Calf mortality and population growth in the Delta caribou herd after wolf control

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Abstract A program to control wolves (*Canis lupus*) in interior Alaska in 1993 and 1994 did not result in expected increases in calf survival in the Delta caribou (*Rangifer tarandus*) herd (DCH). Therefore, the Alaska Department of Fish and Game conducted a study to determine causes of calf mortality during 1995–1997 and monitored recruitment, mortality, and population size annually in the DCH for 6 years after wolf control ended. Despite removal of 60–62% of the autumn 1993 wolf population, wolves still killed 25% of 166 radiocollared calves between birth in mid- to late May and 30 September during 1995–1997. Although autumn calf:cow ratios in the DCH increased after wolf control, similar increases in calf:cow ratios occurred in the adjacent Denali Herd, where wolves were not controlled. Calf:cow ratios following wolf control in 1993 and 1994 were lower than ratios obtained in the same area after wolf control from 1976–1982. We identified 4 factors that contributed to continued low calf:cow ratios in the DCH following the 1993–1994 wolf control program: 1) other predators in combination (i.e., golden eagles [*Aquila chrysaetos*] and grizzly bears [*Ursus arctos*]) were the most significant mortality source for caribou calves, 2) the temporal and spatial extent for wolf removal was inadequate to effectively reduce wolf predation, 3) in 1987 the DCH shifted its main calving area, a move that may have increased predation by golden eagles and grizzly bears, and 4) natality rates and nutritional condition of caribou declined during the 5 years before wolf control coincident with a density-dependent population decline. We conclude that wolf control within the range of the DCH failed because the wolf trapping program did not remove enough wolves and was not conducted long enough to substantially reduce predation by wolves on caribou calves. In addition, wolves that lived outside the control area were responsible for about 40% of the wolf-caused mortality to collared caribou calves, and significant numbers of calves died from unknown, neonatal causes.

Key words Alaska, *Aquila chrysaetos*, calf mortality, *Canis lupus*, caribou, golden eagle, grizzly bear, predator–prey relationships, *Rangifer tarandus*, *Ursus arctos*, wolf, wolf control

From 1989–1993 the Delta caribou (*Rangifer tarandus*) herd (DCH) in the central Alaska Range south of Fairbanks declined from 10,700 to about 4,000 and all hunting was suspended. The decline was primarily caused by high mortality of adult females from wolf (*Canis lupus*) predation and unknown causes, high summer mortality of calves from unknown causes, and high winter mortality of

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calves from wolf predation (Boertje et al. 1996, Valkenburg et al. 1996*a*, 2002). Suboptimal nutrition in caribou may have played a key role in increasing vulnerability of caribou to predation (Boertje et al. 1996, Valkenburg et al. 1996*a*, 2002). The caribou decline was coincident with severe winter weather, lower than normal rainfall, warm summers in some years, a similar decline in the area's Dall sheep (*Ovis dalli*), declines in most other Interior Alaska caribou herds, and increased wolf numbers (Boertje et al. 1996; Valkenburg et al. 1996*a*, 2002; Valkenburg 1997; Mech et al. 1998). To arrest the decline of the DCH and hasten the resumption of caribou hunting, the Alaska Department of Fish and Game (ADF&G) initiated a wolf control program in October 1993. Because the first winter of wolf control was not followed by a substantial increase in the fall calf:cow ratio in the DCH, we conducted a study from 1995–1997 to determine causes of death of newborn caribou calves in summer and their potential vulnerability to predation. In addition, to determine the long-term effects of wolf control on the caribou herd, we monitored herd size, autumn calf:cow ratios, and age-specific mortality and natality of radio-collared caribou in the herd for 6 years after the wolf control program ended.

Among the plausible explanations for lack of a large response in autumn calf:cow ratios in the DCH after wolf control were: 1) most wolf packs remained; the members of remaining wolf packs were efficient calf predators, and kill rates of calves were thus not substantially reduced; 2) calves were being killed by predators other than wolves; and 3) suboptimal nutrition was reducing natality or resulting in a high neonatal mortality rate independent of predation. In this paper we briefly review the wolf control program, present results of the 3-year calf mortality study, and discuss possible short-term and long-term effects of the wolf control program on the DCH.

Study area

From 1989–2002 the DCH ranged over an 11,000-km^2 area that included almost all of Game Management Unit (GMU) 20A, a 1,000-km^2 area of northern GMU 13, and a 400-km^2 area of western GMU 20D (Figure 1). The caribou herd's summer range (including the calving area) was an 8,500-km^2 area of montane treeless alpine tundra and subalpine shrubs. From 1987–1997 >80% of all parturient caribou cows used a 500–1,000-km^2 area of GMU 13 for calving (about 10 May–5 Jun) before returning north to traditional summer range. Gasaway et al. (1983) and Boertje et al. (1996) described the topography of GMU 20A in detail.

By Alaskan standards, GMU 20A is a relatively productive area with 6 species of large mammals: wolves, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), moose (*Alces alces*), caribou, and Dall sheep. Black bears were common on the northern edge of the caribou summer range. Smaller carnivores and herbivores included coyotes (*Canis latrans*), wolverines (*Gulo gulo*), red foxes (*Vulpes fulva*), lynx (*Lynx canadensis*), golden eagles (*Aquila chrysaetos*), marmots (*Marmota caligata*), beavers (*Castor canadensis*), and porcupines (*Erithizon jubatum*).

It may be significant that the DCH used a differ-

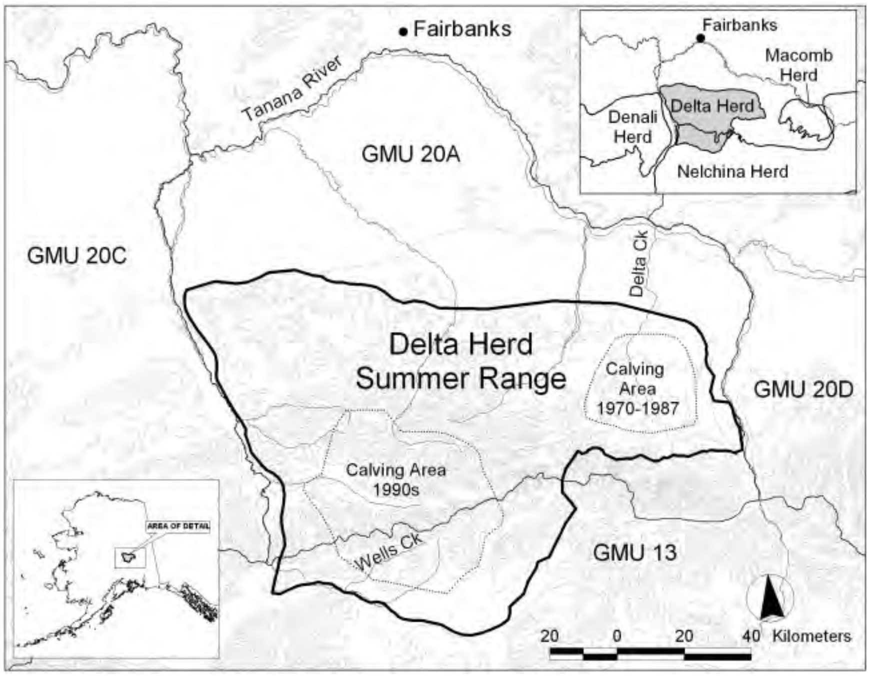

Figure 1. Map shows entire summer range of Delta Herd (solid line), which surrounds historic and recent calving areas. Inset shows juxtaposition of experimental vs. control caribou herd ranges.

ent calving area (Delta Creek) during the 1970s and early 1980s than it did during the 1990s (Wells Creek) (Figure 1). The Delta Creek calving area was more compact, drier, less rugged, and typically had an earlier snowmelt than the Wells Creek calving area. In addition, judging from the numbers of golden eagles and coyotes observed during fieldwork, the Wells Creek calving area and adjacent mountainous terrain probably had higher numbers of golden eagles and lower numbers of coyotes than the Delta Creek calving area.

Methods

Estimating wolf abundance

We estimated the precontrol (Oct 1993) wolf population during 400 hours of aerial surveys conducted before and during the start of the wolf control program. Pilot–observer teams in light 2-place aircraft searched for wolf tracks as soon as snow fell in October. Wolves were tracked down whenever possible, and numbers and colors of wolves in each pack were recorded. At the end of winter 1993–1994, all observations of wolves, wolf tracks, and known numbers of trapped wolves were used to estimate the autumn 1993 population. Radiocollars were not used to estimate wolf numbers prior to 1996. We estimated the autumn 1994 wolf population in a similar manner with approximately 275 hours of surveys, but the control program was terminated in early December 1994, and wolves were not surveyed again until autumn 1995. The postcontrol wolf population in 1994 and 1995 was estimated by subtracting number of wolves removed by control and harvest from the autumn population each year (Boertje et al. 1996). We estimated autumn wolf numbers during 1995–2001 with aerial surveys, radiotelemetry of collared wolves, and harvest data.

The wolf control program

Alaska Department of Fish and Game employees and private trappers killed wolves using traps, snares, and occasionally by shooting free-ranging wolves from the ground. Shooting from aircraft was prohibited. Traps and snares were set throughout most of the DCH's range; however, the authorized control area did not include the main caribou calving area (in GMU 13), where there was at least one pack of 11–13 wolves. Beginning in mid-October 1993, 2 experienced department trappers, using 2 Robinson R-22 helicopters (Robinson Helicopters, Torrance, Calif.) , set snares at baited sites or wolf-killed moose and caribou carcasses within the caribou range in GMU 20A. The trappers were assisted by 2–4 pilot–observer teams in Piper Super Cubs (New Piper Aircraft Corporation, Vero Beach, Flor.) or Bellanca Scouts (American Champion, Rochester, Minn.) that searched for wolf tracks and kill sites. Department trappers also trained private trappers with traplines in the area to catch wolves more effectively and provided them with locations of wolf-killed moose and caribou that were found on their traplines. Trappers were also encouraged to trap wolves from the pack in the caribou calving area in GMU 13. The plan was to remove entire packs if possible. Trapping continued until snowmelt in mid-April 1994, then resumed in October 1994. The department's involvement in the wolf control program ended in early December 1994, but from 1995–2001 public trapping and hunting of wolves continued.

Calf mortality study

During mid- to late-May from 1995–1997, we monitored a total of 98 radiocollared known-age female caribou that were judged to be pregnant (Bergerud 1964, Whitten 1995). We radiocollared (Telonics, Inc., Mesa, Ariz.) 81 of the 98 calves that were expected from these females. Of the remaining expected calves, 2 grew too old to be easily caught and 15 were never seen because they probably were either killed by predators or stillborn. We also collared 88 calves of uncollared cows, and these were temporally distributed based on the timing of births among collared cows. In all, we radiocollared 169 calves.

Calves <2 days old were caught by landing a Robinson (R-22) helicopter nearby and running them down on foot. We then radiocollared calves, weighed them, and determined their sex. For comparison, we also obtained data on calf mass in the adjacent Fortymile and Nelchina herds. Mortality sensors were activated when collars remained motionless for one hour. We monitored signals with a Super Cub or Bellanca Scout once or twice daily until 5 June, twice a week until 31 July, and then weekly through 30 September. When we heard a mortality signal, we flew to the site in the helicopter, usually within 1–3 hours before 5 June and within 48 hours until 30 September. After 30 September, we located radiocollared calves monthly and retrieved dead calves when it was convenient to do so (usually within a week of their discovery). We based determination of cause of death on tracks in snow or soft ground, characteristic feeding patterns of predators, hair, feces, and other evidence (Whitten et al. 1992; Adams et al. 1995*a*, *b*; Boertje and Gardner 1998).

Estimating population size and autumn calf:cow ratios in the DCH and adjacent herds after wolf control

We estimated herd size in late June in the DCH by counting postcalving aggregations of caribou (Davis et al. 1979, Valkenburg et al. 1985). We photographed groups larger than about 200 with either 35-mm or 240-mm cameras and counted animals in the photographs later. We found postcalving aggregations by visually searching the entire summer range of the herd using 4–6 aircraft. All aircraft were equipped with radiotracking gear and tracked the 40–120 radiocollars that were active in the herd each year. Population estimates for the Denali Herd were derived by counting female caribou older than calves with the help of radiocollars in early June and then extrapolating for other sex–age classes by using autumn composition counts (L. G. Adams, United States Geological Survey [USGS], personal communication). We derived population estimates for the Macomb Herd from total counts of rutting groups in early October and then rounding them up to the nearest 25 caribou.

To compare summer calf survival (i.e., survival of calves younger than 4 months) in the DCH where wolf control did occur to adjacent herds (Macomb and Denali) where it did not, we compared autumn calf:cow ratios. We monitored autumn calf:cow ratios and population sizes in the DCH and the Macomb Herd with data collected by ADF&G biologists and in the Denali Herd with data collected by USGS biologists (DuBois 2001). Approximately 15–120 radiocollared females were present in each herd annually, and sampling for population composition was allocated based on distribution of these females. We used a helicopter to classify groups by age and sex and sampled 19–100% of all females in each herd annually. We compared autumn calf:cow ratios within the DCH, Denali, and Macomb herds during 1993 (immediately before wolf control) to 1994 (immediately after wolf control) using chi-square analyses. We determined whether the change in calf:cow ratios differed between herds during the 2 years before wolf control and the 2 years after wolf control in the DCH using an ANOVA analysis with contrasts. We also evaluated trends in autumn calf:cow ratios within the DCH, Denali, and Macomb herds with logistic regression that included an overdispersion factor (McCullagh and Nelder 1989).

Estimating mortality of radiocollared female caribou >4 months old in the DCH

In the DCH, beginning in 1979, we radiocollared cohorts of 15–20 female calves at 10 months of age and monitored them monthly to determine mortality rates. Beginning in 1991, we collared cohorts of 10–20 female calves in early October at 4 months of age. Therefore, when the wolf control program began in 1993, cohorts of known-age females were available in the caribou population for determining mortality rates before and after wolf control. Because mortality rates of radiocollared females aged 4–16 months were higher than those of caribou older than 16 months, they were considered separately. Mortality rates of age-classes of radiocollared female caribou older than 16 months were similar and were pooled to increase sample sizes. We calculated mortality rates between 1 October and 30 September annually as the number of caribou that died during the year divided by the number alive at the beginning of the year. We compared mortality rates of radiocollared female caribou older than 4 months using chi-square analyses.

Estimating mass of newborn calves in herds adjacent to the DCH during and after wolf control

As an index of vulnerability to predation, we compared mass of newborn calves in the DCH with those collected by other researchers in adjacent Fortymile and Nelchina herds. We compared mean mass of annual samples of male and female calves using *t*-tests.

Results

Wolf numbers

Wolf control during winter 1993–1994, combined with public trapping, reduced the wolf population on the caribou summer range to 40% of the precontrol, autumn 1993, estimate (Table 1). In addition to 77 wolves killed on the summer range, 22 wolves in 2 packs were killed on the adjacent DCH winter range. In 1994–1995 the wolf population on the summer range was reduced to 43% of the precontrol estimate. However, no wolves were killed on the main calving area (i.e., Wells Creek

Table 1. Estimates of wolf numbers within the summer range of the Delta caribou herd[a], Alaska, 1993–1994 through 2000–2001.

Year	Autumn wolf estimate	Number of wolves removed in ADF&G control program	Number of wolves removed by public hunting and trapping	Spring wolf estimate (% of autumn wolf estimate)
1993–1994[b]	159	77	19	63 (40)
1994–1995[c]	116	36	12	68 (59)
1995–1996	144	0	34	110 (76)
1996–1997	133	0	26	107 (80)
1997–1998	129	0	26	103 (80)
1998–1999	161	0	58	103 (64)
1999–2000	97[d]	0	27	70 (72)
2000–2001	108[d]	0	42	66 (61)

[a] Wolves included in these estimates were from packs that ranged throughout the mountains and foothills of Game Management Unit 20A and the Wells Creek Pack. Packs that ranged entirely on the flats of Game Management Unit 20A were not included.

[b] Wolf control began in Oct 1993 after the autumn wolf estimate.

[c] Wolf control ended in Dec 1994. Calf mortality studies were conducted during 1995, 1996, and 1997.

[d] After 1998 the Wells Creek Pack was not monitored, and was not included in estimates of wolf numbers.

area) in either year, and at least 11–13 wolves were present there. After wolf control ended in December 1994, wolf numbers increased to near precontrol levels (Table 1). Eleven to 16 wolves were present in the Wells Creek Pack from May 1995 through 1998 (after 1998 there were no radiocollars in the Wells Creek Pack and it was no longer monitored).

Mortality rates and causes of mortality in DCH calves during May–September

During 14 May–30 September 1995 through 1997, all but 4 deaths of radiocollared caribou calves were attributable to predation, primarily by wolves, grizzly bears, and golden eagles (Table 2). Four radiocollared calves died from unknown causes. Because there were no significant between-year differences in the proportions of calves killed by wolves, bears, or eagles ($P > 0.15$), we pooled data from the 3 years to compare mortality rates of different predators. Of the radiocollared calves that died, wolves killed 39%, grizzly bears killed 31%, and golden eagles killed 23%. Wolves killed significantly more calves than golden eagles ($\chi^2 = 5.52$, $P = 0.02$, df = 1), but not significantly more than bears ($\chi^2 = 1.11$, $P = 0.29$, df = 1), and bears did not kill significantly more calves than eagles ($\chi^2 = 1.72$, $P = 0.19$, df = 1) (Table 2). The combined predation by grizzly bears and golden eagles exceeded predation by wolves ($\chi^2 = 3.7$, $P = 0.05$, df = 1).

The calves of 15 of the 98 (15%) known-aged radiocollared female caribou that were judged to be pregnant were never seen (neonatal mortality in Table 2). Causes of death of these calves were not known, but the magnitude of neonatal mortality in the DCH was similar to that found in other studies (cf. Whitten et al. 1992, Boertje and Gardner 1998).

Table 2. Mortality of radiocollared calves and calves of radiocollared females by cause in the Delta caribou herd, Alaska, from birth to 30 September 1995–1997.

		Proportion dying (%)							
	Year	Neonatal[a]	Wolf	Grizzly bear	Golden eagle	Coyote	Unknown	Total	Capture induced
All radiocollared calves	1995	na	13/43 (30)	9/43 (21)	7/43 (16)	0/43 (0)	0/43 (0)	29/43 (67)	2/45 (4)
	1996	na	9/50 (18)	11/50 (22)	6/50 (12)	1/50 (2)	4/50 (8)	31/50 (62)	0/50 (0)
	1997	na	19/73 (26)	13/73 (18)	11/73 (15)	2/73 (3)	0/73 (0)	45/73 (62)	1/74 (1)
Total			41/166 (25)	33/166 (20)	24/166 (14)	3/166 (2)	4/166 (2)	105/166 (63)	3/169 (2)
All calves of known-aged radiocollared cows	1995	7/31 (23)[b]	5/31 (16)	5/31 (16)	3/31 (10)	0/31 (0)	1/31 (3)	21/31 (68)	1/32 (3)
	1996	4/33 (12)	5/33 (15)	8/33 (24)	3/33 (9)	0/33 (0)	1/33 (3)	21/33 (64)	0/33 (0)
	1997	3/31 (10)	5/31 (16)	7/31 (23)	1/31 (3)	2/31 (6)	0/31 (0)	18/31 (58)	0/31 (0)
Total		14/95 (15)	15/95 (16)	20/95 (21)	7/95 (7)	2/95 (2)	2/95 (2)	60/95 (63)	1/96 (1)

[a] Neonatal mortality refers to calves that died prior to or within 2 days after birth, before we had a chance to collar them.

[b] Includes 1 due to breached birth where both cow and calf died.

Table 3. Population size estimates for the Denali, Delta, and Macomb caribou herds before and after wolf control in the range of the Delta Herd, Alaska, during 1989–2000.

Year	Delta herd	Denali herd[a]	Macomb herd
1989	10,690	3,210	na
1990	8,700	3,180	775
1991	5,755	2,660	600
1992	5,877	2,340	600
1993[b]	3,661	1,970	500
1994[c]	4,341	2,140	550
1995	4,646	2,170	500
1996	4,019	2,060	600
1997	3,699	2,070	600
1998	3,829	1,790	600
1999	3,625	1,690	700
2000	3,227	1,730	675

[a] Autumn population estimate.

[b] Wolf control begins in the Delta herd's range in winter 1993–1994.

[c] Wolf control ends in Dec 1994.

Table 4. Late September–early October calf:100 cow ratios in the Delta, Denali, and Macomb caribou herds, Alaska, 1990–2000.

Year	Delta herd calves:100 cows (*N*)	Denali herd[a] calves:100 cows (*N*)[b]	Macomb herd calves:100 cows (*N*)
1990	17 (268:1567)	17 (130:777)	17 (63:373)
1991	8 (101:1248)	7 (72:1067)	9 (36:392)
1992	11 (96:913)	16 (103:643)	14 (45:328)
1993[c]	4 (48:1109)	6 (54:849)	18 (48:268)
1994	23 (328:1433)	20 (128:648)	13 (34:256)
1995	20 (219:1085)	19 (131:683)	10 (31:321)
1996	21 (209:1015)	13 (103:820)	30 (101:340)
1997	18 (202:1103)	16 (124:777)	18 (55:309)
1998	16 (155:949)	12 (87:718)	25 (68:270)
1999	19 (77:415)	14 (92:667)	22 (75:338)
2000	11 (71:646)	7 (52:730)	11 (42:388)

[a] Unpublished data from L. G. Adams, USGS.

[b] Sample size, calves:cows.

[c] Wolf control occurred in the range of the Delta Herd during Oct 1993–Dec 1994.

Of the 41 collared calves killed by wolves, 17 (41%) were killed in the GMU 13 portion of the calving area where wolf numbers were not reduced. There was no between-year difference in the proportion of calves killed by wolves in GMU 20A and GMU 13 ($\chi^2=0.08, P=0.95$, df=2).

Changes in population size of the DCH and adjacent herds before and after wolf control

Population size in the DCH declined rapidly from 1990 to 1993 but stopped immediately following the first winter of the wolf control program in 1993–1994 (Table 3). The herd then increased at a rate of about 12% per year for 2 years before declining slowly again through 2000. The Denali Herd also followed a similar pattern of population fluctuation (Table 3). The Macomb Herd appeared to decline between 1990 and 1995, and then increased slightly, but population changes were not as great as those in either the DCH or the Denali Herd (Table 3).

Autumn calf:cow ratios in the DCH and adjacent herds before and after wolf control

After the first winter of wolf control in the DCH, autumn calf:cow ratios increased from 4:100 to 23:100 in the DCH ($\chi^2>10.0, P<0.001$, df=1), and from 6:100 to 20:100 in the adjacent Denali Herd ($\chi^2>10.0, P<0.001$, df=1). However, calf:cow ratios did not change in the Macomb Herd ($\chi^2=3.25, P=0.07$, df=1) (Table 4). The change in mean calf:cow ratios within herds between 1992–1993 and 1994–1995 (i.e., the 2 years before and the 2 years after wolf control in the DCH) was no greater in the DCH where wolf control did occur than it was in the Denali Herd where wolf control did not occur ($t=1.10$, $P=0.31$, df=6). In the DCH, the 2-year mean autumn calf:cow ratio was 7.4:100 immediately before wolf control (i.e., in 1992 and 1993) and 21.5:100 after wolf control, and in the Denali Herd, the 2-year means were 11.2 and 19.5, respectively. However, the change in calf cow:ratios was higher in the DCH than in the Macomb Herd ($t=3.47, P=0.01$, df=6), where the mean calf:cow ratio was 15.8:100 during 1992–1993 before wolf control in the DCH and 11.5:100 during 1994–1995 after wolf control in the DCH. After wolf control ended there was a slight but significant downward trend in calf:cow ratios during 1994–1998 in the DCH ($t=-5.93$, $P=0.01$, slope=–0.095) but not in the Denali Herd ($t=-2.28$, $P=0.11$, slope=–0.138) or the Macomb Herd ($t=1.19$, $P=0.32$, slope=0.210).

Mortality of radiocollared females older than 4 months in the DCH before and after wolf control

Mortality of radiocollared 4–16-month-old female caribou declined from a mean annual rate of 60%

(15/25) during 1 October 1992–30 September 1994 (before and during wolf control) to a mean annual rate of 38% (9/24) during 1 October 1994–30 September 1996 (after wolf control) (χ^2= 4.56, P=0.03, df=1) (Table 5). However, the number of radiocollared 4–16-month-old females known to have been killed by wolves did not decline between periods (χ^2=0.004, P=0.95, df=1) (Table 5). In the 2 years before and during wolf control (i.e., 1 Oct 1992–30 Sep 1994), wolves killed 5 of 25 radiocollared 4–16-month-olds. In the 2 years after wolf control (1 Oct 1994–30 Sep 1996) wolves killed 6 of 29 that died. During these 2 periods, 9 of these radiocollared caribou died from unknown causes in summer that could have included wolf predation. Even if all of these unknown mortalities had been from wolf predation, there still would have been no difference in the numbers of 4–16-month-old caribou killed by wolves between periods (χ^2=0.97, P=0.33, df=1).

There was no change in mortality rates of radiocollared female caribou older than 16 months between the 2 years before and during wolf control (i.e., from 1 Oct 1992–30 Sep 1994) and the 2 years after wolf control (1994–1996) (12.5% vs. 12.2%, χ^2 =0.003, P=0.96, df=1) (Table 5). Wolves were known to have killed 5 of these radiocollared females during the former period and 7 during the latter period (Table 5).

Body mass of newborn calves in the DCH

Although mean body mass of radiocollared newborn male calves did not change during the 3 years of the study (P>0.2) (Table 6), radiocollared newborn female calves were significantly lighter in 1996 than in 1995 (t=3.01, P=0.004) or 1997 (t= 2.11, P=0.04). However, mean masses of both male and female newborn calves in the DCH were not

Table 5. Annual total mortality[a] of radiocollared known-aged female Delta Herd caribou, Alaska, 1991–2001.

	Proportion dying (%) (cause of death) by age class			
Year[b]	Calves (4–16 months old)	Yearlings (16–30 months old)	Older than yearlings (>30 months old)	Yearlings and older (>16 months old)
1991–1992	5/12 (42) (2 wolf, 2 unknown predator, 1 unknown)	0/4 (0)	5/31 (16) (3 wolf, 1 unknown, predator, 1 unknown)	5/35 (14)
1992–1993	8/15 (53) (3 lynx, 3 unknownpredator, 2 unknown)	1/11 (9) (1 unknown)	5/30 (17) (4 wolf, 1 coyote)	6/41 (15)
1993–1994	7/10 (70) (5 wolf, 1 unknown, 1 poached)	0/7	4/32 (13) (3 unknown, 1 wolf)	4/39 (10)
1994–1995	5/15 (33) (3 wolf, 2 unknown predator)	2/7 (29) (1 grizzly, 1 hunting)	5/41 (12) (3 wolf, 1 unknown predator, 1 breached birth)	7/48 (15)
1995–1996	4/14 (29) (3 wolf, 1 unknown)	1/11 (9) (1 wolf)	4/39 (10) (3 wolf, 1 unknown predator)	5/50 (10)
1996–1997	6/13 (46) (2 wolf, 3 unknown predator, 1 unknown)	3/14 (21) (3 wolf)	3/42 (7) (2 wolf, 1 unknown)	6/56 (11)
1997–1998	3/17 (18) (2 wolf, 1 unknown)	1/19 (5) (1 wolf)	5/49 (10) (1 wolf, 1 avalanche, 1 poached, 2 unknown)	6/68 (9)
1998–1999	7/15 (47) (5 wolf, 2 unknown)	0/15 (0)	5/49 (10) (3 wolf, 2 unknown)	5/64 (8)
1999–2000	8/13 (62) (6 wolf, 2 unknown)	3/10 (30) (1 unknown, predator, 2 unknown)	7/55 (13) (2 wolf, 1 unknown predator, 4 unknown)	10/65 (15)
2000–2001	3/14 (21) (2 wolf, 1 grizzly)	0/9 (0)	8/56 (14) (3 wolf, 5 unknown)	8/65 (12)
Totals	56/138 (41) (30 wolf, 10 unknown predator[b], 11 unknown[b], 3 lynx, 1 grizzly, 1 poached)	11/107 (10) (3 unknown[b], 5 wolf, 1 unknown predator[b] 1 grizzly, 1 hunting)	51/424 (12) (25 wolf, 18 unknown[b], 4 unknown predator, 1 poached, 1 coyote, 1 breached birth, 1 avalanche)	62/531 (12)

[a] Mortality rate was calculated from 1 October–30 September each year.

[b] Most of these died in summer when it was difficult to determine cause of death. Wolves and grizzly bears are the most likely cause of death.

Table 6. Body mass of newborn caribou calves in the Delta Herd compared with 2 other nearby Alaskan herds, 1994–1997.

	Males			Females		
Herd and year	Mass (kg)	SE	N	Mass (kg)	SE	N
Delta 1995	8.72	0.29	26	8.31	0.24	19
Delta 1996	8.39	0.23	22	7.40	0.19	28
Delta 1997	8.33	0.21	40	7.99	0.20	35
$\bar{x}$	8.48			7.90		
Fortymile 1994[a]	7.60	0.19	22	7.47	0.26	22
Fortymile 1995[a]	8.45	0.14	24	7.68	0.16	25
Fortymile 1996[a]	8.47	0.23	26	8.05	0.16	32
Fortymile 1997[a]	8.43	0.21	24	7.88	0.18	32
$\bar{x}$	8.24			7.77		
Nelchina 1996[b]	8.26	0.24	23	7.19	0.19	17
Nelchina 1997[b]	8.43	0.18	30	7.91	0.21	30
$\bar{x}$		8.35			7.55	

[a] Data from Boertje and Gardner (1998:33).
[b] Unpublished data from R. Tobey, ADF&G.

significantly lower ($P > 0.2$) than in the nearby Nelchina and Fortymile herds during 1995–1997 (Table 6).

Discussion

Effects of wolf control on summer calf mortality and autumn calf:cow ratio

Despite overwinter wolf reductions to 40–43% of precontrol (autumn 1993) numbers within the caribou calving and summer range of the DCH during 1994 and 1995, wolves caused at least 25% of the deaths of all radiocollared caribou calves from birth in mid- to late May through 30 September 1995–1997. We likely underestimated predation during these calf mortality studies because "neonatal" causes also probably included some instances of early predation that we did not have a chance to observe. We also may have underestimated predation by wolves because eagles were abundant on the calving area and they often followed wolves. Wolves sometimes wounded caribou calves or made multiple kills that immediately were scavenged by eagles. In 3 cases where eagles were judged the most likely cause of death, wolves also were known to have been nearby at the approximate time of death.

Although the estimated autumn calf:cow ratio in the DCH increased following the first year of wolf control, it did not reach the relatively high level (45:100) seen following control in the mid-1970s, and was not substantially different from calf:cow ratios in the 2 adjacent herds where control did not occur (Boertje et al. 1996). If wolf control had also occurred on the GMU 13 portion of the calving area and all calves killed by wolves there had been spared from other predation through September, the autumn calf:cow ratio could potentially have increased by an average of 4 calves:100 cows annually. Again, assuming no compensatory mortality, if wolves had been completely removed from both the GMU 13 and GMU 20A DCH summer ranges, the autumn calf:cow ratio could have increased by an average of about 15 calves:100 cows. These potential increases still would not have brought calf numbers up to the levels seen during the late 1970s (i.e., 38:100 vs. 45:100). The 14 calves (15%) that apparently died from unknown neonatal causes (Table 2) could indicate that nutrition-related neonatal mortality was higher in 1995–1997 than during the mid-1970s, although there was no indication that calf weights were low.

Natality of 2-year-old DCH caribou probably was higher during the late 1970s than during the mid-1990s, but this difference probably was not sufficient to explain why autumn calf:cow ratios were higher after wolf control during the 1970s than during the 1990s. Although more 2-year-olds were parturient during 1980–1983 (9/27) than during 1994–1997 (1/41) ($\chi^2 = 12$, $P > 0.001$, df = 1) (Valkenburg et al. 2002), these calves rarely survived to autumn (Adams et al. 1995*b*, Mech et al. 1998). Parturition rate in cows 3 years old and older did not differ between the 2 periods ($\chi^2 = 0.02$, $P = 0.87$, df = 1) (Valkenburg et al. 2002).

It was possible that neonatal mortality (nonpredation or unknown mortality occurring within the first 48 hours of life) was higher in the DCH during 1994 and 1995 than during the 1970s, but the 15% rate found during 1995–1997 was similar to rates reported by Whitten et al. (1992) for the Porcupine Herd during a period of population increase. In addition, newborn calf weights in the DCH were similar to those in adjacent herds (i.e., the Nelchina and Fortymile), where fall calf:cow ratios were higher (Boertje and Gardner 1998; Tobey 2001).

Effects of wolf control on population growth and mortality of older calves and adults in the DCH

The DCH increased for 2 years after wolf control, but there was no clear evidence of cause and effect. The herd declined rapidly from about 10,700 in

1989 to 3,700 in 1993, but fluctuated between 3,600 and 4,600 from 1994–1997 (Boertje et al. 1996, Valkenburg et al. 2002). Because mortality of radiocollared caribou 4–16 months old and radiocollared caribou older than 16 months did not decline significantly after wolf control, it is apparent that the population decline stopped primarily due to increased calf survival over summer. This increased survival could not unequivocally be attributed to wolf control because calf survival also improved in the adjacent Denali Herd, where wolves were not reduced by trapping (Mech et al. 1998). Wolf numbers also declined in the range of the Denali Herd, where wolf control did not occur, but the decline was probably caused naturally by food stress (Mech et al. 1998). A similar natural decline in wolf numbers in GMU 20A was less likely to have occurred in the absence of wolf control because of the higher density of moose as alternate prey for wolves in GMU 20A (Boertje et al. 1996).

The similarity in body mass of newborn calves in the DCH and the adjacent Nelchina and Fortymile herds, where calf survival to fall was relatively high, suggests that newborn DCH calves would have survived well in the absence of predators (Boertje and Gardner 1998; Table 6). Although reduced nutritional condition and lower calf mass usually are accompanied by lower calf survival (Espmark 1980; Reimers et al. 1983; Skogland 1985; Adams et al. 1995*a*,*b*), some large herds like the George River, Nelchina, and Western Arctic can maintain relatively high autumn calf:cow ratios despite declines in nutrition (Crête et al. 1996, Valkenburg et al. 1996*b*, 2002). In these herds, however, caribou:wolf ratios were relatively high and predators may not have been numerous enough to bring calf:cow ratios down despite increased vulnerability of calves. In the Nelchina Herd autumn caribou:wolf ratios ranged from about 100:1 to about 150:1 from 1985–1995, whereas in the Delta and Denali herds ratios fluctuated between 15:1 and 50:1 (Boertje et al. 1996). In relatively small herds like the Delta, where predator:prey ratios were relatively high and alternate prey were present, vulnerability to predation is likely to be a more important factor in caribou population dynamics.

Conclusions

Although calf survival increased and the population decline in the DCH stopped after wolf control, cause and effect could not be established, and it appears the wolf control program was largely unsuccessful, except that it may have stopped the herd from declining further. Mortality of caribou older than 16 months did not decline significantly after control, and the increase in calf survival over summer also occurred in an adjacent herd where wolf control did not.

We conclude that wolf control during 1993–1994 did not result in expected large increases in calf survival to autumn primarily because the trapping program did not remove enough wolves during the 14 months in which it was implemented, and secondarily because neonatal mortality from unknown causes and mortality from grizzly bears and golden eagles was significant. Of the 3 plausible explanations proposed to explain continued low autumn calf:cow ratios despite wolf control, none could be entirely rejected. The first (i.e., that not enough wolves were removed) was most strongly supported.

Management implications

Ideally, when controversial and difficult programs such as wolf control are implemented, adequate biological information should be available so that outcomes can reasonably be predicted. In the case of this program, it would have been useful to conduct at least one year of calf mortality study before the wolf control program was implemented. This approach would also have provided some data for evaluating the effects of prey switching and functional responses of the major caribou predators (Dale et al. 1994). Ensuring that wolf control programs have adequate political support would also be highly desirable so that the chances of premature termination can be avoided. Premature termination of projects such as this results in wasted effort and equivocal biological results.

Acknowledgments. We thank J. Larrivee and L. Larrivee (Pollux Aviation, Inc., Fairbanks), B. Scotton, F. Mörschel, D. Reed, and K. Whitten for assistance with fieldwork, and L. Adams, R. Boertje, C. Gardner, and R. Tobey for suggestions on study design and for unpublished data on caribou and wolves in Denali National Park, data on newborn calf mass from the Fortymile and Nelchina herds, and wolf and caribou data from the Nelchina Herd. We also thank J. Ver Hoef for help with statistical analyses. Funding was provided by the State of Alaska and the Federal Aid in Wildlife Restoration program.

Literature cited

ADAMS, L. G., B. W. DALE, AND L. D. MECH. 1995*a*. Wolf predation on caribou calves in Denali National Park, Alaska. Pages 245–260 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35. University of Alberta, Edmonton, Canada.

ADAMS, L. G., F. J. SINGER, AND B. W. DALE. 1995*b*. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59: 584–594.

BERGERUD, A. T. 1964. A field method to determine annual parturition rates for caribou. Journal of Wildlife Management 28: 477–480.

BOERTJE, R. D., AND C. L. GARDNER. 1998. Factors limiting the Fortymile Caribou Herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Research Report. Projects W-24-1 through W-24-5. Study 3.38. Juneau, Alaska, USA.

BOERTJE, R. D., P. VALKENBURG, AND M. E. MCNAY. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60: 474–489.

CRÊTE, M., S. COUTURIER, B. J. HEARN, AND T. E. CHUBBS. 1996. Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George caribou herd. Rangifer Special Issue 9: 27–36.

DALE, B. W., L. G. ADAMS, AND R. T. BOWYER. 1994. Functional responses of wolves preying on barren-ground caribou in a multi-prey ecosystem. Journal of Animal Ecology 63: 644–652.

DAVIS J. L., P. VALKENBURG, AND S. J. HARBO. 1979. Refinement of the aerial photo-direct count-extrapolation caribou census technique. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Research Report. Project W-17-11. Job 3.25R. Juneau, Alaska, USA.

DUBOIS, S. D. 2001. Macomb Herd caribou management report of survey–inventory activities. Pages 73–89 *in* C. Healy, editor. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-27-2 and W-27-3. Project 3.0. Juneau, Alaska, USA.

ESPMARK, Y. 1980. Effects of maternal prepartum undernutrition on early mother–calf relationships in reindeer. Pages 485–496 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings second international reindeer/caribou symposium, Roros, Norway. Direktoratet for Vilt og Ferskvannsfisk, 17–21 September 1979, Trondheim, Norway.

GASAWAY, W. C., R. O. STEPHENSON, J. L. DAVIS, P. E. K. SHEPHERD, AND O. E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs No. 84.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. Second edition. Chapman and Hall, London, United Kingdom.

MECH, L. D., L. G. ADAMS, T. J. MEIER, J. W. BURCH, AND B. W. DALE. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, USA.

REIMERS, E., D. R. KLEIN, AND R. SORUMGAARD. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. Arctic and Alpine Research 15: 107–118.

SKOGLAND, T. 1985. Life history characteristics of wild reindeer (*Rangifer tarandus tarandus* L.) in relation to their food resources; ecological effects and behavioral adaptations. Papers of the Norwegian State Game Research Institute Series 3, No. 14. Direktoratet for Wildlife and Freshwater Fish, Trondheim, Norway.

TOBEY, R. W. 2001. Nelchina herd. Pages 90–105 *in* C. Healy, editor. Caribou management report of survey–inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-27-2 and W-27-3. Project 3.0. Juneau, Alaska, USA.

VALKENBURG, P. 1997. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Research Report. Grants W-23-5 and W-24-1 through W-24-4. Project 3.37. Juneau, Alaska, USA.

VALKENBURG, P., D. A. ANDERSON, J. L. DAVIS, AND D. J. REED. 1985. Evaluation of an aerial photocensus technique for caribou based on radiotelemetry. Pages 287–299 *in* T. C. Meredith and A. M. Martell, editors. Proceedings of the Second North American caribou workshop, 28–29 September 1983. McGill Subarctic Research Paper 40.

VALKENBURG, P., J. L. DAVIS, J. M. VER HOEF, R. D. BOERTJE, M. E. MCNAY, R. M. EAGAN, D. J. REED, C. L. GARDNER, AND R. W. TOBEY. 1996*a*. Population decline in the Delta caribou herd with reference to other Alaskan herds. Rangifer Special Issue 9: 53–62.

VALKENBURG, P., M. A. KEECH, R. A. SELLERS, R. W. TOBEY, AND B. W. DALE. 2002. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Final Report. Grants W-24-5 and W-27-1 through W-27-5. Project 3.42. Juneau, Alaska, USA.

VALKENBURG, P., J. M. VER HOEF, AND R. L. ZARNKE. 1996*b*. Investigation and improvement of techniques for monitoring recruitment, population trend, and nutritional status in the Western Arctic Caribou Herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Research Report. Projects W-24-1 through W-24-4. Study 3.40. Juneau, Alaska, USA.

WHITTEN, K. R. 1995. Antler loss and udder distention in relation to parturition in caribou. Journal of Wildlife Management 59: 273–277.

WHITTEN, K. R., G. W. GARDNER, F. J. MAUER, AND R. B. HARRIS. 1992. Productivity and early calf survival in the Porcupine Caribou Herd. Journal of Wildlife Management 56: 201–212.

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Associate editor: *Murray*