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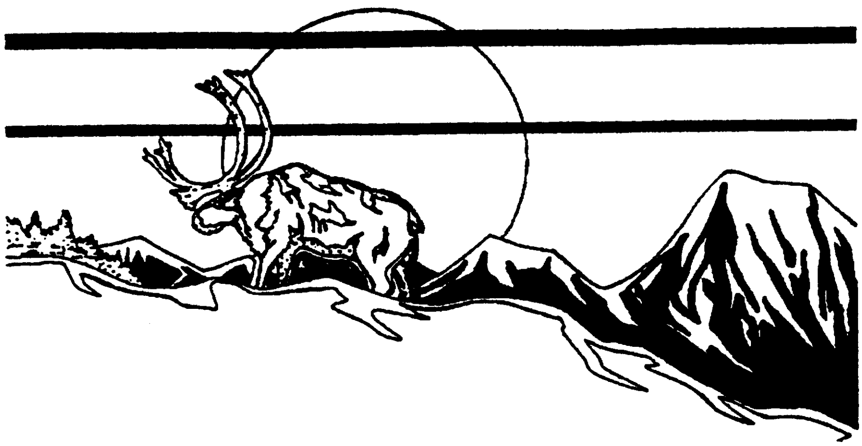

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Population decline in the Delta caribou herd with reference to other Alaskan herds

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Abstract: After growing continuously for nearly 15 years, the Delta caribou herd began to decline in 1989. Most other Interior Alaskan herds also began declining. In the Delta herd, and in other herds, the declines were caused primarily by high summer mortality of calves and increased natural mortality of adult females. Other minor causes included increased winter mortality of calves, and reduced parturition rates of 3-year-old and older females. The decline in the Delta herd also coincided with increased wolf (*Canis lupus*) numbers, winters with deeper than normal snow, and warm summers. Mean body weight of annual samples of 10-month-old female calves was consistently low during the decline. Except in some of the smallest Interior Alaskan herds, we conclude that evidence for population regulation in Alaskan caribou is weak, and that herds are likely to fluctuate within a wide range of densities due to complex interactions of predation and weather. Unless wolf numbers are influenced by man, the size of a caribou herd in a given year is likely to be largely a function of its size during the previous population low and the number of years of favorable weather in the interim.

Key words: rainfall, *Rangifer*, snow, temperature, weather, wolves

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Introduction

Caribou herds in Alaska and elsewhere have fluctuated in size over time, and the factors involved in these fluctuations have been widely debated (Leopold & Darling, 1953; Skoog, 1968; Van Ballenberghe, 1985; Messier *et al.*, 1988; Bergerud & Ballard, 1989; Seip, 1991; Eberhardt & Pitcher, 1992; Bergerud, 1993). Several caribou herds in Alaska were intensively studied during late 1970s and 1980s when herds were generally increasing (Davis *et al.*, 1991; Cameron *et al.*, 1993; Adams *et al.*, 1994; Whitten, 1994). This paper reports results of a continuing study of limiting and regulating factors in the Delta caribou herd, during the period of population decline from 1979 to 1993 and compares more limited data from other Alaskan herds.

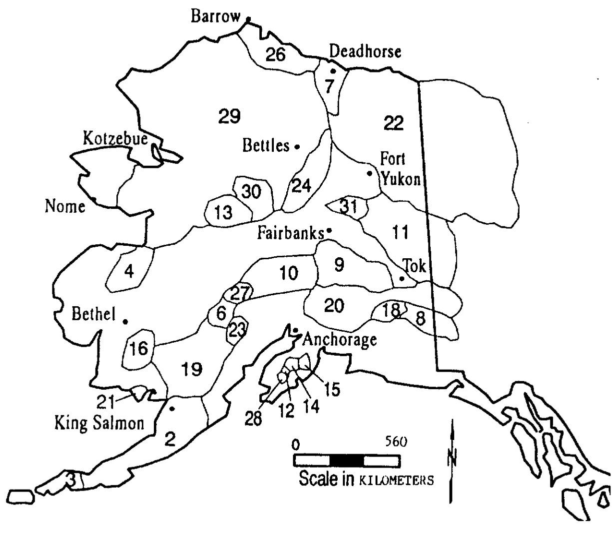

Fig. 1. Distribution of 31 caribou herds in Alaska.

Study area and population

The Delta caribou herd is one of 31 herds composing a total population of about 880,000 caribou in Alaska (Table 1, ADF&G files). About 750,000 of these caribou occur in the 3 largest herds: Western Arctic (29), Porcupine (22), and Mulchatna (19) (Numbers correspond to herd numbers in Fig. 1 and Table 1). Most of the other herds occur in the mountainous areas of Interior Alaska and range in size from a few hundred to about 40,000 caribou. The Delta herd (9) occupies an area of about

Table 1. Estimated size and crude density of Alaskan caribou herds.

Herd no.[a]	Herd name	1993 population estimate	Total range size (km^2)	Crude density caribou/km^2	Population trend since 1989
1	Adak (western Aleutians)[b]	750	376	2.0	up
2	Ak. Peninsula (north)	18,000	33,500	0.5	down
3	Ak. Peninsula (south)	2,500	4,900	0.5	stable
4	Andreafsky	<50	unknown	—	unknown
5	Beaver Mountains	649	6,000	0.1	unknown
6	Big River	750	11,500	<0.1	unknown
7	Central Arctic	23,444[c]	54,000	0.4	stable
8	Chisana	850	9,000	<0.1	down
9	Delta	3,661	12,500	0.5	down
10	Denali	1,890	10,000	0.2	down
11	Fortymile	21,884[c]	50,000	0.4	down
12	Fox River	75	500	0.2	up
13	Galena Mountain	275	10,500	<0.1	up
14	Kenai Lowlands	100	1,500	<0.1	stable
15	Kenai Mountains	300	1,000	0.3	stable
16	Kilbuck Mountains	2,500	10,000	0.3	up
17	Macomb	500	3,500	0.1	down
18	Mentasta	880	25,000	<0.1	down
19	Mulchatna	110,000	103,000	1.1	up
20	Nelchina	40,361	75,000	0.5	stable
21	Nushugak Peninsula	750	2,000	0.4	up
22	Porcupine	165,000	335,000	0.5	stable
23	Rainy Pass	500-1,000	9,000	0.1	unknown
24	Ray Mountains	700	17,000	<0.1	up
25	Sunshine Mountains	800	8,000	0.1	unknown
26	Teshekpuk	27,630	24,000	0.9	up
27	Tonzona	800	6,500	0.1	down
28	Killey River	100	500	0.2	up
29	Western Arctic	450,000	350,000	1.5	up
30	Wolf Mountain	650	8,500	<0.1	stable
31	White Mountains	1,000	8,000	0.1	up
	TOTAL (approximate)	880,000			

[a] Numbers shown on fig. 1.
[b] Not shown on fig. 1.
[c] 1992 estimate.
[d] Stablilized through harvest.

12,000 km^2 of the northcentral Alaska Range. Its calving, summer, and autumn ranges are alpine tundra and its winter range is alpine tundra, muskeg, lowland black spruce (*Picea mariana*) and white spruce (*Picea qlauca*) forest. Adjacent herds include the Macomb herd (17) to the east, Denali herd (10) to the west, White Mountains herd (31) to the north, and Nelchina herd (20) to the south.

Until the early 1970s the Delta herd was considered one of many rather insignificant groups of caribou in Alaska. It was relatively small in size, ha an inaccessible range, and management and researc efforts were concentrated on the larger, road-acces sible Fortymile and Nelchina herds. However, afte the decline of the Fortymile and Nelchina herds i the early 1970s, the Delta herd received more atten tion from hunters, and consequently, from th Alaska Department of Fish and Game (ADF&G Efforts to determine population identity and recru itment had begun in the late 1960s, but the first sys tematic census was not done until 1973. In 1979 ADF&G identified the need for a long-term population dynamics study of an Interior caribou herd, and began intensive research on the Delta herd. Initial studies were to determine the causes of low calf production and/or survival prevalent in the herd from 1971 to 1974. However, after a wolf control program primarily to benefit moose (*Alces alces*), the Delta herd increased rapidly (Gasaway *et al.*, 1983), and data collected through 1989 was representative of a growing population.

From 1979 to 1989 the Delta herd grew continuously from 4,191 to 10,690 (Davis *et al.*, 1991). From 1979 to 1982 the herd grew rapidly (λ = 1.20), because harvest was light, adult female mortality was low, and natality and calf survival were high (Davis & Valkenburg, 1985). From 1982 to 1985 the herd grew slowly from 7,335 to 8,083 caribou (λ = 1.03) because it was limited primarily by harvest, but also by increased adult mortality from wolf predation, and decreased calf survival (Davis *et al.*, 1987). From 1985 to 1989 the herd grew at a moderate rate (λ = 1.07) primarily because of high natural mortality of adult females and high calf mortality (Davis *et al.*, 1991). Since 1989 the Delta herd has been in a rapid decline. In this paper we review recent data on the Delta herd and other Interior herds in the light of current models of population regulation and limitation in caribou. We consider the influence of the following factors in caribou population declines: general density dependence, nutrition, predation, weather, harvest, immigration, and habitat loss.

Methods

We annually estimated population size, recruitment of calves to autumn, and age-specific natality rates of females in the Delta herd. In most years we also collected data on weights of 10-month-old female calves, and mortality rates and causes of death of radiocollared females older than 10 months. Starting in 1991 we also began weighing and collaring 4-month-old females. Movements and distribution of radiocollared caribou in the Delta herd and surrounding herds were monitored to detect immigration or emigration.

Population censuses (total counts) were conducted during mid June to mid July each year and followed techniques described by Davis *et al.* (1979) and Valkenburg *et al.* (1985). We estimated calf recruitment to September/October and April with helicopter surveys. Allocation of sampling effort was based on the distribution of radiocollared females. Natality rates of radiocollared females were estimated by looking for distended udders, hard antlers, or calves at heel from a Piper Super Cub or Bellanca Scout aircraft during the calving period (15 May 1 Jun) (Bergerud, 1964; Davis *et al.*, 1991). Weights

Table 2. Harvest, adult natural mortality, natality and recruitment in the Delta caribou herd, 1976-1993.

Year	Estimated harvest M	Estimated harvest F	Mortality[a] of females >1 year % dying (n)	Natality[a] rate of females >2 years % parturient (n)	Sept.-Oct. calf:cow (n)	April calf:cow (n)
1976	0	0	–	–	45 (258/572)	–
1977	0	0	–	–	42 (319/756)	–
1978	0	0	–	–	39 (126/324)	–
1979	0	0	0 (11)	–	65 (115/177)	–
1980	104	0	0 (29)	–	49 (288/585)	–
1981	268	73	0 (39)	77 (13)	41 (319/776)	–
1982	274	77	7 (47)	70 (10)	37 (318/860)	29 (205/708)
1983	1,302	234	4 (55)	77 (22)	46 (307/665)	49 (194/396)
1984	507	191	4 (50)	90 (31)	36 (222/613)	51 (256/499)
1985	614	117	22 (48)	93 (41)	36 (232/629)	44 (302/694)
1986	841	183	10 (39)	83 (40)	29 (329/1141)	–
1987	644	38	10 (43)	89 (28)	31 (320/1026)	29 (285/976)
1988	555	22	15 (46)	88 (32)	35 (631/1802)	21 (161/774)
1989	681	18	11 (48)	83 (30)	36 (432/1218)	16 (84/651)
1990	552	83	15 (40)	72 (39)	17 (265/1567)	9 (97/1082)
1991	456	22	23 (40)	71 (35)	8 (102/1245)	–
1992	0	0	20 (30)	96 (28)	11 (99/918)	–
1993	0	9	47	30 (23)	4 (46/1113)	–

[a] Data from radiocollared females.

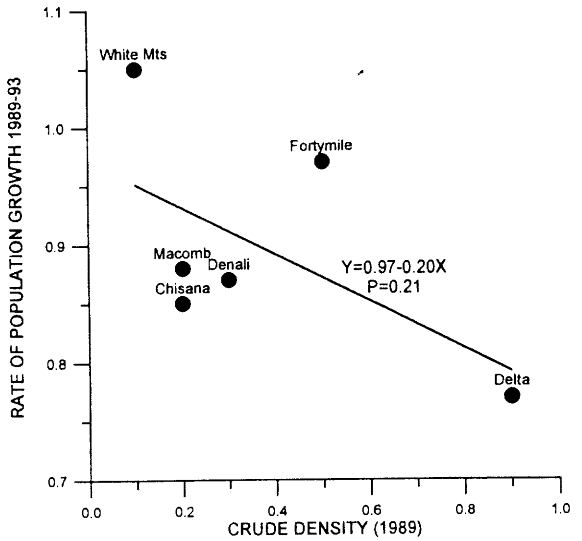

Fig. 2. Linear regression of crude caribou density versus annual average population growth rate (λ).

of 4- and 10-month-old female calves were sampled by immobilizing 9-15 animals from a helicopter in October or April, respectively. Mortality rates of female caribou were estimated with radiocollared individuals. When a mortality was detected, we used a helicopter or ground transportation to investigate the cause of death.

Because weather data were not available within the range of the Delta herd, we used a method of spatial interpolation (universal block kriging; Cressie, 1991:155) to calculate 3 weather variables (snow depth on 1 Mar and 1 Apr, mean Jun, Jul and Aug temperature, and total rainfall during 15 Jun-15 Aug) for the range of the Delta herd using surrounding climate and snow stations (National Oceanic and Atmospheric Administration, Climatological Data--Alaska; U.S. Dept. Agric., Soil Conservation Service--Alaska Snow Surveys). These weather variables were plotted and compared with data on caribou parturition (natality) rates and September/October calf:cow ratios.

Results and discussion

Immediate causes of the decline in the Delta herd

The proximate or immediate causes of decline of the Delta herd from 1989 to 1993 are clear. In order of importance they were: 1) high natural mortality of calves from birth to late September during 1990-1993, 2) high natural mortality of females older than calves primarily from wolf predation, 3) high mortality of radiocollared calves from September/October to April during 1991-1993, and 4) relatively low natality rates of adult females during 1990, 1991, and 1993 (Table 2).

Density-dependent resource limitation

Evidence for density-dependent resource limitation in the Delta and other Interior Alaskan herds was ambiguous. Although there was a weak relationship between density and population growth rate between 1989 and 1993 (Fig. 2). Some low density herds (e.g., Denali and Mentasta) declined, while others that had as high or even higher densities than the Delta herd did not decline (Table 3). However, the greatest decline occurred in the Delta herd which also had the highest density of caribou.

Table 3. Recruitment (fall calf:100 cow ratio) in 7 Interior Alaska caribou herds from 1980 to 1993.

	Herd calf:100 cow ratio in fall						
Year	Chisana	Denali	Fortymile	Macomb	Mentasta	Nelchina	White Mtns.
1980	23[a]		61[b]	13	42	42	–
1981	–	–	31	33	40	43	–
1982	21	–	27	26	39	54	–
1983	–	–	33	24	28	27	31
1984	–	41	–	40	29	34	–
1985	–	28	36	31	46	46	31
1986	33	38	28	–	–	42	–
1987	28	37	37	–	12	51	–
1988	31	33	30	32	18	48	33
1989	15[a]	30	24	34	15	39	36
1990	11	17	29	17	–	33	–
1991	1	7	16	9	2	45	13
1992	0	16	30	14	6	40	23
1993	2	6	28	18	4	24	22

[a] Fixed wing count only.
[b] Count probably not representative of herd.

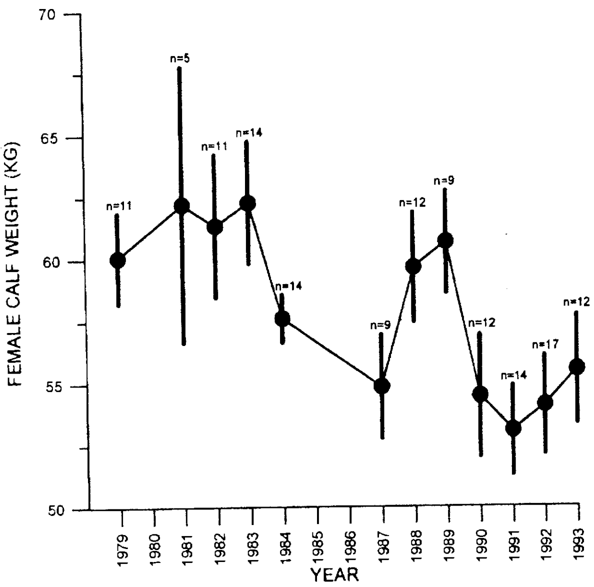

Fig. 3. Mean weight and standard error bars of samples of female calves weighed in April 1979-1993.

Nutrition as a limiting factor

Nutrition in the Delta herd apparently was poorer from 1990 to 1993 than in most prior years. However, it is not clear how decreased nutrition may have contributed to reduced population performance. Body weights of 10-month-old Delta calves have generally been lower since 1989 (Fig. 3), and the parturition rate of females was significantly lower in 1990 and 1991 than from 1984 through 1989 (χ^2 = 9.99, $P < 0.01$) (Table 2). In 1993 natality was very low. Since 1979 body weight of 10-month-old calves (which presumably reflects overall body condition in the Delta herd) has been a reasonably good predictor of calf survival to autumn (Fig. 4). This correlation may reflect increased vulnerability of calves to mortality factors during their first summer of life in years when overall herd nutrition is suboptimal prior to calving (Adams *et al.*, 1994). Poor survival of offspring in populations of animals with suboptimal nutrition has been widely reported (Skogland, 1985).

It is tempting to conclude that the reduced natality rate in the Delta herd in 1993, and perhaps in 1990 and 1991, contributed to the caribou decline. However, in 1993 natality rates in the adjacent Denali herd and in the Chisana herd were at least twice as high as in the Delta herd, and autumn calf:cow ratios were similar (6:100 in the Denali, 4:100 in the Delta, and 2:100 in the Chisana) (Adams, pers. commun.; Valkenburg, 1993). In addition, in 1992 natality in the Delta herd was the highest recorded, and the autumn calf:cow ratio was among the lowest recorded (Table 2).

The cause of the low natality in the Delta herd in 1993 is unknown, however, weather in May and September 1992 was unusual and the growing season was short. Persistent cold and snow in May resulted in the latest leaf out ever recorded in Fairbanks (25 May), and *Eriophorum* flowers were not available to caribou in the Alaska Range until after 15 May. Subsequently, on 11 September an arctic storm system moved into Interior Alaska from the northwest and by 15 September there was over 60 cm of heavy, wet snow on the ground throughout the range of the Delta herd. The Delta herd left the Alaska Range en masse, and together with many hundreds of caribou from the Denali herd, they arrived near Fairbanks about 27 September. Many of these caribou wintered north of the normal range of the Delta herd in black spruce forest immediately adjacent to Eielson Air Force Base and in areas north of Fairbanks. During winter 1992-1993 many Delta and some Denali caribou were mixed with White Mountains caribou in the White Mountains north of Fairbanks and with Nelchina caribou in the Chulitna Mountains southeast of Cantwell. In late April and May, caribou from these 4 herds began separating and by mid June all radio-collared caribou had returned to their respective herds. Natality rates of the Delta, Denali, and Nelchina herds were all lower than normal, but natality in the White Mountains herd remained high (Valkenburg, 1993). Snow conditions were severe in all autumn and winter ranges from September through December. After December snow remained deep in the forested winter ranges north of the Alaska Range, but was reduced by wind and warm temperatures in the Alaska Range

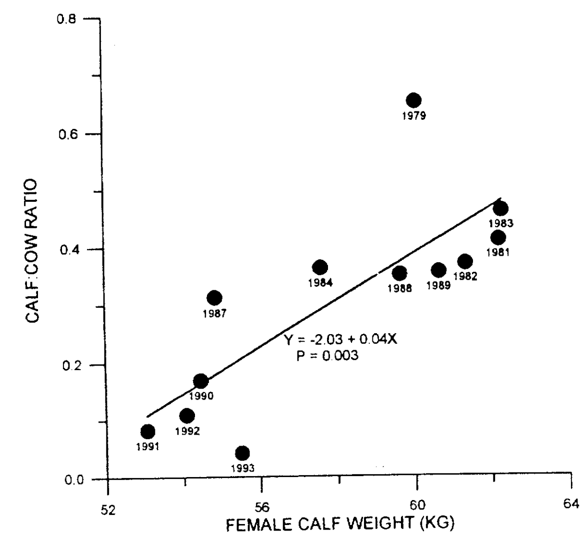

Fig. 4. Linear regression of female calf weight in April on September-October calf:cow ratio (data from Table 2).

where most of the Denali herd and about half of the Delta herd wintered.

Predation

There is compelling evidence that predation by wolves has been a major influence on the Delta herd over time. After wolf control in the mid-1970s the Delta herd became the most rapidly growing caribou herd in the state (Davis *et al.*, 1983; Gasaway *et al.*, 1983). In the mid-1980s, as wolf density approached precontrol levels, recruitment of caribou calves decreased and mortality of adults increased (Table 2). During 1983-1993 in the Delta herd, wolves were implicated in 23 out of 26 cases where the cause of death of adult radiocollared female caribou could be determined. In 26 additional cases, the precise cause of death could not be determined primarily because many of these caribou died during summer. In summer it was difficult to find evidence of hemorrhaging, so even if the kill site had been visited by bears or wolves, it was not possible to determine if the predators were scavenging or whether they killed the caribou. Long bones were recovered at about 50% of the winter kill sites, and in no case was malnutrition (as indicated by marrow fat content of less than 20%) documented as a possible contributing or direct cause of death.

In the recent decline, we did not determine causes of neonatal calf mortality. However, in the adjacent Denali herd (10) and the nearby Mentasta herd (18), wolf and grizzly bear predation were the major causes of high calf mortality (Adams, pers. comm.; Jenkins, pers. comm.). Grizzly bear densities are lower and wolf densities are higher in the range of the Delta herd than in the Denali herd (Dean, 1987; Mech *et al.*, 1991; Boertje, 1993; Reynolds, 1993) and it therefore appears probable that wolves are more important as predators of calves in the Delta herd than in the Denali herd.

Prior to summer 1989 our data suggests that moose were the primary prey of wolves, but shortly thereafter, wolves switched to eating caribou. In February-March 1989, just prior to the caribou decline, we investigated prey selection in 4 wolf packs in the Delta herd's range-by tracking collared individuals 2-3 times daily. Caribou and moose were abundant within the ranges of all packs. By weight, moose comprised two-thirds and caribou one-third of the wolves' diet (assuming 1 average moose = 3 average caribou). During the 30-day period, the 4 wolf packs studied killed 16 moose, 23 caribou, and 2 sheep. The small wolf packs killed as many caribou as the larger ones. At that time caribou and moose were both increasing (McNay, 1990; Boertje, 1993). Subsequently, coincident with severe winter weather, wolves increased, caribou declined and moose continued to increase until 1992 (Boertje, 1993). Comparative data from radiocesium (CS-137) concentrations in wolves corroborated this behavioral switch in prey selection over time (Boertje *et al.*, 1992). In addition, Mech *et al.* (1994) presented evidence that wolves included a higher proportion of caribou in their diet after 1989 in the range of the Denali herd.

Because much of the evidence for wolf predation as the main limiting factor in the Delta herd is circumstantial, we cannot be absolutely certain that the Delta herd would not have declined if wolf numbers had been substantially lower. If wolves are effectively removed from the calving and summer ranges of the Delta herd during the ongoing control program (winters 1993-1994 and 1994-1995) and the herd fails to recover, we will accept this as strong evidence that wolves were not the cause of the high calf mortality.

Another important question is whether wolves could have caused a decline in caribou without the presence of adverse weather. From 1985 on, wolves were an important limiting factor. The April 1988 and 1989 calf:cow ratios suggested increased overwinter mortality of calves prior to the onset of severe winters. However this probable decrease in recruitment, prior to the onset of severe weather, was insufficient to cause the herd to decline. In addition, wolves did not show a concurrent numerical response--wolf numbers remained relatively stable from 1985 to 1989 prior to the onset of bad weather (Boertje, 1993).

Wolf predation as a density dependent limiting factor

Bergerud (1993) proposed a conceptual model of population regulation in woodland caribou where wolf predation acts in a density dependent way and maintains caribou density at low levels (i.e., $<0.1/km^2$) because caribou lose the ability to effectively 'space out' from wolves at higher density. Although this model may fit some of the smallest Alaskan herds, clearly there are many herds which survive for long periods at moderate densities and neither 'space out' nor 'space away' from wolves. Furthermore, we found no clear relationship between caribou:wolf ratio or caribou equivalents:wolf ratio and caribou growth rate (Table 4, Figs. 5 and 6). It appears that Interior Alaskan caribou herds undergo extended periods of slow growth punctuated by short periods of rapid decline. Superficially, this may appear to be density-dependent predation, but growth rate of caribou may be more sensitive to influence of stochastic environmental factors rather than caribou density.

Table 4. Characteristics of 6 Interior Alaska caribou herds, 1980-1993.

Herd (Herd No., Fig. 1)	Crude density caribou/km² 1989, 1993	Size in 1989 relative to existing historical estimates	Mean annual population growth 1980-89(λ)	Mean annual population growth 1989-93(λ)	1989 fall caribou:wolf ratio	1989 fall caribou equiv.:wolf	1989 caribou population size
Chisana (8)	0.2, 0.1	mod	1.07	0.85	unknown	unknown	1,540
Delta (9)	0.9, 0.3	high	1.11[a]	0.77	56:1	230:1	10,690
Denali (10)	0.3, 0.2	low	1.09	0.87[b]	20:1	55:1	3,250
Fortymile (11)	0.5, 0.5	low	1.09	0.97	85:1	150:1	22,766[h]
Macomb (17)	0.2, 0.1	mod	1.04	0.88	27:1	120:1	686[i]
Mentasta (18)	0.2, 0.1	mod	1.00[e]	0.77	34:1[f]	62:1[g]	2,687
Nelchina (20)	0.8, 0.8	mod	1.09[a]	1.03[a]	73:1	235:1	40,317
White Mtns. (31)	0.1, 0.1	n. a.[c]	1.10[d]	1.05	18:1	76:1	930

[a] Growth rate reduced by harvest.
[b] The population peak actually occurred in 1990.
[c] This area was formerly considered part of the range of the Fortymile herd, the herd was first recognized in the late 1970s.
[d] Growth rate is approximate because the 1980 population estimate was poor.
[e] Population estimates during the period ranged from 2,393 to 2,697 but no trend was apparent.
[f] Assuming a fall population of 80 wolves within the range of the herd (data from Tobey, 1991).
[g] Assuming about 750 moose within the caribou range (data from Tobey, 1990).
[h] 1990 population estimate.
[i] Interpolated between 1988 and 1990 estimates.

Weather as a cause of declines

Because the declines of Interior Alaskan caribou herds were nearly simultaneous, and because there appeared to be a nutritional link in the Delta and Denali herds (i.e., reduced body weight and reduced natality rate), it appeared likely that a widespread factor such as weather was involved in the declines. We examined 3 weather variables: winter snow depth as a contributing factor to adult mortality and summer calf survival, and summer temperature and rainfall as factors contributing to lower natality (presumably through reduced body condition during

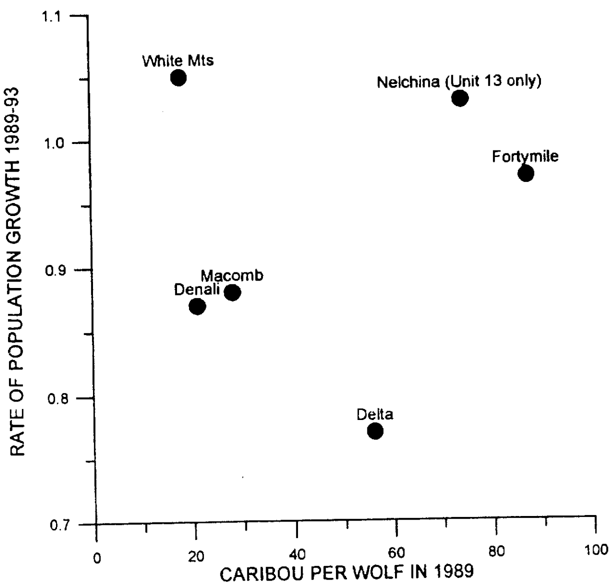

Fig. 5. Scatter plot of annual average population growth rate (λ) versus caribou:wolf ratio for 6 Interior Alaska caribou herds.

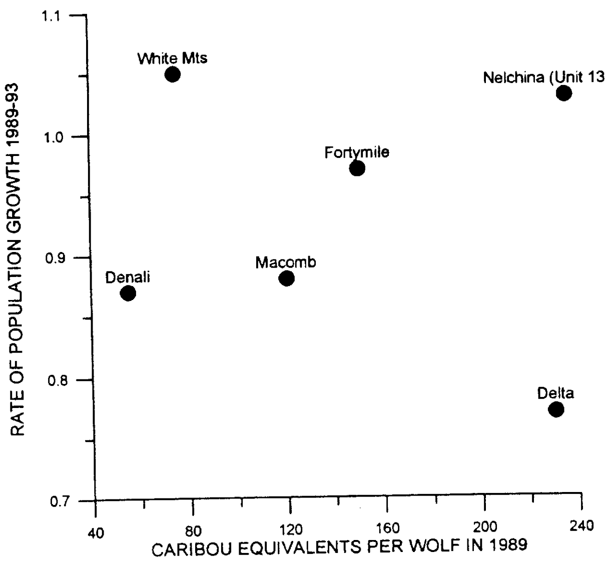

Fig. 6. Scatter plot of annual average population growth rate (λ) versus caribou equivalents:wolf ratio for 6 Interior Alaska caribou herds.

the rut) and decreased calf survival the following summer (through reduced body condition of calves at birth). The caribou decline in the Delta herd was coincident with 4 of the most severe winters since 1972 and followed 3 warm summers (Fig. 7). This was probably also true for the Macomb and Denali herds where weather was similar. However, in east central Alaska on the winter ranges of the Chisana, Mentasta, and Nelchina herds only the winter of 1989-1990 was severe, and snow depth barely exceeded 70 cm (snow data from Northway). The Chisana and Mentasta herds declined rapidly (Table 3) but the Nelchina herd continued to grow even though both wintered in contiguous and overlapping areas.

Harvest, emigration, and habitat destruction

Harvest, emigration, and destruction of winter range by fire and industrial development were potential factors that were either proposed as previous or potential causes or documented as contributing factors in previous declines of Alaskan or other caribou (Leopold & Darling, 1953; Skoog, 1968; Bergerud, 1974). These factors can be completely ruled out as factors in the current declines of the Delta and other Interior herds. In some herds (Denali and Macomb) harvest did not occur during the decline. In other herds, harvest was restricted to low levels and primarily to bulls (Chisana, Delta, Mentasta, Fortymile). Despite the inclusion of about 200 radiocollars in Interior caribou herds annually during the 1980s and 1990s and the occurrence of intermingling on winter ranges during 1989-1993, only 2 10-month-old collared females were documented as dispersing (both dispersed from the Macomb herd; 1 to the Nelchina herd and 1 to the Fortymile herd). From 1980 to 1993 no major fires occurred on Interior caribou winter ranges, and some low density herds declined. Large-scale human developments have not occurred on Interior caribou ranges in Alaska. Two herds, Nelchina and Central Arctic, have had their ranges bisected by the Trans-Alaska Pipeline. Central Arctic caribou have been displaced from their former calving areas (Whitten & Cameron, 1985); however, population consequences of this displacement have not been clearly documented. The Nelchina herd crosses the pipeline each spring and autumn without incident.

Conclusion

Evidence gathered during the current declines of the Delta and other Interior herds has led us to conclude that changed weather patterns increased vulnerability of caribou to predation and resulted in a numerical and behavioral response in wolves

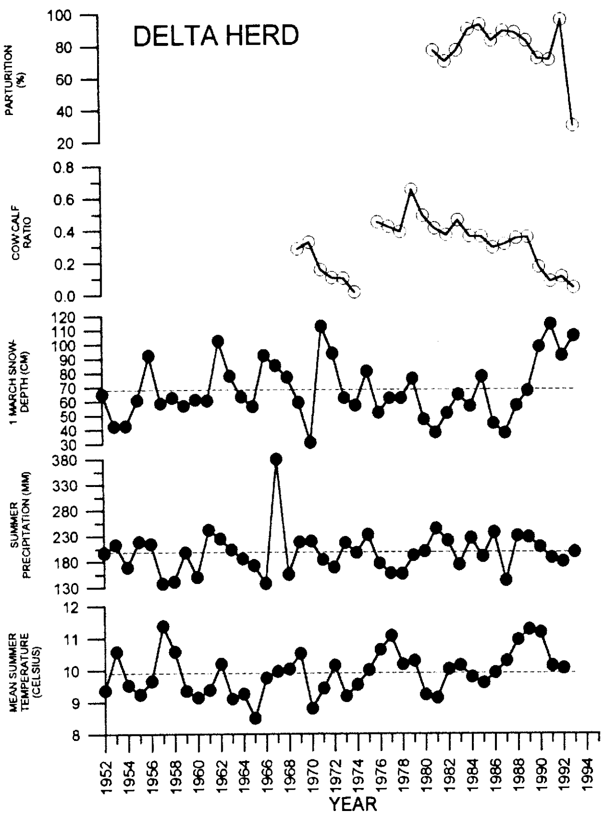

Fig. 7. Plot of parturition rate and autumn calf:cow ratio in relation to snow depth, summer precipitation, and summer temperature in the range of the Delta herd.

which in turn resulted in declines in many caribou herds. We therefore propose a conceptual model for Interior Alaskan herds that incorporates stochastic weather events that interact with predation and nutrition to limit herd size within a wide range of densities. The upper and lower bounds of population size would be a function of the amount of suitable habitat, the length of good or bad climatic periods, and interactions between predators and alternate prey. Only in rare circumstances would absolute food shortage become a major limiting factor. Food availability could be a limiting factor in some cases and may have a strong relationship with weather and predation because weather could make food unavailable and wolves could prevent caribou from foraging optimally. Vulnerability of caribou to predation would vary largely independent of density, and the size of a particular herd at a given time would primarily be a function of the size to which it was reduced during the last decline and the number of intervening years with favorable weather. Additional stochasticity could result from, as yet, largely unpredictable behavioral responses of wolves to numbers and vulnerability of all major prey species. In the recent Alaskan declines, there were no clear relationships between the rate of population decline, density, and numbers of alternate prey (Figs. 2, 5, and 6; Table 4).

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