 Mar	1995 Jan	1995 Mar	1996 Jan	1996 Mar	1997 Jan	1997 Mar	1998 Jan	1998 Mar	Mayo (22,130 km ²) 1995 Mar	Wolf Lake (6,970 km ²) 1994 Mar
Wolves (no.)	178 ^a	120	55	81	44	75	38	52	30	55	33	58	52	96–107	45–52	45–52
Packs (no.)	28	26	11	20	12(1) ^b	18	11	12	7(3) ^b	13	9(6) ^b	14	14	15	8	9
Pack density (packs/1,000 km ²)	1.4	1.3	0.6	1.1	0.6	0.9	0.6	0.6	0.4	0.7	0.5	0.7	0.7	0.7	1.2	0.9
Mean pack size (±SE)	5.6 ±0.6	4.2 ±0.4	3.8 ±0.5	3.7 ±0.4	3.1 ±0.3	3.8 ±0.6	2.7 ±0.2	3.9 ±0.6	3.4 ±0.7	3.4 ±0.7	2.8 ±0.7	3.8 ±0.5	3.4 ±0.4	6.1 ±0.8	5.5 ±0.8	4.9 ±0.4
Density (wolves/ 1,000 km ²)	8.9	6.0	2.8	4.1	2.2	3.8	1.9	2.6	1.5	2.8	1.7	2.9	2.6	4.3–4.8	6.5–7.4	4.5–5.1
Survey coverage rate (km ² /hr)	205		72		100	95		102		100		222		316	162	223
Wolf mortalities:																
Yukon Fish and Wildlife			54		32	36		17		12						
Natural mortality			1		4					1						
Public			10		1	1		5		9		6				
Total			58 ^c		37	37		22		22		6				
Reduction from 1992 population (%)		33	69	54	75	58	79	71	83	69	81	67	71			
Rate of increase (λ)		0.67		1.5		1.6		1.5		1.7		1.8				

^a Total pre-treatment wolf population in February 1992 was the sum of the 1992 count area (15,000 km², 125 pack wolves and 13 lone wolves) plus the number counted in the extension area (5,000 km²) 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 sterilized.

^c Numbers declined by 58 wolves from February 1992 to January 1993. Cause was not determined.

before and 44.2 calves (90% CI: 36.0–51.7) during treatment ($P > 0.90$). There was no annual pre-treatment information for the Wolf Lake caribou herd.

Before treatment, Aishihik herd recruitment was higher than for the Chisana caribou herd ($P < 0.05$, 2-tailed test), and less

than for the Ibex caribou herd ($P < 0.01$). Recruitment in the Aishihik caribou herd remained higher than for the Chisana caribou herd during wolf treatment ($P < 0.01$), and higher than for the Wolf Lake caribou herd ($P < 0.01$), which averaged 26.3 calves per 100 cows (90% CI: 20.0–31.2). Aishihik

caribou herd recruitment increased during treatment and it was not different than the high but declining recruitment rates for the Ibex herd ($P > 0.60$).

The Aishihik caribou herd lost proportionately fewer calves between July and October during treatment (7–18%) compared to 2 years before wolves were reduced (34–41%). Calf losses from July to October were lower for the Aishihik caribou herd than for the Wolf Lake caribou herd (17–60%) during all treatment years ($P < 0.01$).

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

Adult Caribou Survival Rate

Survival of adult caribou was the same in the treatment and control herds. Adult survival in the Aishihik caribou herd was 0.94 in 1991–1992 and 0.49 in 1992–1993, making any estimate of pre-treatment trend difficult. Survival during treatment averaged 0.89 ± 0.01 (SE), similar to the Wolf Lake caribou herd (0.89 ± 0.04 [SE]) (Table 6). Survival in the Chisana caribou herd was not different before (0.77 ± 0.06 [SE]) and during treatment (0.83 ± 0.05 [SE], $P > 0.07$). Adult survival in the Chisana caribou herd was not different than in Aishihik caribou herd before ($P > 0.90$) or during treatment ($P > 0.20$).

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

Caribou Pregnancy Rate and Forage Quality

Caribou response was not related to changes in pregnancy rates. The Aishihik

caribou herd had high pregnancy rates before (96–100%) and during treatment (88–100%; Table 7). The average annual pregnancy rate for the Aishihik caribou herd was $95\% \pm 2.93$ (SE) during wolf treatment, the same as for the Wolf Lake caribou herd ($94\% \pm 4.09$ [SE]).

Pregnancy rate was high in all herds except for Chisana. A total of 201/216 cows tested were pregnant (1.57–12.58 ng progesterone/mL); 9 of the 15 cows that were not pregnant (0.09–0.97 ng/mL) were from the Chisana caribou herd. Because sample sizes were small for this herd we combined both progesterone and June udder counts for a better estimate of pregnancy rates. Estimated pregnancy rates were 50% in 1993, 86% in 1994, 93–95% in 1995 and 1996, and 82% in 1997. Pregnancy was probably low in 1992 when only 1 calf was classified among 1,142 caribou seen 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 diet composition. Lichens constituted $84\% \pm 4$ (SE) of the diets of Ibex caribou, $80\% \pm 12$ (SE) of Aishihik caribou, $70\% \pm 7$ (SE) of Wolf Lake caribou, and $53\% \pm 2$ (SE) of Chisana caribou. The importance of other plant types varied. The frequencies of mosses were highest and lichens were lowest for Chisana caribou. In 2 winters that we studied Chisana food habits the herd used forested lowland areas they did not use in other years.

Caribou Response to Snow Depth and Snowmelt Phenology

Snow depth on the Aishihik caribou herd range never exceeded the threshold of 80–90 cm. Depths reached or exceeded the threshold of 55 cm in 8 of 12 winters when the herd declined (1981–1993) and in 3 of 5 winters when the herd increased (1994–1998). There was no relation between snow depth and Aishihik caribou herd demography.

Snow on the Chisana winter range reached 55–60 cm in 3 of 7 years, and did not exceed 55 cm on the winter range of the Ibex caribou herd in any year. Snow depths exceeded the critical level of 85 cm only in the Wolf Lake caribou herd range. The Wolf Lake caribou herd increased from 1987 to

Table 6. Kaplan–Meier survival rates for adult caribou in the Aishihik and Wolf Lake herds in the Yukon and Chisana herd in Alaska, 1989–1997.

Area	Period	Year	No. at risk	No. of deaths	Annual survival	No. censored	No. added	Variance	Lower 95% confidence bound	Upper 95% confidence bound
Aishihik herd	Before treatment	1991	17	1	0.941	0	11	0.003	0.833	1.000
		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	1.000
		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	1.000
		1997	43	4	0.906	4	0	0.002	0.824	0.990
		Total	236	33		13	64			
Wolf Lake herd		1993	29	1	0.965	0	0	0.001	0.900	1.000
		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	1.000
		1997	45	3	0.933	4	0	0.001	0.863	1.000
	Total	179	17		4	30				
Chisana herd		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	1.000
		1993–1994	19	2	0.895	0	0	0.004	0.764	1.000
		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
	Total	165	34		22	61				

1993 (Table 3) when snow was near or above critical depths every year except 1993, but remained stable after 1993 when snow exceeded 85 cm in only 1 of 4 years. Thus, there was no relation between trends in control caribou herds and snow depth.

None of the study herds experienced late snowmelt in any spring during treatment. Before treatment, the Aishihik and other herds experienced a late snowmelt in 1992. Recruitment was low in Aishihik the next October, 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. We found no evidence that recruitment or changes in herd size were related to snowmelt phenology.

Changes in Moose Population Trends and Abundance

Between 1990 and 1992, before the start of treatment, moose numbers in the Aishihik South area were rapidly declining ($P < 0.05$, $\lambda = 0.71$; Table 4). During treatment, moose numbers stopped declining then rapidly increased ($P < 0.001$, $\lambda = 1.19$), a cumulative difference of 0.48 points in the finite rate of increase. Between 1988 and 1993 moose numbers in the Mayo area did

not change ($P > 0.20$), then increased during treatment ($P = 0.003$, $\lambda = 1.11$) for a cumulative difference of 0.11. There were no pre-treatment trend data for the Onion Creek area but moose numbers also increased rapidly during treatment ($P < 0.001$, $\lambda = 1.16$). Moose numbers in the Big Salmon area were stable ($P = 0.99$) during treatment.

Moose Recruitment, Adult Sex Ratio, and Adult Survival Rates

Moose recruitment in the Aishihik area increased ($P < 0.05$) from 10.4% (90% CI: 5.6–15.5) in 1993 to average 18.8% (90% CI: 16.0–22.1) during wolf treatment. In 1993 in the control areas, recruits made up 10% of

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

Herd	Year					
	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)

the Big Salmon (90% CI: 5.5–14.4) and 12.1% of the Mayo (90% CI: 8.5–16.7) moose populations. Average recruitment rates in the Big Salmon area (15.4%; 90% CI: 11.3–19.9) during the treatment period were no different than pre-treatment levels ($0.05 < P < 0.10$); in Mayo the average recruitment during treatment was 16.0% (90% CI: 11.6–20.5), no different than pre-treatment levels ($0.10 < P < 0.20$). Recruitment in the Ladue control area was 7.4% (90% CI: 3.8–11.9) before treatment, no different than the average of 7.2% (90% CI: 5.5–8.9) during treatment ($P > 0.30$).

Moose recruitment in the Aishihik area before treatment (1993) was not different from the Big Salmon ($P > 0.80$), Ladue ($P > 0.40$), or Mayo ($P > 0.60$) areas. During treatment, moose in Aishihik showed higher recruitment than all control areas in 3 of 5 years; Big Salmon and Mayo areas showed wide variation and in some years exceeded the rates seen in the Aishihik area (Table 4). Average recruitment during treatment was greater than in the Ladue area ($P < 0.01$), but it was not different from the Big Salmon ($P > 0.60$) and Mayo areas ($P > 0.40$).

After adjusting for the effects of the harvest closure, we found that the moose sex ratio did not change in the Aishihik South ($P = 0.48$) or Onion Creek ($P = 0.06$) areas (Table 4). Omitting our adjustment for harvest did not change this finding in the Aishihik South area but resulted in a significant increase in the proportion of mature bulls in the Onion Creek area ($P = 0.02$). Sex ratios did not change in Big Salmon ($P > 0.75$) or in Mayo ($P > 0.40$) during the same period. Based on census interpolation the mean annual natural mortality rate of adult moose during wolf treatment was 0.03 for Aishihik South, 0.02 for Onion Creek, 0.01 for Mayo, and 0.15 for Big Salmon.

Moose Response to Snow Depth and Summer Growing Season

We found no significant relationship ($P > 0.05$) between recruitment rates and season length, GDD in May or June, or maximum snow accumulation in the year preceding or following birth in the Aishihik treatment or control areas.

In all moose study areas in all years, snow depths were less than 80 cm and were not

considered to be limiting to calf moose survival. Before treatment (1977–1993) snow depth in Aishihik exceeded 70 cm only in 1991 and 1992, possibly impeding mobility but not survival. Snow depth did not exceed 70 cm in any year in Mayo and only in 1994 in the Big Salmon area. Thus, snow depth did not limit moose survival in any year.

We ranked the magnitude of changes in growing season length and moose population size for each area (Table 8). The rankings were not correlated and provided no evidence that variation in the length of the growing season was responsible for the relative differences in the performance of moose populations.

Unusually short or long seasons also did 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.

Role of Adult Survival, Recruitment, and Harvest in Moose Response

The combined effects of wolf and harvest reductions resulted in an increase in adult moose numbers that was greater than the individually modeled responses to reduced harvest, increased recruitment, and increased adult survival (Fig. 3).

We estimated a 6–8% harvest rate before wolf reduction, when moose were rapidly declining. Without wolf and harvest reductions, moose would have continued to decline at an annual finite rate of 0.73 in Aishihik South and at a rate of 0.86 in the Onion Creek area. Increased adult survival was the only factor in the moose population response that was sufficient to stop the rapid decline and create a finite rate of change of 0.99 in Aishihik South and 1.06 in Onion Creek (Fig. 3). Overall, increased recruitment was the second most important factor in producing the observed response. The increase in recruitment would have reduced the rate of decline to 0.85 in Aishihik South and 0.94 in Onion Creek, but without the change in adult survival, numbers would not have increased. A reduction in harvest

Table 8. Comparison of growing season length with moose population change in the Yukon, 1983–1998.

Moose population	Average season length (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 are available.

alone would have seen the populations continue to decline at a finite rate of 0.87 in both areas.

When combined with the observed increases in adult survival and recruitment, harvest reduction was an important cause of the moose response in the Aishihik South area but had little effect in the Onion Creek area. In Aishihik South adult and yearling moose numbers increased at a finite rate of 1.19 during treatment. If the pre-treatment harvest of moose had continued each year

during treatment, the rate of change would have decreased to 1.09–1.12. In the Onion Creek block, moose numbers increased at an annual rate of 1.16 during wolf reduction. A continuation of the small pre-treatment harvest would not have changed this.

Dall Sheep Response

Neither treated nor control populations of Dall sheep changed over time (Fig. 4). 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 rate than the control area (Fig. 5) but overall lamb: nursery sheep ratios did not differ between treatment and control periods in any area (Ruby Range: Wilcoxon $Z = -1.73$, $df = 1$, $P = 0.08$; Rose Lake: $Z = 1.36$, $df = 1$, $P = 0.18$).

DISCUSSION

Test of Wolf Predation Hypothesis

Our central hypothesis was that an 80% reduction in wolf numbers would cause higher recruitment and adult survival rates, resulting in increased numbers of caribou, moose, and sheep. We found overall support for the wolf predation hypothesis for moose and caribou, but not for sheep. Key evidence supporting the wolf predation hypothesis was the dramatic change in both caribou and moose population growth, which happened in the treatment area but not in the control areas. We observed sharp reversals in the Aishihik caribou and moose populations from declining to rapidly increasing during wolf treatment. None of the control populations showed similar responses. Controls either did not change, or the changes in the rate of increase were considerably smaller between pre-treatment

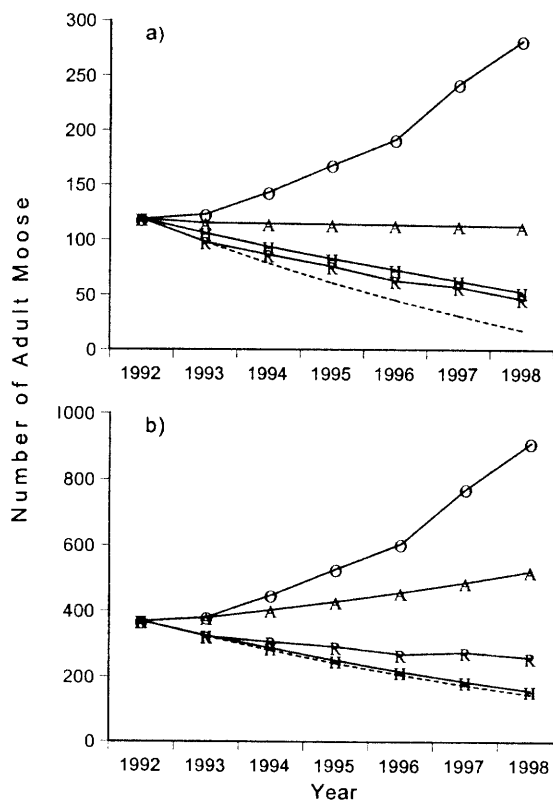


Figure 3. Relative importance of increased adult survival and recruitment, and reduced harvest in producing the observed response in the Aishihik south (a) and Onion Creek (b) moose populations. Symbols show observed response (O), increased adult survival only (A), increased recruitment only (R), reduced harvest only (H), and no response (- -).

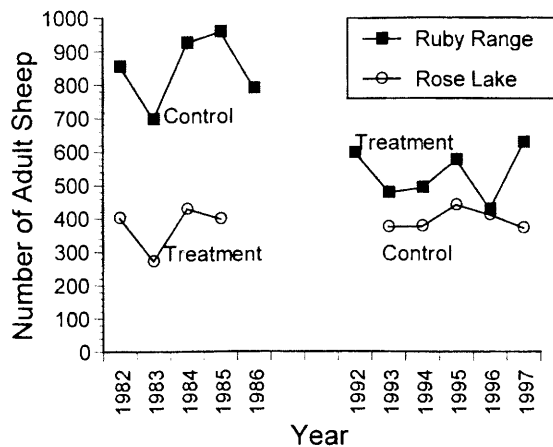


Figure 4. Total number of adult sheep counted in the Ruby Range and Rose Lake sheep study areas in the southwestern Yukon, 1983–1985 and 1993–1997. All regressions of sheep numbers by year ($y = a + bx$) were not significant: Ruby Range 1983–85 (control, $P = 0.72$), Ruby Range 1993–97 (treatment, $P = 0.42$), Rose Lake 1983–85 (treatment, $P = 0.72$), Rose Lake 1993–97 (control, $P = 0.79$).

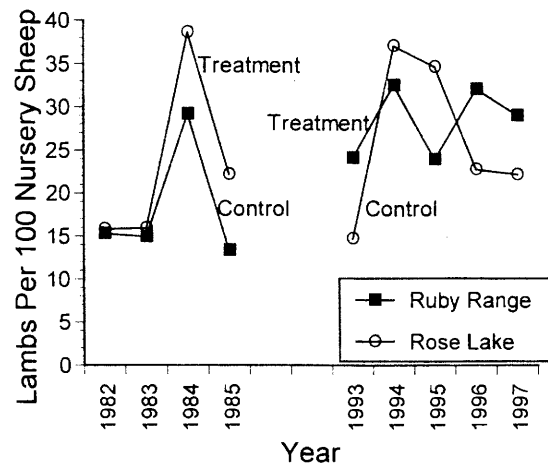


Figure 5. Ratios of lambs/100 nursery sheep in the Ruby Range (control) and Rose Lake (treatment) areas in the southwestern Yukon, 1982–1987; and in Ruby Range (treatment) and Rose Lake (control) areas, 1993–1997.

and treatment periods. Some control populations (i.e., Ibex caribou herd, Mayo moose) increased without wolf reduction. Pre-treatment data shows both controls were stable or slowly increasing. All other controls either remained stable or declined while Aishihik moose and caribou increased.

We found different levels of support for our predictions about changes in recruitment, adult survival, and population responses (Table 10). Predictions of increased caribou recruitment and herd size were supported (P1, P2, P3, P4). When harvest was adjusted for, however, herd size could have grown by a factor of 1.54, less

than the doubling predicted (P4). We had no support for or against prediction P5 because the Ibex caribou herd increased without wolf reduction, the Wolf Lake caribou herd remained stable and the Chisana caribou herd declined. We had evidence against predictions P6 and P7. Adult survival in the Aishihik caribou herd did not increase during treatment and annual survival rate of adults in the Aishihik caribou herd was not different than the rate in the Wolf Lake caribou herd.

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

We found no support for or against moose predictions P4 and P6. Moose numbers also increased in the Mayo control area, and adult survival was comparable between Mayo and Aishihik areas. In the Big Salmon area, moose numbers did not change and adult survival was much lower than in Aishihik.

There was no support for Dall sheep predictions; sheep population size and lamb recruitment rates were unrelated to changes in wolf abundance.

Our inability to accurately predict responses in various population processes reaffirms

Table 9. Results of Wilcoxon Z-value tests for differences in Dall Sheep lamb recruitment between wolf treatment and control areas in southwestern Yukon, 1982–1985 and 1993–1997 (1 degree of freedom for each value).

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

Table 10. Predictions about wolf and ungulate responses (Hayes 1992) and levels of support from our study in the Yukon, 1993–1997.

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.	0
P6) Survival rates of radio-collared adults in the Aishihik herd will increase to 0.90–0.95 during wolf treatment.	0
P7) Adult survival in the control herds will be lower than for the Aishihik herd.	–
Moose	
P1) The proportion of calf moose in the Aishihik area in late winter will increase to 13–20% during wolf treatment.	++
P2) The proportion of calves in control areas will not increase.	0
P3) Aishihik moose densities will increase at a finite annual rate of 1.08–1.12 after wolf treatment.	++
P4) Moose densities in control areas will not increase.	0
P5) Mean annual adult survival rate will increase to 0.96 in the Aishihik area.	++
P6) Adult survival will be higher in Aishihik compared to 2 control areas.	0
Sheep	
P1) The number of adult sheep will increase in treatment area, but not in control area.	–
P2) The lamb to nursery sheep ratio will increase in treatment area, but not in control area.	–

Key: – Prediction not supported; 0 No evidence for or against prediction; ++ Support for prediction.

how difficult it is to generate hypotheses that are relevant to changes in internal structure of managed systems (Walters and Holling 1990). It further demonstrates that our knowledge of wolf–prey systems is incomplete. Nevertheless, after controlling for other factors, the differences in the trends of treated and control populations of moose and caribou is best explained by reduction of the Aishihik wolf population.

Comparison of Treated and Untreated Ungulate Responses

The large scale of our study resulted in us comparing contemporary controls that were experiencing different ecological trends independent of wolf reduction. The uncertainty of the treatment–control outcomes was confounded by the scale of the study and by the concurrent reduction of wolves and harvest. Our modeling showed that harvest reduction played an important role in caribou response but a smaller role in the overall Aishihik moose response. However, harvest closure between 1990 and 1992 was not sufficient to stop the decline of the Aishihik caribou herd. Nor did harvest reduction stop the decline in moose in our model. Reversing population trends happened only when both wolf predation and harvest were reduced. In the following sections we com-

pare the internal responses among treatment and control populations, and we discuss the relative effects of wolf reduction and other factors on observed responses.

Caribou.—The Aishihik caribou herd rapidly declined then increased but the 3 control herds all performed differently. Before treatment, the Chisana caribou herd was the most similar to the Aishihik caribou herd in ecotype and declining trends in adult composition, recruitment, and herd size (Valkenburg et al. 1996). Recruitment and adult survival of Chisana caribou remained low in all study years, and the ratio of adult bulls per 100 cows continued to decline with herd size despite hunting closures. In contrast, the recruitment rate in the Ibex caribou herd was already high before the Aishihik treatment began. Since 1983, recruitment had averaged more than 50 calves per 100 cows, the highest of any naturally limited herd in the Yukon. During treatment, Ibex herd recruitment gradually declined, in contrast to increased recruitment in the Aishihik caribou herd. Ecological conditions were probably unique for the Ibex herd. Hayes et al. (1991) found that wolves rarely preyed on Ibex caribou when herd size was about 150 animals during the mid 1980s. Despite high recruitment this herd apparently began to rapidly

increase only after 1993 when First Nations hunters stopped their harvest (O'Donoghue 1996, Farnell et al. 1998), suggesting that excessive harvest of adults was keeping the herd from increasing. Between 1987 and 1992 the Wolf Lake caribou herd increased at an annual rate of 1.11. During treatment the herd stabilized when calf recruitment averaged 26 calves per 100 cows and annual adult survival rate was typical of stable caribou herds elsewhere (Bergerud 1980, Bergerud and Elliot 1998).

No control herd showed a pattern of increased recruitment and adult sex ratios similar to that observed in the Aishihik caribou herd. Calf recruitment in the Aishihik caribou herd increased and remained high in all years of wolf reduction. However, the consistently high recruitment in the control Ibex caribou herd showed that other ecological factors besides wolf reduction can support high caribou calf survival. Reducing wolves apparently increased calf survival rates between July and October in the Aishihik caribou herd. Neonatal calf survival was similar between the Aishihik and Wolf Lake caribou herds before July (42–46 calves per 100 cows), the period when neonatal vulnerability was highest in the Denali caribou herd in Alaska (Adams et al. 1995). After July (when wolves had the largest effect on calf survival in the Denali herd) the Wolf Lake control herd lost 4 times as many calves as did the treated Aishihik caribou herd.

Survival rates of Aishihik adult caribou did not apparently change in response to lower wolf numbers but our pre-treatment data was too variable to estimate a trend. Survival rates of 0.71–0.83 were reported for declining woodland caribou herds elsewhere in Canada (Fuller and Keith 1981, Edmonds 1988, Farnell and McDonald 1988, Seip 1992, Seip and Cichowski 1996; Stuart-Smith et al. 1997). Farnell and McDonald (1988) reported survival rates of 0.72 during a decline and 0.89 during a rapid increase in the Finlayson caribou herd. We found no evidence that wolf reduction increased adult survival, which was within the range for stable and increasing woodland caribou herds elsewhere (Bergerud 1980).

Comparing changes in composition between the increasing Aishihik and declin-

ing Chisana caribou herds provides evidence of the importance of recruitment to adult sex ratio. When recruitment was high during treatment, the adult sex ratio in the Aishihik caribou gradually increased each year from 29 bulls per 100 cows to 52 bulls per 100 cows by 1998. In the same period, when recruitment was very low the sex ratio in the Chisana caribou herd continued to decline from 39 to 19 bulls per 100 cows. This reversing trend in sex ratio supported the conclusion of Bergerud (1980) that it is mainly through improved recruitment that bull:cow ratios increase.

The Aishihik caribou herd increased at a finite rate of 1.15 during treatment. With continued hunting, the rate of increase could have been reduced to 1.05–1.09. The Wolf Lake herd was stable and the Chisana herd declined. The Ibex caribou herd increased at a rate similar to the Aishihik caribou herd, showing that similar responses can sometimes be initiated without reducing wolf numbers.

With adequate food and no predators, caribou are capable of increasing at a maximum finite rate of 1.35 (Valkenburg 2000). Our study and others (Gasaway et al. 1983, Farnell and McDonald 1988) showed that when wolves are substantially reduced, rates of increase of caribou remained at about half of the intrinsic potential. In these 3 studies about half of the caribou calves still died before October. In our study and in the Finlayson area (Farnell and McDonald 1988) the survival rate of adults did not exceed 0.90 when most wolves were removed, showing that other limiting factors are important in caribou population dynamics.

There was little evidence that pregnancy rate affected caribou response. Except for the Chisana herd in some years, pregnancy rates were similar to woodland caribou in British Columbia (90–97%; Seip and Cichowski 1996), Alberta (86%; Stuart-Smith et al. 1997), and Saskatchewan (94%; Rettie and Messier 1998). Poor summer nutrition and low body condition 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). Lenart (1997) found warm and dry summer weather on the Chisana range decreased alpine summer

forage in 1994 and 1995. The Chisana caribou herd body condition scores ranked second from last among the Yukon herds studied by Kuzyk et al. (1999). We believe that the unfavorable summer conditions caused low body condition scores and pregnancy rates of Chisana caribou in 1993.

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 neonatal survival (Espmark 1980, Adams et al. 1995). Winter diets of the Aishihik, Ibex, and Wolf Lake caribou herds were similar to diets of other caribou herds wintering on lichen range in the Yukon and Alaska (Russell and Martell 1984, Boertje 1985, Russell et al. 1993). Body measurements and body condition scores of these 3 herds were not different from other Yukon herds (Kuzyk et al. 1999). In contrast, the Chisana caribou herd experienced poor winter diet, with the highest proportion of low-nutrition mosses and lowest proportion of fruticose lichen among our study herds. Thus, we found evidence that summer and winter conditions negatively affected the Chisana herd, but other herds were not nutritionally limited.

Farnell et al. (1999) found no evidence that disease limited any of our study herds. Serum samples of 137 Aishihik, 55 Chisana and 59 Wolf Lake caribou were collected between 1991 and 1996. Epizootic hemorrhagic disease was present in 4 of 71 Aishihik caribou tested in 1991, but no evidence of the disease was found thereafter. Chisana caribou showed no disease, and leptospirosis was found in 1 Wolf Lake caribou. This low prevalence of disease is consistent with serological studies of other woodland caribou herds in the Yukon (Farnell et al. 1999) and Alaska (Zarnke 2000).

Haber and Walters (1980) speculated that movement of caribou among herds can explain changes in herd abundance, but telemetry data from North American herds have since discounted this (Thomas 1995). Telemetry studies (Farnell and Russell 1984, Farnell et al. 1998) and new genetic research (Zittlau et al. 2000) showed Yukon woodland caribou herds are discrete and do not exchange among herds at current densities. Nevertheless, we looked for exchange between Aishihik and neighboring herds by

monitoring 81 radiocollared adult caribou in the Aishihik herd, 25 in the Kluane herd, and 45 in the Klaza herd for a total of 2,022 locations. We saw no exchange of radiocollared animals and there was no change in the size of adjacent herds as the Aishihik caribou herd increased. The Kluane herd remained between 180–200 animals from 1993 to 1997. The Klaza herd numbered 441 (90% CI: 428–454) in 1989 and 426 (90% CI: 350–502) in 1996 (R. Farnell, Yukon Department of Environment, unpublished data). We conclude that immigration did not contribute to the change in Aishihik caribou herd size.

Moose.— The Aishihik South and Onion Creek treatment areas were the only places to show a sharp reversal from declining to increasing moose numbers during treatment. Moose abundance in the Mayo area increased. Moose numbers in the Big Salmon area did not change during treatment. Although moose were not counted in the Ladue control area, the consistently low recruitment indicated numbers probably declined there.

The sharp reversal in moose population growth rate in the Aishihik treatment area was primarily the result of improved adult survival, but increased recruitment was also important. Eberhardt et al. (1982) and Nelson and Peek (1982) noted that adult survival can have a profound effect on the rate of increase in long-lived species. The change in adult survival in the Aishihik treatment area exceeded our predictions, increasing from 0.80–0.82 (Ward and Larsen 1995) to 0.97–0.98 during the wolf reduction period. Gasaway et al. (1983) reported a similar increase in adult survival following a wolf reduction experiment in Alaska. Adult survival in the Aishihik area during treatment was higher than the range of 0.90–0.95 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). Adult survival in the Big Salmon area during treatment was similar to survival in the Aishihik area before reduction. In the Mayo area adult survival was even higher than in the Aishihik area during wolf reduction.

High recruitment was the second most important factor in moose population

growth in the Aishihik treatment area. In 2 control areas (Mayo and Big Salmon), recruitment was similar to or higher than that in Aishihik in 2 of 5 years, showing that factors other than wolf reduction can support high calf survival in some years. The Ladue area experienced much lower annual recruitment in all study years. No control area showed the pattern of consistently high calf survival seen in the Aishihik treatment area. Previous studies have also identified changes in recruitment in response to predator reduction as a driving force behind moose population dynamics (Gasaway et al. 1983, 1992; Crête and Jolicoeur 1987; Crête and Messier 1984; Stewart et al. 1977).

After adjusting for harvest, the ratio of bulls per 100 cows did not increase in Onion Creek or Aishihik South. Nor did ratios change in control areas. Increases in bull:cow ratios 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 reduction was not estimated in either study. 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).

The Onion Creek area showed the most rapid rate of increase in our treatment and control moose populations. Moose populations in the Aishihik South and Mayo areas grew at about the same rate. The substantial increase in moose numbers in Mayo deserves special discussion because it was not predicted, underscoring the idea that uncertainty of responses should be expected in large-scale ecological experiments (Walters and Holling 1990). The Mayo response showed that local moose densities in the Yukon can increase in response to either environmental conditions or other factors. In Mayo, large fires burned a total of 980 km² near the survey area in the summer of 1998, a few months before our population count (M. O'Donoghue, Yukon Department of Environment, unpublished data). The largest burn (850 km²) was on the southwestern border of the count area. We did not study radiocollared moose, so we have no evidence of moose moving from the newly burned areas into the Mayo count area.

Temporary migration in response to a forest fire (Gasaway and Dubois 1985) could partially account for the observed population increase.

We examined recent maps to see if large forest fires (>50 km²) near the Aishihik area could have affected moose distribution and abundance in the count areas. Fires burned a 185-km² area outside the 3,400-km² Onion Creek count area in 1996 and no large fires burned near Aishihik South. There was no evidence that wildfires affected moose distribution in the Aishihik area.

We found no evidence that climatic factors affected moose response in any area. Snow depth probably had little effect because threshold levels were not exceeded. Even when snow is deep, moose recruitment may not be affected. In Alaska, snow depths reached 70–80 cm in 4 winters, but the survival of calves was low in only 1 winter (Gasaway et al. 1992). Spring and summer conditions and snow depths were favorable for moose (and caribou), reinforcing the positive effects of reduced wolf predation and lower harvest levels.

Sheep Response

Sheep population dynamics in the Ruby Range treatment area did not differ from the Rose Lake control area during our study. By reversing treatment areas used in a previous study (Barichello et al. 1989), we showed that wolf reduction did not increase survival rates of lambs or cause total numbers to increase. In Alaska, Gasaway et al. (1983) also found that there was no increase in lamb survival in response to wolf reduction. In a subsequent study in the same area, Scotton (1998) found 96% of lamb mortality was caused by predation, including 43–60% by coyotes, 22% by golden eagles, and 4–17% by wolves. Bergerud and Elliot (1998) reported an increase in number and lamb survival rates of Stone's sheep (*O. d. stonei*) when wolf numbers were reduced. A review of their sheep data is less convincing (see their Table 8, page 1563). Total sheep numbers dropped in the wolf reduction period (1983–1985), and sheep numbers show an increase when wolf numbers were recovering in their study area.

Sumanik (1987) found that wolves that preyed primarily on Dall sheep in the south-

west Yukon had larger home ranges, smaller pack sizes, lower density, and lower consumption rates than did wolves that preyed on moose or caribou. 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 (Hayes et al. 1991) adjacent to our study area. Although sheep could be important to the diet of some wolves, wolf predation does not appear to a main factor limiting sheep numbers in the southwest Yukon. However, we did not test for responses in adult sheep survival in our study design.

During treatment, we estimated an average of 28 lambs per 100 nursery sheep in July (range 24–32) in the Ruby Range, near the long-term average of 30 lambs:100 nursery sheep measured throughout the Yukon since 1973 (J. Carey, Yukon Department of Environment, unpublished data). Lamb production in the Yukon shows annual variability ranging from 9 to 67 lambs per 100 nursery sheep in summer (J. Carey, Yukon Department of Environment, unpublished data). Similar variability (8–81 lambs per 100 ewes) has also been reported in Alaska (Nichols 1978). Variation in recruitment has been linked to stochastic weather events (Hoefs 1984, Heimer and Watson 1986, Barichello and Carey 1988). The decline in sheep numbers in the Ruby Range between the 2 treatment periods can be best explained by several years of poor lamb production in the 1980s (Carey and Dehn 1998).

Wolf Reduction

Aishihik wolves were annually reduced by 69–83%, exceeding the sustainable harvest rate of 30–50% (Gasaway et al. 1983, Keith 1983, Peterson et al. 1984). By each January, wolves were able to recover to 36% of the 1992 pre-treatment density. Thus, wolves were substantially reduced in all seasons during treatment years.

Sterilization reduced the wolf rate of increase by apparently stopping 12 breeding events from potentially producing 68 pups between 1994 and 1997, based on an average litter size of 5.7 (Hayes and Harestad 2000*b*). Surgically treated packs were present starting in 1994 (Table 5). Assuming that each pack was capable of reproducing, steriliza-

tion reduced the wolf rate of increase by 11% in 1995, 24% in 1996, 51% in 1997 and 58% in 1998. Mech et al. (1996) and Spence (1998, our study area) found wolf territoriality, pair bonding, and survival rate were not affected by surgical sterilization. Our study and similar research in Alaska (C. Gardner, Alaska Department of Fish and Game unpublished data) indicated sterilization was an effective tool for reducing wolf rate of increase. Keeping wolf pack sizes small reduces predation rates on moose (Thurber and Peterson 1993, Hayes et al. 2000), and possibly on caribou. Continuing research should show how fertility control of wolves affects survival rates of calf and adult moose and caribou, and how treated wolves behave and survive as other wolves move into the Aishihik study area.

We plotted annual rates of increase against the percent of wolves left alive the previous winter (Fig. 6) and compared the results to 4 other wolf reduction studies in Alaska (Gasaway et al. 1983, 1992) and the Yukon (Hayes et al. 1991; R. Farnell, Yukon Department of Environment, unpublished data). We found a 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. Aishihik rates of increase were the lowest of the 4 studies, in part because surgical sterilization slowed numerical response. The X intercept indicated that wolf populations are stable when

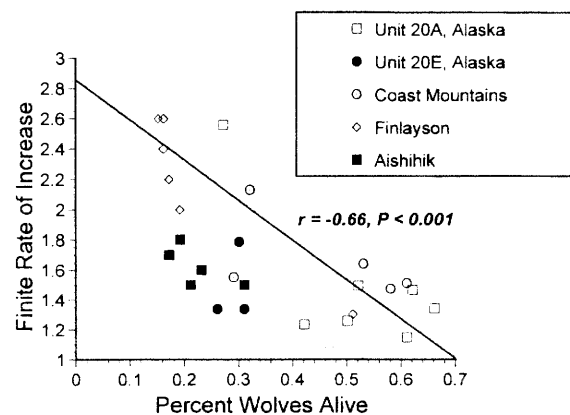


Figure 6. Annual rate of increase of wolves and reduction levels in our study and 4 other studies (Game Management Unit 20A, Gasaway et al. 1983; Game Management Unit 20E, Gasaway et al. 1992; Coast Mountains, Hayes et al. 1992; Finlayson, R. Farnell unpublished data).

annual reductions are less than 30%, supporting Keith (1983), who used different methods to come to the same conclusion. Wolf populations can apparently respond with an annual finite rate of increase of 2.6 when 80% of the wolves in a large area are removed.

Our study supports the conclusion of the National Research Council (1997) that prey populations increase when wolves are greatly reduced over a large area for at least 4 years. Similar rates of increase in the order of 1.14–1.19 were reported for moose and caribou 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). Caribou and moose recruitment in our study increased simultaneously, similar to increases in the studies mentioned above. In previous wolf reduction studies there were no attempts to estimate the contributions of reduced harvest or mild winters to prey responses (National Research Council 1997).

In all of the studies examined, mild winters prevailed during wolf reduction, bolstering ungulate responses. There is evidence that severe winters can initiate ungulate declines in Alaska (Gasaway et al. 1983, Boertje et al. 1996, Mech et al. 1998). To learn about the interaction between weather and wolf predation rates, prey responses to wolf reduction need to be studied during years of adverse weather.

MANAGEMENT IMPLICATIONS

Adaptive Management and Predator–Prey Experiments

Controlled and replicated field experiments on the scale of large-mammal systems are often impractical (Sinclair 1991). Our large-scale study was not ideal because of the following:

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. Without replication we had no interspersion, increasing the risk of bias and stochastic effects (Hurlbert 1984).
3. The treatment area was not random but chosen by public concern, increasing the risk of systematic bias.
4. Hunting of moose and caribou was also stopped, adding a second treatment effect.
5. We did not monitor predation by bears, which are important predators of moose and caribou calves in other areas (Larsen et al. 1989, Gasaway et al. 1992, Adams et al. 1995, Boertje and Gardner 2000). Therefore, we could not evaluate for compensatory predation by bears when wolves were reduced.

The problem of a nonrandom, nonreplicated treatment is shared with other wolf–prey experiments (Gasaway et al. 1983, 1992; Farnell and McDonald 1988). Outcomes of nonreplicated experiments cannot generalize to other areas and results must wait for future opportunities to repeat observations (Sinclair 1991). Nevertheless, previous experimental approaches to wolf–prey systems by Gasaway et al. (1983, 1992) have greatly increased knowledge about effects of predation on northern ungulates. These earlier studies provided the foundation for our experimental design.

The task of selecting effective controls for large-scale ecological studies such as ours can be challenging. It is often difficult to find replicate areas with sufficient pre-treatment data that have similar species composition and population dynamics, ecological processes, topography, climate, and types and levels of human activity—yet are far enough removed from the experimental area so as not to be affected by the treatment. In addition to these confounding factors the cost of monitoring multiple control populations is frequently prohibitive; other Yukon Fish and Wildlife Branch programs were reduced or eliminated to fund this study. These difficulties have undoubtedly contributed to the tendency of predator–prey studies to fall short in this area (National Research Council 1997).

There were ecological differences among our treatment and control caribou populations that confounded responses. Compared to the Wolf Lake caribou herd, the Aishihik, Ibex, and Chisana herds ranged in more arid and windy mountainous terrain

year-round where snow depths were typically light. The average home ranges of herds were similar except for the Ibex caribou herd, which was smaller (Table 3). There was more road access into the ranges of the Aishihik and Ibex caribou herds. There was no road access into the Wolf Lake herd and it was least affected by human activity.

Of our 3 moose control areas, Big Salmon most closely resembled the Aishihik area in species composition. Mayo and Ladue had lower caribou densities. Despite being more arid, wildfires were less frequent in the Aishihik area than in the 3 control areas. The Ladue and Big Salmon areas were more remote and harvest rates were lower than in Mayo and in the accessible parts of the Aishihik area. The Rose Lake sheep control area was perhaps the most ecologically similar to the treatment area. It had similar terrain, species composition, weather, snow depth and human access.

In the end, we observed moose and caribou herds that showed widely variable dynamics. This was important because it reinforces the principle of managing woodland caribou as individual herds (Yukon Department of Environment 1996) and managing moose on a population basis, rather than by prescriptions that are jurisdiction-wide.

Measuring numerical responses to any treatment does not reveal the internal dynamics of change. Differences in age distribution (Page 1989, Gasaway et al. 1992), proportion of adult cows (Van Ballenberghe 1987), physical condition (Peterson 1977, Mech et al. 1998), and calf mass at birth (Adams et al. 1995, Boertje et al. 1996) can all have strong density-independent effects on ungulate responses. Ideally, these factors should be considered as part of future adaptive management experiments.

We approached our study by treating the entire range of the Aishihik caribou herd with wolf reduction in efforts to generate the greatest effect on caribou survival. In some cases it may be possible to design smaller-scale experiments 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 in the seasonal range of an ungulate population

(Spence 1998). For example, wolf numbers were reduced only on the summer range of the Fortymile caribou herd, with increases in calf recruitment as the primary measure of treatment effect (Boertje 1999). Smaller-scale approaches require greater vigilance to 1) ensure that treatment area boundaries reflect the seasonal distribution of prey to optimize the effects of the treatment, and 2) minimize unexpected treatment effects in nearby control areas.

Controlled wolf-prey experiments will always be complicated by problems of scale and human influence (National Research Council 1997, Van Ballenberghe and Ballard 1998). Nevertheless, our knowledge of the nature of wolf-moose-caribou systems were greatly improved by the controlled wolf-prey experiments of Gasaway et al. (1983) and Gasaway et al. (1992). We join Walters and Holling (1990) and others (Sinclair 1991, Boutin 1992, National Research Council 1997) and recommend other wildlife agencies test uncertainty of management actions through adaptive experimental designs.

Wolf-Moose-Caribou Models

Making effective management decisions depends on how well our conceptual models explain the dynamics of predator-ungulate systems. Seip (1991), Boutin (1992), Messier (1994, 1995) and Valkenburg et al. (1996) presented differing models to explain the dynamics of wolf-ungulate systems. Ballard and Van Ballenberghe (1998) summarized 4 predator-moose models, and 2 models have been proposed for single-predator-woodland caribou systems (Valkenburg et al. 1996; Bergerud 1980, 1992). These 2 models have limited application in Yukon wolf-bear-moose-caribou-sheep systems because they examine responses of a single prey to predators with no consideration of interactions.

Concurrent declines of sympatric moose and caribou are well documented in various northern studies including ours (e.g., Gasaway et al. 1983, Gasaway et al. 1992, Bergerud and Elliot 1998). We propose that in the Yukon, woodland caribou declines are linked to falling moose abundance. In this model, wolves increase their predation rate on caribou after moose fall below some low-

density threshold that is probably less than 200 moose/1,000 km² (Hayes and Harestad 2000a). The initial decline of moose could result from the additive effects of high wolf predation and excessive harvest, as appears to have happened in our study area. Alternately, severe winters could independently initiate declines (Boertje et al. 1996). Maintaining high harvest rates could depress moose and woodland caribou populations even further.

The Yukon system could respond in 1 of 3 ways. If there is sufficient lag in the wolf numerical response, moose could be held at low density for a long time while wolves continue to prey on caribou. Extirpation of the caribou could eventually result, especially if harvest on caribou continues. Alternately, a small remnant caribou herd could persist, finding refuge from wolf predation by reducing its range size (Bergerud et al. 1983) and minimizing the number of wolf packs it is exposed to year-round. Moose and caribou could then increase to some higher density after wolves have naturally declined. Finally, a combination of adverse weather and wolf predation could initiate recurrent eruptions and declines in caribou numbers (Boertje et al. 1996, Valkenburg et al. 1996). In no case does it seem likely that moose would become extirpated from the system (Messier 1994, Hayes and Harestad 2000a).

Thomas (1995) proposed that where moose are common, wolf densities of more than 5–8 wolves/1,000 km² can hold woodland caribou herds at low density for long periods. These conditions seem to fit the Yukon. Yukon wolf density equaled or exceeded his threshold range in 14 of 18 wolf survey areas (A. Baer, Yukon Fish and Wildlife Branch, unpublished data), and in all parts of the Yukon woodland caribou remain at densities similar to those reported in Thomas (1995; R. Farnell Yukon Fish and Wildlife Branch unpublished data). In all wolf survey areas moose abundance was the main determinant of wolf numerical response.

Seip (1991) and Bergerud (1996) proposed a model showing that the addition of moose into a simple wolf–caribou system will result in higher wolf density (numerical response) and a subsequent increase in predation on caribou. In areas where wolves,

moose and caribou use similar habitat in summer, caribou lose the advantage of their “spacing-away” strategy to avoid predation (Seip 1991,1992). Although the models of Seip (1991) and Bergerud (1996) could apply to small isolated caribou herds elsewhere, it does not fit the Yukon system and management plans to protect vulnerable caribou herds by reducing moose numbers might cause the opposite effect. Woodland caribou herds are contiguous throughout the Yukon, and their use of space overlaps with moose year-round, except perhaps summer. As wolves continue their pattern of home range use when moose numbers decline, the attraction to preying on caribou could increase because wolf encounter rates with moose should decline. Ultimately, the fate of a caribou herd should depend on how strong a compensatory effect wolf predation will exert, and how quickly wolf numbers decline in response to lower prey biomass.

Predation by brown bears is an important factor limiting calf survival of moose and caribou. In 2 nearby study areas, brown bears killed 57–58% and wolves killed 15–27% of moose calves (Larsen et al. 1989, Gasaway et al. 1992). Three caribou calf mortality studies in Alaska showed wolves killed 22–25% and brown bears 16–20% of calves (Adams et al. 1995; Boertje and Gardner 2000; P. Valkenburg, Alaska Department of Fish and Game, unpublished data). Dale et al. (1994) provided a model to explain why wolf reductions have been successful in areas where bear predation is an important factor limiting prey. The model shows that when 2 predators have antiregulatory responses (i.e., predation rate increases as prey numbers decrease), reduction of 1 predator causes the total predation rate to shift to an inversely density-dependent function (i.e., predation rate decreases as prey increase), allowing prey to increase to higher density. We expected a moderate response in moose to wolf reduction because brown bears were common and were not treated in our study (Table 10). However, we saw strong responses in both moose and caribou populations, supporting the idea that neither bear nor wolf predation compensated for reduced wolf numbers. Boertje and Gardner (2000) did not observe compensatory predation by bears

after wolves were reduced in the Fortymile caribou range, supporting our results.

No single model explaining wolf–bear–moose–caribou systems will prevail (Thomas 1995, Ballard and Van Ballenberghe 1998) and we should not be surprised when system dynamics change over time (Pielou 1991). Although there is currently evidence for a low density single-stable-state model for moose in Yukon and Alaska (Gasaway et al. 1992, Hayes and Harestad 2000a), the 2-stable-state system has not been fully tested (National Research Council 1997), nor have the effects of wolf predation on sympatric moose and caribou populations been sufficiently studied. As a result, caution must be used when selecting a conceptual model for management purposes.

Managing Harvest

In other studies, sharp declines in caribou abundance were caused by excessive harvest rates of 7–19% (Gasaway et al. 1983) and 10% (Farnell and McDonald 1988). Harvest rates of 2% were sustainable for the Fortymile caribou herd (Gasaway et al. 1992). Male–female harvests of 2–10% had little effect on growth rates of the Delta caribou herd when environmental conditions were positive (Boertje et al. 1996). Harvests of 4–19% contributed strongly to the rapid decline in moose (Gasaway et al. 1983), but harvests of 2–6% had little influence on growth rates of moose (Gasaway et al. 1992, Boertje et al. 1996). Generally, harvest rates become unsustainable when they exceed recruitment (Gasaway et al. 1983, 1992), especially during periods of adverse winters or short growing season when twinning rates of moose and caribou calf survival rates are lowest (Boertje et al. 1996).

Annual harvest of 5–8% was an important factor causing the decline in moose and caribou before we began our study. Harvest rates greater than 5–6% for moose (Gasaway et al. 1992, Boertje et al. 1996) and 3% for caribou (Bergerud 1980) are probably unsustainable in Alaska and the Yukon where bears and wolves are at naturally regulated levels. We recommend that in the Yukon maximum harvest rates should be set conservatively at 2% for caribou and 5% for moose, unless there is evidence that populations are increasing. Harvest rates should be

set well below recruitment rates, and when adverse weather depresses recruitment for sustained periods there may not be a sustainable harvest (Boertje et al. 1996, Hayes and Harestad 2000a).

Both wolf control and harvest reduction were necessary to cause the high rate of recovery of the Aishihik caribou herd, and to a lesser extent moose. We recommend that reduction of wolves be accompanied by a substantial harvest reduction to provide the greatest benefit from wolf management actions.

Proactive Wolf Management or Recovery Plans

Subsistence use of wildlife is an important part of the culture and economy of northern communities (National Research Council 1997). The Yukon Wolf Conservation and Management Plan (Yukon Wolf Planning Team 1992) recommended that instead of using broad-scale wolf control to recover already depressed ungulate populations, wildlife managers should avoid such situations. The challenge will be to find publicly acceptable methods that are adequate to increase ungulate populations but will not imperil predator populations. Spence (1998) developed a model that suggested a reduction of wolf pack sizes on important summer range of the Aishihik herd could allow caribou to increase. A similar model is being studied in Alaska, where public trapping, live relocation, and surgical sterilization of wolf packs on the summer range of the Fortymile caribou herd has resulted in increased caribou numbers (Boertje and Gardner 2000). Other proactive methods to sustain higher moose and caribou densities through habitat enhancement could include wildfires, prescribed burning, mechanical crushing of preferred forage, and well managed forestry practices (Klein 1982, Schwartz and Franzmann 1989; Collins 1996).

Fertility Control of Wolves

In the future, broad-scale lethal wolf control programs will be rare in the Yukon, as they have become in Alaska and other parts of Canada. Our study was the first to show that wolf predation could be reduced by using a combination of lethal and nonlethal techniques. Surgical sterilization of wolves proved to be more publicly acceptable than

killing wolves. Surgical procedures were safe and did not change wolf social behavior (Spence 1998). Our study showed fertility control was effective in reducing the rate of increase of wolves over a large area. In 1990, a wide range of stakeholders endorsed the continued use of fertility control and wolf trapping in the Aishihik area to reduce predation losses as part of long-term management (Alsek Renewable Resources Council 2000). We recommend that fertility control be considered whenever there is a management plan to hold wolf densities below natural levels for sustained periods.

Public Involvement in Management Decisions

Public sentiments about the roles of natural predators and the ethics of predator control are diverse. Conflicts are intense among people with different interests (National Research Council 1997). Our experiment was the first wolf control program to be developed using ethical and scientific guidelines formulated by a citizens' team. Our study followed the intent of the Yukon Wolf Conservation and Management Plan (Yukon Wolf Planning Team 1992). We used harvest reduction and wolf control to increase moose and caribou numbers without losing broad public and political support. Although wolf control is unacceptable to some segments of society (Hummel 1995), the Yukon government stayed committed to the study mainly due to strong support from people in communities, First Nation governments, and wildlife management advisory groups. In contrast, public opposition prompted the governor of Alaska to cancel 3 wolf control programs because the programs did not satisfy the public majority interpretation of the Alaskan Wolf Conservation and Management Policy (National Research Council 1997). We recommend that management plans that include predator reductions be guided by careful planning that integrates biological information with the diversity of social values held by stakeholder groups and local communities. In this way, socially directed management actions can be sustained by broader public support.

Balancing Public Interest

Even with conservative harvest rates and optimal habitat, densities of 45–417 moose/

1,000 km² (Gasaway et al. 1992) and 30–242 caribou/1,000 km² (Bergerud 1980; Valkenburg et al. 1996) will likely be the norm in most areas of the Yukon and Alaska where predation remains unmanaged. In accessible areas, predation and subsistence demands of local people for wild food can combine to exceed the sustainable supply of ungulates. Most Yukon residents agree that the consumptive interests of people should be balanced with the needs of predators (Yukon Wolf Planning Team 1992). In the Yukon there are ways to balance these conflicting values. Management options could include using the Yukon Protected Areas Strategy (Yukon Department of Environment 1998) to reserve areas where large-mammal systems would be managed for natural change and predators would not be manipulated to benefit people's use of ungulates. In other areas, some reduction of wolf predation using socially acceptable methods could be considered to allow people a fair share of wildlife without compromising the long-term viability of predator populations.

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