Perhaps Aldo Leopold (Flader and Callicott 1991:345–346) provided the best guidance we may hope for with these words:

"I have no illusions about the speed or accuracy with which an ecological conscience can become functional. It has required 19 centuries to define decent man-to-man conduct and the process is only half done; it may take as long to evolve a code of decency for man-to-land conduct. In such matters we should not worry too much about anything except the direction in which we travel."

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INCREASES IN MOOSE, CARIBOU, AND WOLVES FOLLOWING WOLF CONTROL IN ALASKA

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Abstract: Short-term studies in our study area and southeast Yukon have previously documented substantial increases in moose (*Alces alces*) and caribou (*Rangifer tarandus*) following wolf (*Canis lupus*) control. To provide long-term information, we present a 20-year history beginning autumn 1975 when precontrol wolf density was 14 wolves/1,000 km². Private harvest and agency control kept the late-winter wolf density 55–80% ($\bar{x}$ = 69%) below the precontrol density during each of the next 7 years. Wolf numbers subsequently recovered in ≤4 years in most of the study area and increased further to between 15 and 16 wolves/1,000 km² during a period of deep snowfall winters. The post-hunt moose population increased rapidly from 183 to 481 moose/1,000 km² during the 7 years of wolf control (finite rate of increase, λ_r = 1.15) and increased more slowly during the subsequent 12 years (λ_r = 1.05) reaching a density of 1,020 moose/1,000 km² by 1994. The Delta caribou herd increased rapidly during wolf control (λ_r = 1.16), more slowly during the subsequent 7 years (λ_r = 1.06), then declined for 4 years (λ_r = 0.78) from a peak density of 890 caribou/1,000 km². This decline coincided with declines in 2 adjacent, low-density herds (240–370 caribou/1,000 km²). These caribou declines probably resulted from the synergistic effects of adverse weather and associated increases in wolf numbers. Reduced caribou natality and calf weights were associated with adverse weather. Wolf control was reauthorized to halt the Delta herd's decline in 1993. Similar subarctic, noncoastal systems without effective wolf control have supported densities of 45–417 moose/1,000 km² ($\bar{x}$ = 148, n = 20), 100–500 caribou/1,000 km², and 2–18 wolves/1,000 km² ($\bar{x}$ = 9, n = 15) in recent decades. In our 20-year history, 7 initial winters of wolf control and 14 initial years of favorable weather apparently resulted in 19 years of growth in moose, 14 years of growth in caribou populations, and a high average autumn wolf density after control ended (12 wolves/1,000 km²). Benefits to humans included enjoyment of more wolves, moose, and caribou and harvests of several thousand additional moose and caribou than predicted if wolf control had not occurred. We conclude from historical data that controlling wolf populations, in combination with favorable weather, can enhance long-term abundance of wolves and their primary prey, and benefits to humans can be substantial.

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Key words: Alaska, *Alces alces, Canis lupus*, caribou, harvest, moose, predator-prey relationships, *Rangifer tarandus*, weather, wolf, wolf control.

Wolf predation can and often does reduce the abundance of primary ungulate prey (Bergerud 1980, Gasaway et al. 1983, 1992; Bergerud and Snider 1988, Van Ballenberghe and Ballard 1994, Adams et al. 1995). Several Alaska Department of Fish and Game (ADF&G) wolf control programs have been initiated in Alaska where humans desired elevated moose or caribou populations; however, most programs were terminated after 1 or 2 winters for a variety of political and scientific reasons (Gasaway et al. 1983:44–45, 1992; Harbo and Dean 1983, Ballard et al. 1987). Since 1960, only 2 agency programs, 1 in our study area and 1 in southeast Yukon, have strongly reduced precontrol wolf numbers for several winters with the objective of increasing moose and caribou numbers (Gasaway et al. 1983, Farnell and MacDonald 1988, Larsen and Ward 1995). In both studies, substantial short-term increases in moose and caribou were documented, but long-term case histories are lacking. Wolf control continues to be the focus of political and scientific controversies (Stephenson et al. 1996), in part because of misinformation (Mech 1995) and in part because of the need for information about the long-term effects of temporary control on wolves and the need to evaluate the long-term benefits of wolf control to humans. Also, concerns exist about whether prey will reach high numbers and starve subsequent to wolf control.

Gasaway et al. (1983) summarized data from our study area (Game Manage. Unit 20A) during the 1950s, 1960s, and 1970s, including data from the first 4 of 7 consecutive winters of wolf control by ADF&G. Conclusions were that: (1) wolf predation was causing declines in the moose and caribou populations for several years before wolf control, (2) wolf control may be required periodically where management objectives include maintaining high moose and caribou densities, (3) knowledge of prey : wolf ratios can assist in the initial interpretation of whether wolf predation is an important factor sustaining a moose or caribou decline or maintaining a low ungulate density, and (4) in retrospect, errors were made in managing the moose, caribou, and wolf populations for several years before the mid-1970s' wolf control program.

Moose and caribou populations in the study area were at high densities in the 1960s following a federal predator control program in the 1950s (Hemming 1971, Bishop and Rausch 1974, Gasaway et al. 1983). Deep snow in the mid-1960s and early 1970s and overharvest in the early 1970s "led to a grave management situation" (Gasaway et al. 1983). Overharvest occurred because the effect of increased wolf predation on ungulates was underestimated and because severe winters reduced ungulates. Adult female ungulates were harvested in excess of yearling recruitment. This overharvest was allowed, in part, because of the belief that poor range condition was the major factor causing low yearling recruitment. "Biologists patiently awaited a compensatory rebound in yearling recruitment from improved range that would offset harvest. However, it was a futile vigil—calf moose and caribou became increasingly scarce through 1975. Mortality from severe winters, hunting, and wolf predation were largely additive" (Gasaway et al. 1983:46). As a result, moose and caribou populations declined from the mid-1960s through 1975.

In this report, we examine the long-term effects of wolf control on the abundance of wolves and their primary prey, moose and caribou. We define wolf "control" as the human act of reducing the annual autumn wolf population below levels that the prey population could otherwise support. Alaskans have "controlled" wolves indirectly by altering habitat (e.g., urbanization and homesteading) and directly by harvesting wolves or through ADF&G and (pre-1959) federal control programs. In our study area, wolves have been controlled only by ADF&G and (pre-1959) federal control programs, but we reference other study areas where control was by private interests.

We present a 20-year history of wolves, moose, caribou, and weather beginning summer 1975, immediately before a 7-year ADF&G wolf control program. We end with winter 1994–95 data collected following the beginning of a second ADF&G wolf control program. Our objectives were to (1) document 20-year population trends of wolves, moose, and caribou during and after the 1970s' wolf control, (2) compare wolf and prey densities and harvests in this area with similar noncoastal Alaska-Yukon study areas where predators and prey are unexploited or lightly harvested, (3) discuss factors other than wolf predation that may affect moose and caribou populations in the study area, (4) evaluate conclusions of Gasaway et al. (1983), and (5) present a conceptual model for wolf-moose-caribou relationships in this system.

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STUDY AREA

Our study area (17,000 km^2) in Interior Alaska south of Fairbanks (Fig. 1) was described at

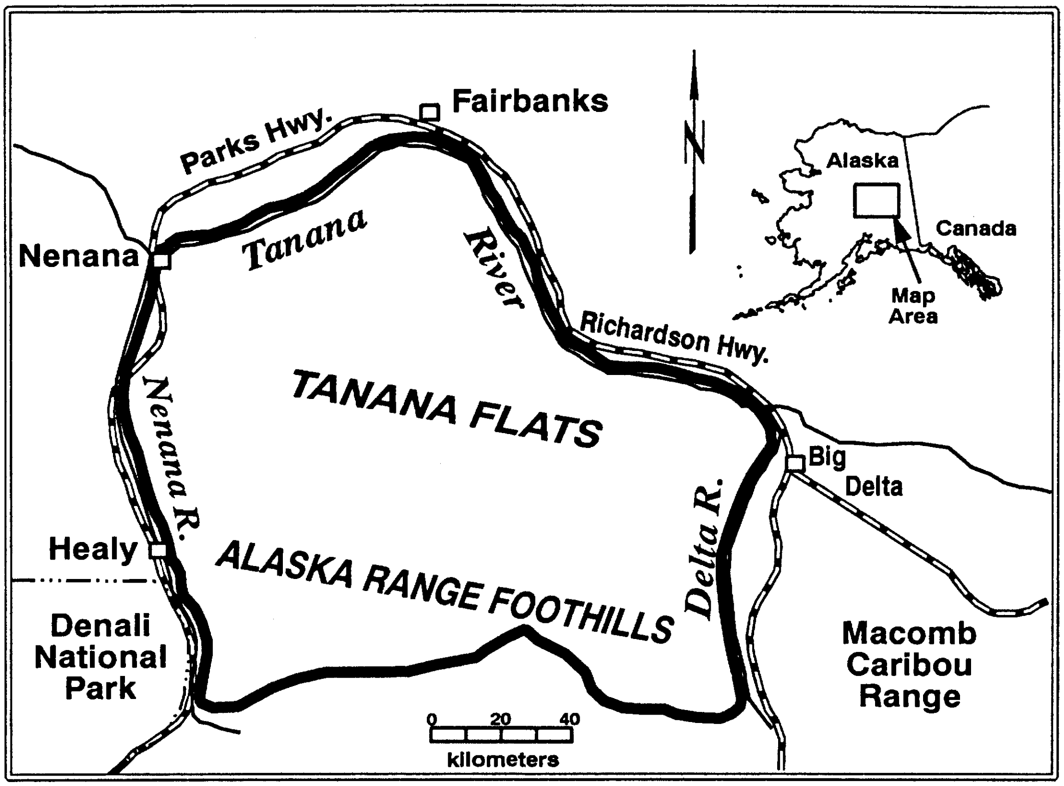

Fig. 1. Study area in Interior Alaska where wolves were controlled during 7 winters, 1975–76 through 1981–82. Wolves were controlled in a 10,000 km² portion of the 17,000 km² study area during winters 1993–94 and 1994–95.

length by Gasaway et al. (1983). The southern portion of the area (9,700 km²) included the northern foothills and mountains of the Alaska Range. Elevations ranged from 110 to 4,000 m; however, ungulates and their predators seldom ranged above 2,000 m. The northern portion of the area (7,300 km²) consisted of poorly drained lowlands with elevations from 130 to 300 m (Tanana Flats). Less than 5% of the study area was accessible by road, but seasonal trails provided access to small-scale mining operations in the foothills. The only significant human settlements were located along the study area boundaries. The area was centered around 64°10′ latitude and 147°45′ longitude.

Wolves, black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) were found in the study area. Their prey included moose, caribou, Dall's sheep (*Ovis dalli*), beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), and ground squirrels (*Spermophilus undulatus*). We restricted our discussion primarily to wolves, moose, and caribou. The effect of bear predation in the study area was low compared with wolf predation (Gasaway et al. 1983:30). Dall's sheep were minor prey of wolves in the study area (Gasaway et al. 1983, Valkenburg 1992). Snowshoe hares have been relatively scarce since the early 1970s, except for moderate levels in the early to mid-1980s. Ground squirrels were found only in the Alaska Range.

METHODS

Estimating Wolf Abundance and Harvest

We estimated wolf abundance and distribution by counting wolves and wolf tracks in snow during aerial surveys (Gasaway et al. 1983, 1992). Experienced pilots and observers flew wolf surveys on clear days usually during late winter (Feb–Apr), 1–5 days after fresh snowfall. To assist with surveys, we radiocollared 1 or 2 wolves in each of several wolf packs during winters 1987–88, 1988–89, and 1991–92. A pack contained 2 or more wolves. In winters 1987–88 and 1988–89, 41–44% of the packs contained radiocollared wolves, and in winter 1991–92, 21% contained radiocollared wolves. Techniques for radiocollaring and radiotracking followed Gasaway et al. (1992). We solicited additional information from local trappers, hunters, and pilots each year. Estimates of wolf numbers from winters 1975–76 through 1978–79 came from Gasaway et al. (1983:11) using similar methods.

We estimated autumn population size as the sum of wolves and wolf tracks counted during surveys plus wolves harvested before surveys. We increased this sum by 10% to account for single wolves not associated with packs (Mech 1973). Late winter population size was the autumn population size minus the total number of wolves known killed. We assumed that immigration offset emigration and natural mortality in this exploited population. Wolf density was based on 17,000 km², the total area <2,000 m in elevation used by packs mostly or entirely within the study area. Some pack movements extended slightly beyond the study area border, but within about 17,000 km².

Regulations allowed wolf hunting during 10 August–30 April, and wolf trapping during 1 November–31 March. Mandatory reporting forms provided information on wolf harvest locations and numbers of wolves in the pack before harvest. Private traplines occurred throughout most of the study area, and trapping and snaring were by far the most common methods used to harvest wolves in the study area. Regulations allowed private hunters to use fixed-wing aircraft for wolf hunting during all but 3 winters. Private hunters using aircraft were required to land before shooting, except during 3 winters, 1980–81 through 1982–83. Department aerial gunners flew in helicopters and fixed-wing aircraft during the 1970s' control program. Entire packs were shot when possible. During the 1993 and 1994 control programs, ADF&G used primarily snares to kill wolves; traps and ground shooting were used to a limited extent.

Estimating Moose Abundance, Rate of Increase, Harvest, and Twinning Frequency

During November 1978, 1984, 1988, 1991, and 1994 we estimated moose densities and the respective approximate 90% CIs in the study area using stratified random sampling (Gasaway et al. 1986). A sightability correction factor for undercounting bias was estimated by resurveying portions of sample units at a higher search intensity, except in 1994. We surveyed the entire study area in 1978 and 1988; moose habitat totalled 13,044 km² in 1988. Moose habitat included the entire study area, exclusive of large lakes, below the upper limits of vegetation characteristically used by moose. In 1984, we derived a total population estimate by surveying the foothills portion of the study area (Fig. 1) and adding results from a 1982 similar survey of the Tanana Flats. We allowed for a 6% annual rate of increase between 1982 and 1984, because this was the mean rate of increase between 1982 and 1988 surveys on the Tanana Flats. In 1991, we surveyed 7,843 km² in a portion of the flats and foothills and extrapolated to 13,044 km², based on growth rates observed between 1988 and 1991 in the 7,843 km². Survey methods in 1994 were similar to those in 1991, except we sampled from 10,131 km² and assumed a conservative sightability correction factor (1.05). To test for significant differences between any 2 estimates of population size, $\hat{\mu}_i$ and $\hat{\mu}_j$, we tested the H_0: $\hat{\mu}_i = \hat{\mu}_j$ using

$$Z = \frac{\hat{\mu}_i - \hat{\mu}_j}{\sqrt{\text{var}(\hat{\mu}_i) + \text{var}(\hat{\mu}_j)}}$$

We rejected the H_0 at $\alpha = 0.05$ if $|Z|$ was >1.96.

We flew in 3 to 5 trend areas during the remaining years to estimate composition of the moose population during late October–early December. We chose widely scattered trend areas where relatively high densities of moose could be reliably observed. These trend areas varied in size from 160 to 230 km² and were flown at an intensity of 1.5–2.3 min/km². Composition of moose observed in these areas was similar to composition in more extensive stratified random surveys (ADF&G, unpubl. data).

We derived population size for years when population surveys were not flown by calculating the annual finite rate of increase (λ_c; Bergerud and Elliot 1986) based on annual estimates of harvest, a 7% mean annual adult natural mortality (Gasaway et al. 1983:Table 13), and annual recruitment, R, from aerial surveys:

$$\lambda_c = \frac{0.93(1 - M_h)}{1 - R}$$

where

$$M_h = \frac{\text{estimated number of moose harvested}}{\text{estimated number of moose prehunting}}$$

and

$$R = \frac{\text{number of yearling bulls} \times 2}{\text{number of moose older than calves}}$$

To derive the 1979 population size, for example, we multiplied the population size measured in 1978 by the 1979 λ_c. This method predicted the 1984, 1988, 1991, and 1994 population estimates well within their approximate 90% CIs. To derive population size for the 3 years before 1978 we divided by the appropriate λ_c. We assumed an average post-wolf control recruitment in 1989, when no surveys were flown.

To derive rates of increase between 2 estimates of population size, we calculated a constant annual finite rate of increase (λ):

$$\lambda = e^r$$

where

$r = (\ln P_2 - \ln P_1)/(t)$

P_1= first estimate of population size

P_2= second estimate of population size

t = time interval between estimates in years.

To derive annual finite rates of increase using 3 or more estimates of population size (λ_r), we regressed the ln of population estimates over the survey years to estimate the slope (m) of the line, and calculated $\lambda_r = e^m$.

To estimate the total number of moose harvested, we multiplied the reported moose harvest by 1.15 to account for unreported moose and mortally wounded moose that were lost (Gasaway et al. 1983). The reported moose harvest was the number of moose reported killed by hunters after a reminder letter was sent to hunters who failed to return mandatory mail-in harvest reports. About 69–70% of harvest reports were received after reminder letters each year.

We estimated the frequency of twin calves among cows with newborn calves in the Tanana Flats during 20–28 May using fixed-wing aircraft (Piper Supercub or Bellanca Scout). These surveys were flown during 9 of the 20 study years. During 1989, we followed the Supercub in a helicopter and verified that the Supercub surveys were accurate. A 2-sample Chi-square test with continuity corrections was used to test for differences between twinning rates in 1993 versus the remaining years when the prior growing seasons were much longer (Snedecor and Cochran 1980:125).

Estimating Caribou Abundance and Harvest

Initial studies in the 1970s described 2 caribou herds in this study area, but by 1986 separate herds were not distinguishable. We refer to caribou in the study area as the Delta caribou herd. We used aerial-photo, total-search, and radiosearch techniques to annually estimate minimum numbers of Delta caribou during mid-June to mid-July 1979–93 (Valkenburg et al. 1985). We used similar census techniques in the adjacent Macomb caribou herd (Fig. 1). Gasaway et al. (1983) interpolated census estimates of the Delta herd for 1975–78 using censuses in 1973 and 1979 and annual trend data collected during postcalving and autumn composition surveys. Experience has shown that we cannot necessarily detect annual trends in caribou numbers by comparing 2 consecutive censuses; the degree of underestimation varies and is strongest when adverse weather interrupts the census and caribou are poorly aggregated. To help evaluate annual trends, we examined calf recruitment during September or October, natural mortality rates of radiocollared caribou, and harvest.

Caribou occupied 12,000 km^2 in the study area during the late 1980s, based on monthly flights during which we located 39–48 radiocollared caribou. This 12,000 km^2 includes virtually all portions of the study area used by caribou for >1 year during the 20-year study. Davis et al. (1991) depicted annual caribou distribution in the study area during 1979–89.

Procedures for estimating total and female caribou harvest varied depending on the type of harvest reporting system. We applied a correction factor to general season hunts (1983–91), because harvest was reported by mandatory mail-in report cards without the benefit of reminder letters. Correction factors were derived during 1986–91 by interviewing successful hunters in the field. To avoid biased reporting, hunters were not told the purpose of these interviews. The interviews and subsequent mail-in harvest reports were treated as a mark-recapture sample to estimate total harvest. To derive total harvest from general season hunts in 1983–85, we multiplied reported harvest by 1.74, the average correction factor calculated during 1986 (1.78) and 1987 (1.71). We considered harvest reports collected from permit hunts (1980–91) to be accurate estimates of total harvest because reminder letters were sent to permittees and 97% of reports were returned.

Estimating Caribou Natality Rates and Body Weights

We estimated natality rates of radiocollared females ≥36 months old by documenting the presence or absence of a calf, hard antlers, and/or a distended udder (Whitten et al. 1992). Radiocollared females were observed at least 3 times each year during 15–31 May 1984–93 from a Bellanca Scout. The flights were augmented in some years by ground and/or helicopter surveys of several hundred caribou within a few days of the median calving date.

We weighed an average of 11 10-month-old female caribou annually during 1979–93 to monitor variation in mean body weight among cohorts. Calves were darted from a Robinson R-22 helicopter using immobilizing doses of 1 mg carfentanil citrate (Wildnil®, Wildlife Pharmaceuticals, Fort Collins, Colo.) and 65 mg xylazine hydrochloride (AnaSed®, Lloyd Laboratories, Shenandoah, Ia.), and antagonist doses of 100 mg naltrexone hydrochloride (Trexonil®, Wildlife Pharmaceuticals) and 10 mg yohimbine hydrochloride (Antagonil®, Wildlife Pharmaceuticals).

Estimating Weather Parameters

We used snow and temperature data from Fairbanks because data from alternative sites were incomplete; rainfall data (15 Jun–15 Aug) came from Healy (Natl. Weather Serv., Fig. 1). To compare snowfall among winters, we plotted daily snow depth, connected the points, and measured the area under the curve (Gasaway et al. 1983). The number of snow-free days was the number of days during which no measurable snow was on the ground; this was used as an index to the length of the growing season. We also compared the sum of mean monthly temperatures during May–August and during the oestrid fly season (1 Jul–31 Aug; Boertje 1985*a*).

RESULTS

Wolf Abundance and Harvest

Wolves numbered about 239 in the study area during autumn 1975, immediately before wolf control. Public harvest and ADF&G control efforts kept the late winter wolf numbers 70–80% below precontrol numbers during each of the next 5 years and 55–60% below precontrol numbers during the subsequent 2 years (Table 1, Fig. 2). Following these 7 winters, no complete surveys were flown for 3 winters. By autumn 1985, the wolf population had increased to near precontrol densities in most of the study area except along the Tanana River (Fig. 1). Wolf numbers appeared nearly stable (n = 184–195) during autumn 1985–88. By autumn 1991, 9 winters after control ended, wolf numbers (n = 267) exceeded the precontrol population size and wolf density had increased along the Tanana River. A second wolf control program during winters 1993–94 and 1994–95 reduced the precontrol wolf population (n = 262) by 62 and 56% (Table 1).

Public wolf harvests continued throughout the study area during the 11 winters without wolf control, but harvests were too low to significantly reduce the annual autumn population size. These harvests ranged from 23–67 wolves (12–25% of the respective autumn populations) during winters when surveys were flown; harvests of 14–55 wolves during the remaining winters were probably <25% of the respective autumn populations (Table 1). In other studies, winter harvest rates of ≥28% have reduced annual autumn wolf populations (Peterson et al. 1984, Fuller 1989, Gasaway et al. 1992).

Moose Abundance and Harvest

Estimates of the prehunting moose population ranged from 2,500 in 1975, immediately before wolf control, to 13,800 in 1994, a 5.6-fold increase in 19 years (Table 2). These estimates suggest λ_r was 1.15 (90% CI = 1.145–1.161) during the 7 years of wolf control (1975–82) and 1.05 (90% CI = 1.047–1.058) during the 12 years after wolf control (1982–94). Between the 1978 and 1984 surveys of population size, λ was 1.14, and between the 1984 and 1994 surveys, λ_r was 1.06 (90% CI = 1.048–1.066, Fig. 2). The moose population apparently increased between early winter 1988 and 1994 surveys (P = 0.01, λ_r = 1.06, 90% CI = 1.055–1.069; Fig. 2) despite reduced yearling : adult female ratios during early winters 1990–93 (Table 3).

Harvest was restricted in a variety of ways to assure that hunting was a minor factor affecting moose population growth and to retain a minimum male : female ratio of 30:100. Harvest rates of male moose ranged from 2 to 6% ($\bar{x}$ = 4%) of the prehunting population during this 20-

Table 1. Estimates of wolf population size and harvest in a 17,000-km² area <2,000 m in elevation, encompassing all wolf pack territories completely or mostly in the study area during 1975–95, Interior Alaska.

	Wolf population				Wolf harvest				
	Autumn		Late winter		No. wolves killed			% reduction of precontrol population by late winter ($\bar{x}$)	% of autumn population killed
Winter period	No. wolves	Density (wolves/1,000 km²)	No. wolves	No. survey hours	ADF&G	Public	Total		
Wolf control began Feb 1976									
1975–76	239	14.1	60–80	324	67	78	145	67–75 (71)[a]	61
1976–77	125	7.4	70–80	325	27	26	53	67–71 (69)[a]	42
1977–78	100	5.9	55–65	111	39	4	43	73–77 (75)[a]	43
1978–79	80	4.7	45–55	101	18	12	30	77–81 (79)[a]	38
1979–80	64–84	4.4	50–70	60	3	11	14	71–79 (75)[a]	19
1980–81	100–125	6.6	87–111	40	0	13	13	54–64 (59)[a]	12
1981–82	130–157	8.4	91–118	60	20	19	39	51–62 (56)[a]	27
Wolf control ended Apr 1982									
1982–83					0	14	14		
1983–84					0	24	24		
1984–85					0	23	23		
1985–86	195	11.5	171	50	0	24	24	N.A.[b]	12
1986–87					0	37	37		
1987–88	191	11.2	155	100	0	36	36	N.A.	19
1988–89	184	10.8	152	215[c]	0	32	32	N.A.	17
Adverse weather began									
1989–90					0	31	31		
1990–91					0	55	55		
1991–92	267	15.7	200	125	0	67	67	N.A.	25
1992–93					0	55	55	N.A.	
Wolf control began Oct 1993									
1993–94	262	15.4	100	400	98	64	162	62[d]	62
1994–95	180	10.6	114	275	36	30	66	56[d]	37

[a] Calculated as 100(239 − late winter no.)/239.
[b] N.A. = not applicable.
[c] Value includes 150 hr radiotracking 11 packs.
[d] Calculated as 100(262 − late winter no.)/262.

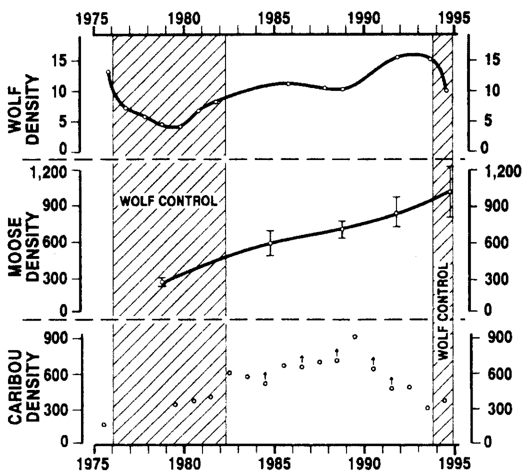

Fig. 2. Estimated and relative densities of wolves, moose, and caribou per 1,000 km² in the study area, 1975–94. The approximate 90% CIs are shown for moose population estimates; the 1984 and 1991 estimates were significantly different ($P = 0.02$) as were the 1988 and 1994 estimates ($P = 0.01$). Wolf, moose, and caribou densities were based on areas of 17,000 km², 13,044 km², and 12,000 km² (see Methods).

year history (Table 2). Regulations prohibited harvest of female moose. Hunting was largely restricted to 1–10 September during wolf control and 1–20 September or 1–30 September after wolf control. Hunting restrictions based on antler size were initiated in a trail-accessible portion of the study area during the last 5 autumns to prevent the male:female ratio from declining below 30:100.

Caribou Abundance and Harvest

The Delta caribou herd numbered about 2,200 in summer 1975 before wolf control (Gasaway et al. 1983). Numbers peaked at 10,690 in 1989 and declined to 3,660 in 1993 (Table 2). The finite rate of increase (λ_r) was 1.12 (90% CI = 1.100–1.135) during the first 14 years (1975–89) of this study; λ_r was 1.16 (90% CI = 1.137–1.191) during wolf control (1975–82) and 1.06 (90% CI = 1.025–1.086) after wolf control (Table 2, Fig. 2). Subsequently, the herd declined during 4

Table 2. Moose and caribou population size and harvest in the study area during 1975–94, Interior Alaska.

	Moose				Caribou			
Summer or autumn	Prehunting[a] population	No. per wolf posthunting	Estimated no. M harvested	% population harvested	Summer population	Estimated harvest[b]	Estimated no. F harvested	% population harvested
1975	2,500	10	72	3	2,200	0	0	0
Wolf control began Feb 1976								
1976	2,800	21	71	3	2,700	0	0	0
1977	3,300	32	58	2	3,100	0	0	0
1978	3,600	44	92	3	3,500	0	0	0
1979	4,400	58	150	3	4,191	0	0	0
1980	5,100	44	238	5	4,478	104	0	2
1981	5,800	38	319	6	4,962	268	73	5
Wolf control ended Apr 1982								
1982	6,600		335	5	7,335	274	77	4
1983	7,900		459	6	6,969	1,302	234	19
1984	8,100		451	6	>6,260[c]	607	191	<10
1985	8,500	41	416	5	8,083	614	117	8
1986	9,200		483	5	>7,804[c]	841	183	<11
1987	9,400	47	347	4	8,380	644	38	8
1988	9,700	51	404	4	>8,338[c]	555	22	<7
1989	10,300		429	4	10,690	681	18	6
Adverse weather began								
1990	10,500		426	4	>7,886[c]	552	83	<7
1991	11,500	41	439	4	>5,755[c]	456	22	<8
1992	11,600		283	2	5,877	0	0	0
1993	12,300	47	444	4	3,661	0	0	0
1994	13,800	78	450	3	4,341	0	0	0

[a] Estimated by adding no. moose harvested to Nov population estimates and rounding to nearest 100 moose. Nov population estimates were flown during 1978, 1984, 1988, 1991, and 1994 and annual finite rates of increase (λ_c) were calculated to derive other population estimates (see Methods).

[b] Some caribou were harvested during the winter following the indicated autumn.

[c] Conservative estimates based on incomplete photocensuses.

years (1989–93, λ_r = 0.78, 90% CI = 0.550–1.089); this decline coincided with declines in 2 adjacent low-density herds and 4 years of adverse weather beginning with winter 1989–90 and summer 1990. The herd appeared to increase during the last year of this study following renewed wolf control during winter 1993–94.

Harvest was restricted in a variety of ways to ensure that hunting was a minor factor affecting herd demographics, except during 4 years (1983–86) when the objective was to stabilize herd growth. A secondary objective was to maintain a male : female ratio ≥30:100. No caribou were harvested during the autumn preceding wolf control or during the 4 subsequent autumns (Table 2). Initial harvests during 1980–82 consisted of only 2–5% of the herd, and the female harvest averaged 1% of the herd. During the subsequent 4 autumns (1983–86), harvest averaged 11% of the herd and the female harvest averaged 2% of the herd. In 1986 the goal of stabilizing herd size was reconsidered, and more conservative harvests were enacted thereafter. During 1987–91, harvests averaged 6% of the herd and the female harvest averaged <1% of the herd. During the herd's 4 years of decline (1990–93), harvest was reduced slightly during the first and second years and eliminated the last 2 years and in 1994 (Table 2).

Adverse Weather and Changes in Wolf, Moose, and Caribou Populations

The snow-depth index was significantly greater during the 4 winters 1989–90 through 1992–93 compared with the prior 14 winters (P = 0.006, n = 18, Mann-Whitney test, Fig. 3). During 1992, the number of snow-free days totaled only 126, the lowest compared with a range of 160–199 ($\bar{x}$ = 176, SE = 2.3) in the remaining 19 years. Thus the 1992 growing season was the shortest by ≥34 days. During 1990–92 summer precipitation was significantly lower (P = 0.035, n = 14, Table 3), but no significant difference occurred in summer (May-Aug) temperatures (P = 0.53, n = 17) or temperatures during the oestrid fly season (P = 0.90, n = 17). However,

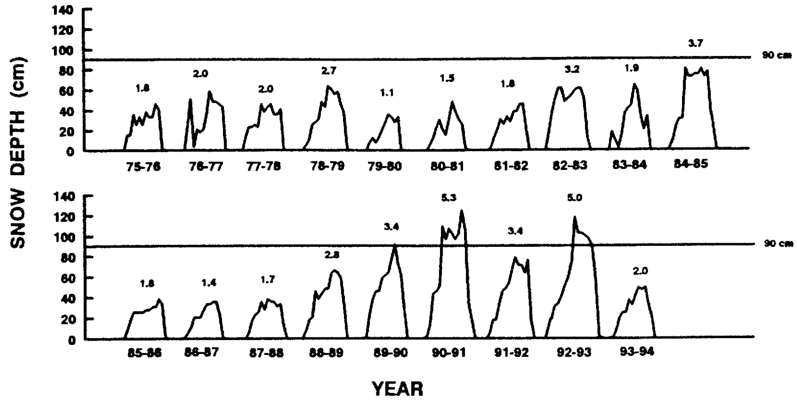

Fig. 3. Accumulated snow depth on the ground during winters 1975–76 through 1993–94 at Fairbanks, Alaska. Curves were generated from daily snow depth measurements. Snow depth index (shown above each curve) was calculated by dividing the area under each curve by the area of lowest snowfall, 1969–70 from Gasaway et al. (1983). Snow depth of 90 cm, indicated by the solid line, was considered the critical depth for calf moose survival (Coady 1974, Gasaway et al. 1992).

summer 1990 was the warmest and one of the driest during this study (Table 3).

Estimated wolf numbers increased 45% from 184 in autumn 1988 to 267 in autumn 1991, possibly as a result of deep snow increasing vulnerability of prey, e.g., calf moose (Peterson et al. 1984) and caribou (Ballard et al. 1987:36, Adams et al. 1996, Mech et al. 1996). Wolf numbers almost doubled during these same years in adjacent Denali National Park (Adams et al. 1996).

During the 4 autumns of 1990–93, which followed deep-snowfall winters (Fig. 3), significantly reduced yearling moose recruitment occurred ($P = 0.005$, $n = 17$, Mann-Whitney test) compared with the previous 13 autumns (Table 3). Snow reached critical depths for calf moose (Coady 1974) during winters 1989–90, 1990–91, and 1992–93 (Fig. 3). Although overwinter calf survival (i.e., yearling recruitment) declined, calf survival to autumn was not reduced compared with the earlier 13 years ($P = 0.91$, $n = 17$). The only evidence of significantly reduced production ($\chi^2 = 4.233$, 1 df, $P = 0.04$) was the absence of twins in late May 1993, which followed the short growing season of 1992.

Caribou calf recruitment to autumn declined significantly ($P = 0.003$, $n = 18$, Mann-Whitney test) during the 4 years of adverse weather, compared with the previous 14 autumns (Table 3). Declines in the Delta herd recruitment resulted in part from significantly reduced ($P = 0.022$, $n = 10$) natality rates during 1990, 1991, and 1993 compared with other study years (Table 3). Natality in 1992 was the highest recorded, yet recruitment to autumn was similar to values in 1990, 1991, and 1993. The lowest caribou natality rate reported for Alaska caribou (30%, Table 3) occurred following the short growing season of 1992. Calf weights in early April also declined significantly during 1990–93 compared with 1979–89; $\bar{x} = 53.8$ kg versus 59.8 kg ($P = 0.014$). Significantly reduced caribou calf recruitment was associated with declines in the Delta and adjacent Denali and Macomb herds during 1990–93 (Table 4).

DISCUSSION

Moose

Gasaway et al. (1983) documented that wolf predation was substantially limiting moose numbers in the study area immediately before the 1970s' wolf-control program. Evidence included increased moose numbers and calf and yearling recruitment during wolf control (Tables 2 and 3). Moose calf recruitment did not increase significantly in adjacent areas without wolf control, except where moose migration from the study area was evident (Gasaway et al. 1983: 22).

Wolf control and favorable weather apparently had long-lasting positive effects, because moose attained much higher densities than in areas without predator control. Gasaway et al. (1992) concluded that moose densities will fluctuate within a range of 45–417 moose/1,000 km^2 ($\bar{x} = 148$ moose/1,000 km^2, $n = 20$) in large areas (>2,000 km^2) of Alaska and the Yukon where moose are major prey of wolves and bears,

Table 3. Moose and caribou recruitment, moose twinning rates, rainfall, and summer temperature for the study area, 1974–94, Interior Alaska.

	Moose				Caribou			Weather	
Yr of Sep–Nov surveys	5-month-old calves : 100 ad F[a]	17-month-old yrl : 100 ad F[a,b]	n[c]	% births that were twins in preceding May[d]	4-month-old calves : 100 F older than calves	n[c]	Natality rate of radio-collared F ≥ 36 months old[e]	Total rainfall in preceding 15 Jun–15 Aug (cm)	Sum of $\bar{x}$ monthly temperature in preceding May–Aug (C)
1974	19	5	413		2	868			
1975	15	10	353	10 (31)	<13[f]	839			
Wolf control began Feb 1976									
1976	51	32	143	13 (23)	45	572			55.8
1977	49	44	274		42	756		6.5	58.8
1978	61	50	213		39	324			55.2
1979	57	52	122		65	177		15.2	56.1
1980	62	47	195		49	585		14.2	52.1
1981	46	39	300		41	776		13.9	51.4
Wolf control ended Apr 1982									
1982	38	42	673		37	860		22.5	53.5
1983	40	43	121		46	665		13.9	56.3
1984	34	23	1,370		36	613	90 (31)		53.0
1985	36	26	317		36	629	93 (41)	12.4	53.5
1986	35	27	236		29	1,141	83 (40)	12.1	56.1
1987	37	20	876	10 (50)	31	1,026	89 (28)	12.2	59.4
1988	50	28	1,741	13 (60)	35	1,802	88 (32)	14.6	62.2
1989				16 (51)	36	1,218	83 (30)	17.0	58.5
Adverse weather began									
1990	52	17	422	22 (33)	17	1,567	72 (39)	9.9	63.4
1991	37	16	1,411	21 (24)	8	1,245	71 (35)	9.4	56.7
1992	39	15	193		11	918	96 (28)	10.3	52.8
1993	42	21	936	0 (30)	4	1,113	30[g] (23)	12.2	60.7
Adverse weather ended, wolf control began Oct 1993									
1994	52	25	677	18 (51)	23	1,433	67 (30)	10.0	59.0

[a] Ad F are F ≥ 28 months old. To estimate no. ad F, we subtracted no. yrl M from total no. F older than calves.
[b] No. yrl M were doubled to estimate total yrl.
[c] n equals the total no. ad F moose or F caribou older than calves that were classified.
[d] No. F observed with neonates is in parentheses.
[e] No. radiocollared F ≥ 36 months old in parentheses.
[f] Survey was flown 11–12 Jun 1975; <13 calves: 100 F would have been present during Sep or Oct.
[g] Low natality rate in 1993 was confirmed by helicopter survey; 41% natality rate was observed among 604 F older than calves.

and where moose, wolves, and bears are not controlled by harvest. In contrast, posthunting moose density in our study area increased from 183 to 1,020 moose/1,000 km^2 by 1994. This 1994 density is 6.9 times higher than the average moose density in areas with uncontrolled wolf and bear populations.

The Alaska-Yukon conceptual model, where moose are held at low levels well below food-limited densities by wolf and bear predation, is supported by data on the effects of wolf control (Gasaway et al. 1992, Larsen and Ward 1995), by data on abundant supplies of high quality moose browse in adjacent Denali National Park (Risenhoover 1987), and by data on the absence of significant ungulate diseases in noncoastal Alaska (Zarnke 1991, 1993; Gasaway et al. 1992: 26). Support is also evident in early accounts from Native Alaskans (Coady 1980), archeological data (Yesner 1989), and reviews on predation (Bergerud and Snider 1988, Gasaway et al. 1992, Messier 1994, Van Ballenberghe and Ballard 1994).

Increased density of moose allowed for increased harvest. Estimated annual harvest of moose ranged from 22 to 37 male moose/1,000 km^2 ($\bar{x}$ = 32) during 1982–94 in the study area contrasted with 0–18 male moose/1,000 km^2 ($\bar{x}$ = 5) in stable or increasing moose populations with near-natural predator levels (Gasaway et al. 1992:Table 11).

Gasaway et al. (1983:30) concluded that factors other than reduced wolf predation could not adequately explain the rapid increase in moose numbers that began with wolf control. They inferred, however, that low snow accumulation maximized moose survival and the effects of wolf control. We concur. Favorable snow

Table 4. Calves:100 female caribou older than calves in the Delta herd and adjacent Denali and Macomb herds during September–November 1981–93, Interior Alaska.

	With wolf control 1976–82		Without wolf control			
	Delta		Denali		Macomb	
Yr	Calves: 100 F	n[a]	Calves: 100 F	n	Calves: 100 F	n
1981	41	776	—[b]	—	33	215
1982	37	860	—	—	26	148
1983	46	665	—	—	24	152
1984	36	613	41	375	40	210
1985	36	629	28	654	31	295
1986	29	1,141	38	547	—	—
1987	31	1,026	37	631	—	—
1988	35	1,802	33	678	32	377
1989	36	1,218	30	830	34	370
Deep snowfall winters and dry summers began[c]						
1990	17	1,567	17	777	17	373
1991	8	1,245	7	1,067	9	392
1992	11	918	16	643	14	328
1993	4	1,113	6	849	18	268

[a] n equals the no. F caribou older than calves that were classified.
[b] Dashes indicate no data were collected.
[c] Significant reductions in calf recruitment to autumn occurred during 1990–93 in the Delta ($P = 0.007$, $n = 13$, Mann-Whitney test), Denali ($P = 0.014$, $n = 10$), and Macomb herds ($P = 0.011$, $n = 11$) compared with data from 1981–89.

conditions existed from winter 1975–76 until winter 1989–90, when critical snow depth was reached for calf moose (Coady 1974, Fig. 3) and a significant decline in yearling recruitment to autumn was first observed (Table 3).

We concur with Gasaway et al.'s (1983:30) inference that bear predation was a minor factor limiting moose in the 1970s, because moose recruitment increased simultaneous to wolf control without a reduction in bears. Grizzly bears are uncommon on the Tanana Flats (43% of the study area), where moose from throughout the study area tend to congregate during calving and summer (Gasaway et al. 1983:Fig. 4). Reynolds (1993) reported densities of 16.7 to 22.8 grizzly bears/1,000 km² in a 3,160-km² portion of the foothills during 1981–92, but bear predation was not studied.

We agree with Caughley and Gunn (1993) that herbivore nutritional status can change independently of herbivore numbers or density in systems with high annual variations in weather. We surmise that the absence of moose twins and the low caribou natality in 1993 are examples of the effects of nutritional stress. We suggest that the relatively short growing season during 1992 contributed to the absence of moose twins and to the low caribou natality rates in 1993 (Table 3). Schwartz and Hundertmark (1993) and Gasaway et al. (1992:24) concluded that twinning rates of <5% indicate nutritional stress in moose populations. Twinning rates in late May in the study area ranged from 10 to 22% during survey years since 1960 except 1993 ($n = 16$). These rates did not correlate with moose density ($r = {}^-0.18$, $P = 0.50$, $n = 16$). The absence of twins in 1993 was not a major factor limiting the moose population, as evidenced by moderately high calf survival to autumn 1993 (42 calves/100 ad F, Table 3).

Caribou

Gasaway et al. (1983) documented that wolf predation was exerting substantial control over the Delta caribou herd immediately before wolf control. Evidence included increased Delta caribou calf recruitment during the initial years of wolf control and the lack of similar strong increases in the adjacent Denali and Macomb herds.

Wolf control and favorable weather apparently had long-lasting positive effects on Delta caribou. We documented the increase in density of Delta caribou from 183 to 891 caribou/1,000 km² during the 14 years following the initiation of wolf control. In contrast, densities in the adjacent Denali and Macomb herds remained between 100 and 370 caribou/1,000 km² throughout the study period (Adams et al. 1996). Bergerud (1980:Fig. 10) reviewed the population dynamics and densities of 19 caribou herds and indicated that uncontrolled predation commonly sets the density at ≤400 caribou/1,000 km², which is consistent with the densities observed in the Denali and Macomb herds. Coastal caribou ranges with few alternate prey have recently supported higher caribou herd densities up to 1,500 caribou/1,000 km² (Valkenburg et al. 1996).

Bergerud (1980) proposed that maximum caribou density imposed by food supplies or dispersal would be well above 800 caribou/1,000 km². Data collected during high Delta herd densities support Bergerud's hypothesis. Range studies indicated that lichen biomass and annual production were not limiting growth of the Delta caribou herd during the late 1980s (Fleischman 1990). However, snow may have strongly limited caribou access to lichens during some winters. The slow growth rates of lichens, and caribou selection for lichens, make lichens susceptible to overgrazing. Radiotelemetry studies using several hundred different caribou indicate that dispersal was a negligible factor limiting growth of the Delta, Denali, or Macomb herds during 1975–94 (Davis and Valkenburg 1991, Valkenburg et al. 1996).

We hypothesize that adverse weather and wolf predation acted synergistically to cause the Delta herd's decline during 1990–93, similar to findings on the adjacent Denali caribou herd (Adams et al. 1996, Mech et al. 1996). Although we consider adverse weather as the initiating factor that led to the decline, increased wolf predation was a necessary contributor to reduced abundance. Wolf predation was the most common known cause of death among collared caribou (Valkenburg et al. 1996). Adverse weather was characterized by deep snow, a short growing season, low rainfall, and an unusually warm and dry summer. Deep snow can affect caribou by decreasing mobility, increasing energy expenditure, and decreasing forage intake and selection (Boertje 1985*a*,*b*, 1990). More days with snow can increase energy expenditure of caribou and decrease forage intake, selection, and quality (Boertje 1985*b*, 1990). Unusually warm, dry summers can adversely affect caribou by increasing oestrid fly harassment and reducing diet quality (Boertje 1984, 1985*a*,*b*, 1990; Chapin et al. 1992; Russell et al. 1993:143). Increased oestrid fly harassment increases caribou energy expenditure and decreases forage intake (Boertje 1985*a*).

Nutritional stress in the Delta and Denali herds was indicated by both reduced caribou production and reduced calf weights during years of adverse weather. Increased vulnerability to predation was inferred from significant declines in calf weights. Adams et al. (1996) reported decreased pregnancy rates and caribou birth weights during 1990 and 1991 in the Denali herd compared with prior years. Wolf predation was the most important cause of death among radiocollared Denali caribou calves during 1987–91, but the overall neonatal mortality rate was inversely correlated with average birth weight among years ($R^2 = 0.96$).

We do not infer from these indices of nutritional stress that the capacities of the Delta, Denali, and Macomb ranges to support caribou were compromised by the 1989 densities. Failure of caribou to increase rapidly with favorable weather and wolf control would be convincing support for this hypothesis. Belief in this range-limitation hypothesis in the early 1970s led to overharvests while biologists futilely awaited compensatory rebounds in yearling recruitment from improved range. Range limitation per se is unlikely to occur in the Delta herd while densities remain at or below current management objectives of 500–700 caribou/1,000 km² (Bergerud 1980, Fleischman 1990).

The simultaneous declines in all 3 herds suggest a conceptual model for caribou where adverse weather can cause decreased production and increased vulnerability to predation over a wide range of densities (Valkenburg et al. 1996). In this conceptual model, uncontrolled wolf predation can exacerbate declines in caribou numbers. This model is supported by Ballard et al. (1987:36), Mech et al. (1996), and Adams et al. (1996) who observed increased wolf predation on caribou when snow was deep and herds were at low densities (<400 caribou/1,000 km²).

We examined calf recruitment in the Delta, Denali, and Macomb herds to test the hypothesis that the decline of the Delta herd during 1990–93 was a result of its high density in 1989. All 3 herds exhibited significant reductions in calf recruitment ($P \leq 0.014$) during 1990–93 compared with prior years (Table 4). In all 3 cases, lowered calf recruitment was sufficient to cause significant declines in the herds. The 1989–90 peak densities varied from 890 caribou/1,000 km² in the Delta herd to 240/1,000 km² in the Macomb herd and 370/1,000 km² in the Denali herd (Adams et al. 1996). We conclude that a decline in the Delta herd would likely have occurred during 1990–93 even if density had been lower.

Wolves

Wolf density has been repeatedly shown to correlate positively with prey density or prey biomass where wolves are lightly harvested (Keith 1983, Fuller 1989, Gasaway et al. 1992). Thus, we expected relatively high wolf densities in the study area following increases in moose and caribou. During the decade following the control program, autumn wolf density increased to between 15 and 16 wolves/1,000 km², well above the average value (9 wolves/1,000 km²) reported for 15 noncoastal Alaska and Yukon study sites where wolves and bears were not controlled and moose and usually caribou were prey (Gasaway et al. 1992:Table 11). The density of 15–16 wolves/1,000 km² is the third highest among 26 Alaska-Yukon moose or moose-caribou systems with and without wolf control reported to date ($\bar{x} = 8$ wolves/1,000 km², range

= 1–20, Peterson et al. 1984; Gasaway et al. 1992; Mech et al. 1996).

Evidence suggests that wolf numbers in adjacent Denali National Park, and possibly in the study area, increased partly in response to increased prey vulnerability rather than simply increased prey numbers. For example, Mech et al. (1996) found that during the second and third of 4 consecutive deep-snowfall winters, wolves greatly increased the proportion of caribou cows and calves in their diet compared with data from the late 1980s. Mech et al. (1996) and Adams et al. (1996) indicate that deep snowfall made caribou more vulnerable. They concluded that these newly-vulnerable prey allowed for increased wolf numbers. We hypothesize that the significantly drier summers of 1990–92, the hot and dry summer of 1990, and the short growing season of 1992 may have been contributing factors in the Delta, Denali, and Macomb herds' increased vulnerability to predation. Increased vulnerability of moose calves and caribou to wolf predation has previously been related only to deep snowfall (Peterson et al. 1984, Ballard et al. 1987:36, Adams et al. 1996, Mech et al. 1996).

MANAGEMENT IMPLICATIONS

Since the mid-1970s this study area has proven to be the most intensively managed in Alaska in terms of ADF&G costs to survey wolves and ungulates and to reduce predation for promoting increased ungulates. Hunters annually numbered about 3,000 in this area during the late 1980s. Local residents broadly support elevated numbers and harvest of moose and caribou in this area. This support stems primarily from a strong local tradition of hunting, awareness of the enhanced value of land with abundant wildlife, a cumulative increase in restricted hunting seasons elsewhere in Interior Alaska, and awareness of the area's high densities and harvest of ungulates during the 1960s following federal predator control in the 1950s.

Wolf control in the 1970s and favorable weather in the late 1970s and 1980s apparently allowed for 19 years of growth in moose and 14 years of growth in caribou populations. Data are insufficient to allow us to predict the outcome of a similar control program given several years of adverse weather.

Wildlife abundance and use in the 1980s and 1990s were substantially greater as a direct result of the 1970s' wolf control. Elevated prey densities supported elevated wolf densities on average ($\bar{x}$ = 12 wolves/1,000 km^2 after wolf control, $\bar{x}$ = 10 overall, Table 1) compared with similar systems without wolf control ($\bar{x}$ = 9, Gasaway et al. 1992:Table 11). High wolf densities in the study area have been a clear benefit to wolf conservation and to recreational use and enjoyment of wolves, wolf sign, and wolf sounds.

Other long-term benefits attributed to wolf control include additional harvests of 1,700 to 5,600 ($\bar{x}$ = 4,500) moose from 1979 to 1994 (16 yr) and additional harvests of 3,500 to 6,100 ($\bar{x}$ = 4,800) caribou from 1981 to 1991 (11 yr). These estimates are the difference between actual harvests (Table 2) and derived 5% harvests of minimum, maximum, and mean densities of moose and caribou in similar systems without wolf control (Gasaway et al. 1992:Table 11, Bergerud 1980:Fig. 10), assuming 13,044 km^2 of moose habitat and 12,000 km^2 of caribou habitat. Projected future benefits of wolf control in our study area include harvests of >800 moose annually as the moose population reaches its upper management objective and harvests of female moose are permitted.

The degree of wolf control during the 1970s was less than initially planned, yet results exceeded expectations in terms of allowing for growth of moose and caribou populations. Initial objectives were to reduce the wolf population until an autumn moose:wolf ratio of 100:1 was achieved. Instead, moose:wolf ratios never exceeded 58:1 during the control program (Table 2). During the 12 autumns following the control program, moose:wolf ratios ranged from about 40:1 to 51:1. Gasaway et al. (1983) accurately predicted that with ratios >30:1 in the study area, wolf predation would not limit growth of the moose population, assuming favorable weather and no excessive harvest.

Gasaway et al. (1983) also accurately predicted that managers would have difficulty in maintaining high caribou densities for extended periods without reducing predation in the study area. Ten years after this prediction, wolf control was again initiated in the study area because of rapidly declining caribou numbers. Gasaway et al.'s (1983) prediction that moose would also eventually decline from adverse weather and predation was not supported by current results.

Gasaway et al. (1983) noted the significance of not waiting for prey to reach extremely low numbers before initiating wolf control. Wolf control in the 1970s was timely because control halted ongoing declines of moose and caribou. Had wolf control occurred after ungulates declined further, harvest and ungulate numbers during the 1980s and 1990s would have been lower. Population declines can be more rapid than recovery because there are no biological constraints on declines.

Unlike excessive harvest during moose and caribou declines in the early 1970s, harvest was conservative during the 1990s. Managers in the 1990s recognized the importance of restricting harvest during periods of adverse weather and high wolf predation. In contrast, managers in the early 1970s continued high harvests "while awaiting a compensatory rebound in yearling recruitment from improved range that would offset harvest" (Gasaway et al. 1983). These past managers largely ignored the effects of predation because of prevailing, untested philosophies about predation having minor effects on prey.

Our current conceptual model of the relationship among wolves, moose, and caribou in the study area is derived from summaries of subarctic, noncoastal Alaska and Yukon wolf-bear-moose-caribou systems (Bergerud 1980, Davis and Valkenburg 1991, Gasaway et al. 1992, Valkenburg et al. 1996). In the absence of periodic or prolonged wolf control, autumn wolf densities have fluctuated in these systems largely between 6 and 12 wolves/1,000 km^2 with extremes of 2–18 wolves/1,000 km^2 (n = 15 study sites, Gasaway et al. 1992:36–38). Management objectives in the study area in 1993 were to reduce wolf densities to 6 wolves/1,000 km^2 by late winter. Wolves recovered to 10.6 wolves/1,000 km^2 by autumn 1994 (Table 1), which is higher than the average autumn densities of 9 wolves/1,000 km^2 in systems without wolf control. Autumn densities of >8 wolves/1,000 km^2 are predicted in the study area during the current wolf control program because of the high moose numbers and corresponding high reproductive capacity of wolves (Boertje and Stephenson 1992). Autumn densities >12 wolves/1,000 km^2 are expected within 1 or 2 years after control terminates because moose are abundant here compared with systems without wolf control (Gasaway et al. 1992). Wolf numbers up to 15–20 wolves/1,000 km^2 are positively correlated with prey abundance in these systems (Gasaway et al. 1992:Fig. 14).

These subarctic noncoastal systems without effective wolf control have supported densities of 45–417 moose/1,000 km^2 and 100–500 caribou/1,000 km^2 since the mid-1970s (Bergerud 1980:Fig. 10, Gasaway et al. 1992, Valkenburg et al. 1996). Current management objectives of 900–1,200 moose/1,000 km^2 and 500–700 caribou/1,000 km^2 in the study area appear achievable assuming periodic wolf control is implemented following years of adverse weather. The upper limits of carrying capacity for moose and caribou with favorable weather have been elusive in this study area given the intermittent adverse weather and exacerbating effects of predation during the mid-1960s, early 1970s, and early 1990s. Indeed, given the wide variation in snow conditions and effects of predation, the concept of a long-term carrying capacity may be inappropriate in this study area. We do know that some Alaska habitats, with reduced wolf numbers and favorable weather, can support densities of 1,000–1,200 moose/1,000 km^2 and 700–1,500 caribou/1,000 km^2 (Davis and Valkenburg 1991, Gasaway et al. 1992:Table 12, Valkenburg et al. 1996).

Assuming moose and caribou numbers decline in this study area, management proposals for elevating numbers might include: (1) improving habitat for moose, (2) restricting harvest to low proportions (≤6%) of the populations and allowing harvest of only male moose and caribou, or (3) reducing wolf numbers through lethal or nonlethal means (e.g., moving and sterilizing wolves, Boertje et al. 1996). Wildlife managers in this study area have no authority to manipulate habitat, but they have encouraged land management agencies to allow the infrequent wildfires to burn suitable areas. Prescribed burns are planned, but burning, without reducing predation, has only resulted in moose densities up to 417 moose/1,000 km^2 in large areas (>2,000 km^2, Boertje et al. 1996). Restricting harvest without reducing predators cannot be expected to accomplish objectives for elevated moose and caribou numbers, because harvests constitute a low proportion of the annual kill of ungulates by predators (5% in other Alaska studies of moose and caribou, Gasaway et al. 1992, Boertje et al. 1995).

Reducing wolf numbers depends largely on cultural, social, economic, and political values as well as information and education and these issues are beyond the scope of this paper (Harbo and Dean 1983, Mech 1995, Stephenson et al. 1996). Ecological and biological issues of wolf control are more easily addressed. For example, obtaining meat from sustainable local wildlife populations is ecologically sound compared with obtaining meat from nonlocal livestock industries dependent on agriculture (Orr 1992). We have shown that periodic wolf control programs can be consistent with the principles of wildlife management and conservation. We conclude that, if periodic wolf control is sanctioned in this area and favorable weather occurs, the long-term densities and harvests of wolves, moose, and caribou will be relatively high compared with similar noncoastal systems without wolf control.

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