

CARIBOU CALF MORTALITY IN DENALI NATIONAL PARK, ALASKA

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Abstract: Calf mortality is a major component of caribou (*Rangifer tarandus*) population dynamics, but little is known about the timing or causes of calf losses, or of characteristics that predispose calves to mortality. During 1984–87, we radiocollared 226 calves (≤ 3 days old) in the Denali Caribou Herd (DCH), an un hunted population utilized by a natural complement of predators, to determine the extent, timing, and causes of calf mortality and to evaluate influences of year, sex, birthdate, and birth mass on those losses. Overall, 39% of radio-collared calves died as neonates (≤ 15 days old), and 98% of those deaths were attributed to predation. Most neonatal deaths (85%) occurred within 8 days of birth. Few deaths occurred after the neonatal period (5, 10, and 0% of calves instrumented died during 16–30, 31–150, and >150 days of age, respectively). Survival of neonates was lower ($P = 0.038$) in 1985, following a severe winter, than during the other 3 years. In years other than 1985, calves born during the peak of calving (approx 50% of the total, born 5–8 days after calving onset) experienced higher ($P < 0.001$) neonatal survival than did other calves. Grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), and unknown large predators (i.e., grizzly bears or wolves) accounted for 49, 29, and 16% of the neonatal deaths, respectively. The rate of bear-caused mortalities declined ($P < 0.001$) with calf age, and bears killed few calves >10 days old. Wolf predation was not related ($P > 0.05$) to calf age and peaked 10 days after onset of calving. Grizzly bear and wolf predation on neonates during the calving season was a limiting factor for the Denali Caribou Herd.

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Calf mortality is an important factor in the population dynamics of many caribou herds, and predation is suspected as the primary cause of mortality (Miller and Broughton 1974, Bergerud 1980, Page 1985, Bergerud and Elliot 1986, Whitten et al. 1992). Herds exposed to predation may lose 50% of the annual calf crop prior to 6 months of age (Bergerud 1980). However, little is known of the relative importance of mortality agents, timing of deaths, or factors that influence extent of calf losses. Studies involving radiocollaring of neonates provided insights about early calf mortality (Page 1985, Mahoney et al. 1990, Whitten et al. 1992, Adams et al. 1995). Also, wolf removal experiments (Gasaway et al. 1983, Farnell and McDonald 1988) and examinations of dead calves (Miller and Broughton 1974; Miller et al. 1985, 1988)

indicated the importance of wolf predation on caribou calves.

The DCH provided a unique opportunity to investigate caribou population dynamics and caribou/predator relationships in a naturally functioning system, where caribou and their predators are not harvested, to enhance our understanding and management of similar, but managed, systems throughout North America. Annual human harvests of caribou from the DCH averaged $<2\%$ prior to 1976 with no hunting since then (Adams et al. 1989). In Denali National Park, caribou are preyed upon by an un hunted complement of predators, including grizzly bears and wolves. Our objectives were to (1) determine the extent and timing of DCH calf mortality, (2) identify mortality causes and relative importance of each, (3) compare predation patterns of carnivores that were major mortality sources, and (4) identify factors that influence calf survival, such as annual snow conditions, sex, birth mass, and birthdate.

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STUDY AREA

The DCH inhabited approximately 10,000 km² in central Alaska, including most of Denali National Park north of the Alaska Range, and areas south of the range east of Mount McKinley. The Alaska Range consisted of mountain peaks >3,000 m, glaciers, and glacial valleys, flanked by lower mountains and broad lowland flats dissected by several major rivers. Permanent snow and ice occurred above 2,400 m, whereas lower mountains and foothills were covered predominantly by alpine sedge (*Carex* spp.) and shrub (*Salix* and *Betula* spp.) tundras. Treeline occurred at about 800 m, with spruce (*Picea* spp.) woodlands and forests, tussock (*Eriophorum* spp.) tundra, and riparian spruce/willow zones below. During this study, most females from the DCH congregated during calving on calving grounds composed of tundra ridges and broad tussock or shrub tundra flats ranging from 500 to 1,900 m in elevation.

Weather in the region was typical of subarctic montane climates, with temperatures ranging from 32 C in summer to -47 C in winter. Annual precipitation at Denali National Park headquarters on the eastern boundary averaged 38 cm, including 190 cm of snowfall (Natl. Park Serv., Denali Park, Alas., unpubl. rec.). Snowfall between 1 September and 31 May was 155, 336, 86, and 103 cm for winters 1983-84, 1984-85, 1985-86, and 1986-87, respectively. During all years except 1985, the calving range of the DCH below 900 m elevation was mostly free of snow at the onset of calving, but in 1985, snow cover was complete at the onset of calving, except for wind-blown ridges. In addition, approximately 20 cm of snow fell on the calving ground during

17-19 May 1985, shortly after the peak of calving.

The DCH declined from about 9,500 animals in the early 1960s to about 1,000 by the mid-1970s (Singer 1987), a period when several other Alaskan caribou herds declined (Klein and White 1978). Severe winters, density-related resource limitation, heavy wolf predation, and overharvest were implicated in these declines (Davis et al. 1980, Gasaway et al. 1983, Van Ballenberghe 1985, Bergerud and Ballard 1988, Valkenburg and Davis 1988, Eberhardt and Pitcher 1992). Unlike in other herds, human harvests could not have been a factor in the DCH's decline (Adams et al. 1989).

During the DCH decline (1963-75), early calf losses appeared to be important in the herd's dynamics. Calf:cow ratios ("cow" included yearling bulls) in summer were <20:100 and averaged 13:100 (Adams et al. 1989). Investigations of nutritional status of the herd indicated the herd and its range were in good condition (Boertje 1981, 1984). Boertje (1981) suggested that early predation on calves, independent of nutritional condition of the herd, was the key factor limiting the population.

During our study, the DCH grew by 6% annually from 2,200 animals in September 1984 to 2,600 by September 1987 (Adams et al. 1989). Fall calf:cow ratios averaged 36:100 by late September each year. The herd shared its range with approximately 2,000 moose (*Alces alces*) (Meier 1987) and 2,400 Dall's sheep (*Ovis dalli*) (Singer and Dalle-Molle 1985). Grizzly bears occurred primarily in upland areas at approximately 30 bears/1,000 km² (Dean 1987). Wolves were found throughout the area at 4-5 wolves/1,000 km² in later winter (Adams et al. 1995). Other predators included black bears (*U. americanus*), coyotes (*C. latrans*), lynx (*Felis lynx*), wolverines (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*).

METHODS

Calf Capture

We radiocollared caribou neonates and monitored them daily, weather permitting, during May 1984-87. In 1984-86, we searched the known calving range of the herd by helicopter or fixed-wing aircraft to locate calving caribou. In 1987, in addition to aerial searches, we monitored 43 radiocollared cows to aid in finding calving caribou.

We attempted to capture any calf that appeared young enough to be caught (i.e., ≤ 3 days old) (Lent 1964, Nowosad 1975). When we observed a young calf, the helicopter landed as close as possible to the cow-calf pair, usually within 5 m, and a person was dropped off to capture the calf by hand. If the helicopter could not be landed near the cow-calf pair because of steep terrain or tree cover, 1 or 2 people were dropped off within 200 m and the helicopter slowly herded the cow and calf toward the hidden capture crew.

Each person handling calves wore clean rubber gloves for each capture to minimize scent transfer between calves. Each calf was radio-collared, sexed, and examined to determine umbilicus condition (bloody, wet, dry, or absent) and hoof characteristics (hardness, rim color, and wear). We noted posture, coordination, umbilicus condition, and hoof characteristics to estimate the calf's age in days (Johnson 1951, Haugen and Speake 1958, Lent 1964, Adams et al. 1989). In 1986 and 1987, we weighed each calf with a hand-held spring scale and a cloth strap positioned around the animal's chest. Handling took < 1.5 minutes/calf.

Radio collars weighed 134 g (1.7% of body mass, on average) and consisted of a motion-sensitive transmitter mounted on a brown elastic collar. Transmitter pulse rate doubled if stationary for 1 hour to indicate mortality. The elastic collar had 3 expansion folds and a break-away seam sewn with cotton thread to allow for animal growth and eventual release of the radio collar.

Monitoring and Mortality Investigation

We observed instrumented calves daily, weather permitting, until at least 31 May of each year by radiolocating them from a PA-18 Super Cub or a Bell 206 Jet Ranger helicopter. In 1984 and 1985, we monitored calves weekly from 31 May until 22 July and 23 June, respectively. In 1986 and 1987, we located calves at least weekly during June and approximately monthly throughout the rest of their first year.

When a mortality was detected during May, we investigated it by helicopter, usually within 5 hours of detection. After May, we investigated mortalities as soon as practical, usually within 1 month. We assumed that deaths after May occurred midway between the dates last observed alive and first mortality signals; often we could

not determine the causes of death. For all calves, we examined carcasses and mortality sites for information on causes of death, including predator signs such as tracks, scats, and hair (Ballard et al. 1979, Adams et al. 1989). We necropsied carcasses either on site or in the laboratory and noted wounding patterns.

Statistical Analyses

We used logistic regression (Feinberg 1980) to examine influences of year, sex, and birthdate on survival to 15 days old (neonatal survival; calves ≤ 15 days old referred to as neonates throughout). The initial regression model included indicator variables for ages at capture (CAPAGE = 1, CAPAGE = 2, and CAPAGE = 3), in place of a general regression constant, to account for staggered entry of calves into our sample over the 3-day range of CAPAGE. We classified calves as early, peak, or late births on the basis of their estimated birthdates falling within 4 days, 5–8 days, or ≥ 9 days of the onset of calving, respectively. Those classes approximated 25, 50, and 25% of the births in the herd, respectively (Adams, unpubl. data). We also compared age-specific patterns of bear- and wolf-caused mortality rates for neonates by logistic regression.

Because we weighed calves in 1986 and 1987 only, we conducted separate logistic regression analyses to evaluate influences of calf mass on neonatal and annual survival for those years. We used analysis of variance (ANOVA) procedures (Zar 1984) to test for differences in capture mass associated with sex, year, birth period, and CAPAGE. Because CAPAGE was significant in the ANOVA ($F = 20.7$; 2, 120 df; $P < 0.001$), we used 3 interaction terms (CAPAGE = 1 \times MASS, CAPAGE = 2 \times MASS, CAPAGE = 3 \times MASS) in our logistic regression model to test effects of mass on survival while allowing for variation in mass with CAPAGE.

We calculated Kaplan-Meier survival estimates, accounting for staggered entry of calves into our sample over the first 3 days following birth, and survival functions (Pollock et al. 1989) for the neonatal period (all years) and the remainder of the year (1986 and 1987 calves only) for calf classes that differed in logistic regression analyses. Using generalized log-rank tests (GLR; Pollock et al. 1989), we compared survival functions. We evaluated differences in cause-specific mortality between 1985 and other years of the

Table 1. Timing and causes of deaths of caribou calves radiocollared as neonates in Denali National Park, Alaska, May 1984–87.

Age class (days)	Cause of death	Year			
		1984 <i>n</i> = 41	1985 <i>n</i> = 55	1986 <i>n</i> = 56	1987 <i>n</i> = 74
1–15	Grizzly bear		12	10	13
	Wolf	7	8	9	10
	Unknown large predator	1	5	1	2
	Golden eagle	4	3		1
	Wolverine		1		
	Drowning			1	
	Perinatal mortality				1
	Total deaths ^a	12 (29%)	29 (53%)	21 (38%)	27 (36%)
16–30	Grizzly bear		2		
	Wolf			1	
	Unknown large predator		1	3	4
	Total deaths ^a		3 (12%)	4 (11%)	4 (9%)
31–60	Wolf				2
	Golden eagle				1
	Undetermined			2	2
	Total deaths ^a			2 (6%)	5 (12%)
61–150	Grizzly bear			1	
	Fall into glacial crevasse				1
	Undetermined			1	3
	Total deaths ^a			2 (7%)	4 (11%)
151–365	Total deaths			0	0

^a No. in parentheses is % mortality during the period.

study with 2 × 2 contingency tables (Feinberg 1980).

RESULTS

We first observed calves between 10 and 12 May each year, and we observed newborn calves for ≤4 weeks following the onset of calving. We captured 233 caribou neonates estimated to be 1, 2, or 3 days old at capture (42, 42, and 16%, respectively). The number of males and females in our sample was similar (117 and 114, respectively; 2 not sexed). Calves born during early, peak, and late periods in our sample totaled 74, 94, and 65, respectively. Five calves were killed by golden eagles on the day of capture at the capture site and these were assumed to be study related. In 1985, 2 calves lost their collars shortly after capture. Therefore, our sample for survival analyses consisted of 226 calves (Table 1).

Masses of calves captured in 1986–87 (*n* = 127 weighed of 130 captured) varied between sexes ($F = 65.3$; 1, 120 df; $P < 0.001$) and with CAPAGE ($F = 20.7$; 2, 120 df; $P < 0.001$), but not between years ($F = 0.05$; 1, 120 df; $P = 0.823$) or among birth periods ($F = 2.61$; 2, 120 df; $P = 0.076$). To estimate birth masses and account for CAPAGE, we subtracted 0.6 kg for

each day of age >1 (Clutton-Brock et al. 1982), on the basis of regression analysis of mass with CAPAGE and sex as independent variables ($R^2 = 0.44$, $P < 0.001$ for regression; coefficient for CAPAGE = 0.64, SE = 0.11, $t = 5.91$, $P < 0.001$). An interaction term for sex and CAPAGE, indicative of different growth rates for each sex, was not significant ($t = 1.54$, $P = 0.125$). Birth mass estimates for males and females averaged 9.0 kg (*n* = 67, SE = 0.11, range 7.5–11.7) and 7.8 kg (*n* = 60, SE = 0.11, range 4.9–9.9), respectively.

For all years of the study, 100 calves (44%) died prior to 30 days of age (Table 1). Of those, 76 died within 8 days of birth. In 1986–87, 13 calves (10%) died between 30 and 130 days of age, with no deaths recorded after that.

Factors Influencing Survival

In analyses of effects of year, sex, and birth period on neonatal survival, indicator variables for peak birth period ($G^2 = 6.80$, 1 df, $P = 0.009$) and 1985 ($G^2 = 4.31$, 1 df, $P = 0.038$) were the only factors ($P < 0.05$) to enter the logistic regression model, indicating increased survival of calves born during the peak period and reduced survival overall in 1985, following winter 1984–85 (Table 2). To determine whether differences

Table 2. Kaplan-Meier survival estimates (Pollock et al. 1989) for caribou calves, Denali National Park, Alaska, during 1984–87 (Early = born within 4 days of calving onset; Peak = born 5–8 days after onset; Late = born > 8 days after the onset).

Year	Birth period	No. at risk	\hat{s}	SE	95% CI
Neonates (1–15 days of age)					
Low snowfall yr ^a					
1984	Early	20	0.450	0.111	0.232–0.668
	Peak	21	0.950	0.049	0.855–1.000
1986	Late		none captured		
	Early	26	0.523	0.099	0.328–0.718
	Peak	18	0.717	0.107	0.507–0.927
1987	Late	12	0.667	0.136	0.400–0.933
	Early	18	0.516	0.123	0.275–0.757
	Peak	23	0.727	0.095	0.541–0.913
Pooled	Late	33	0.517	0.093	0.335–0.699
	Early	64	0.486	0.068	0.352–0.620
	Peak	62	0.800	0.052	0.698–0.901
	Late	45	0.560	0.084	0.395–0.725
	Combined ^b	171	0.662	0.038	0.588–0.735
High snowfall yr ^c					
1985	Early	9	0.667	0.157	0.359–0.975
	Peak	28	0.451	0.095	0.266–0.637
	Late	18	0.388	0.115	0.163–0.613
	Combined ^d	55	0.489	0.068	0.356–0.622
Older calves (16–365 days of age) ^d					
1986		35	0.769	0.065	0.641–0.898
1987		47	0.723	0.062	0.602–0.845

^a Snowfall ≤ 155 cm during previous Sep–May.

^b Early, peak, and late rates weighted by the proportion of calves born within each birth period (0.25, 0.50, and 0.25, respectively; Adams, unpubl. data).

^c Snowfall = 336 cm during previous Sep–May.

^d Survival of calves > 15 days old did not vary among birth periods ($G^2 = 2.79$, 2 df, $P = 0.248$).

in survival attributed to the peak birth period applied to 1985 as well as other years, we substituted 2 interaction terms (1985 \times PEAK and OTHER \times PEAK) for the peak birth period term in the logistic regression model that included the significant year effect. Survival of calves born during the peak period was enhanced only in years other than 1985 (OTHER \times PEAK, $G^2 = 12.91$, 1 df, $P < 0.001$; PEAK \times 1985, $G^2 = 0.03$, 1 df, $P = 0.869$).

We conducted similar analyses of survival beyond 15 days of age for 1986 and 1987 calves (Table 2). For those 2 years, survival from 16 days to 1 year was not affected by year ($G^2 = 0.25$, 1 df, $P = 0.617$), sex ($G^2 = 0.02$, 1 df, $P = 0.888$), or birth period ($G^2 = 2.79$, 2 df, $P = 0.248$).

We hypothesized that low birth mass calves would suffer higher neonatal mortality, as well as throughout their first year, than heavier calves within the same cohort. However, birth mass was not related to survival to 15 days of age ($G^2 = 3.70$, 3 df, $P = 0.296$) or throughout the first year ($G^2 = 3.40$, 3 df, $P = 0.221$) for 1986–87 calves.

Patterns of Survival

As a result of differences described above, we calculated neonatal survival curves for each birth period for 1985 and for the other 3 years combined. In low snowfall years (1984, 1986–87; snowfall ≤ 155 cm during previous Sep–May), survival of calves born early and late, although similar (GLR, $\chi^2 = 1.80$, 1 df, $P = 0.179$), differed from that for calves born during the peak period in 2 ways (Fig. 1a). Survival of calves born early appeared to be poorer than that of peak calves during the first 7 days following birth, whereas calves born late showed poorer survival only during the first 2 days following birth. Oriented in the proper time scale (Fig. 1b), differences in survival indicate that calves born early suffered high losses until late calves began appearing.

In 1985, when snowfall equaled 336 cm during the previous winter, survival between birth periods did not differ ($P = 0.869$), but sample sizes were small (Table 2). Early and peak calves appeared to experience high survival during the first few days following birth (Fig. 1a). Oriented

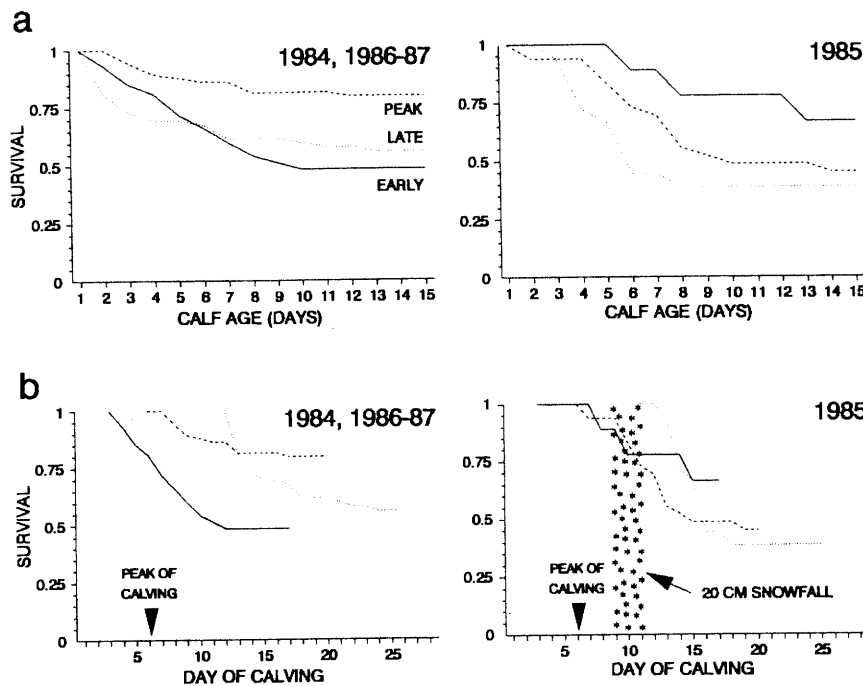


Fig. 1. Survival of caribou calves radiocollared in the Denali Caribou Herd, Alaska, during May 1984, 1986, and 1987 (following low snowfall winters; snowfall ≤ 155 cm during previous Sep–May) and May 1985 (following a high snowfall winter; snowfall = 336 cm during previous Sep–May) by birth period (EARLY = born within 4 days of calving onset; PEAK = born 5–8 days after onset; LATE = born >8 days after onset). (a) Survival versus calf age. (b) Survival curves from Figure 1a oriented in time according to mean birthdate of calves within each sample.

in time, survival was high for these calves prior to day 9 of the calving season or the time of a 20-cm snowfall (Fig. 1b). During and after this snowfall, losses of peak- and late-born calves was high. Survival of calves born during the peak period was lower in 1985 than the other years (GLR, $\chi^2 = 9.80$, 1 df, $P = 0.002$).

Causes of Neonatal Mortality

Of the 89 neonatal deaths, all but 2 were attributed to predation. An additional 11 calves (5% of the total) died by 30 days of age and all were killed by predators (Table 1). Grizzly bears were the most common cause of death for neonates (49% of deaths or 19% of calves instrumented; Table 1).

An average of 29% of neonatal deaths were attributed to wolves each year (11% of calves collared; Table 1). Although fewer deaths were attributed to wolves than grizzly bears, wolf kills were more difficult to identify and may have constituted a larger portion of kills by unknown large predators (16% of neonatal deaths each year on average) than grizzly bears. Compared with grizzly bears, wolves were seldom observed on kills ($n = 13$ and 3 occasions, respectively) and seldom left scats at kill sites ($n = 9$ and 1,

respectively). Further, most wolf kill designations were based on tracks in snow ($n = 9$) or characteristic wounding patterns on partial or whole carcasses ($n = 10$). Wolves completely consuming a carcass in areas with no snow would have left little evidence. As we gained experience identifying wolf kills (i.e., locating wolf hair amidst caribou calf hair and recognizing wounding patterns), the proportion of neonatal deaths due to wolves increased, decreasing that attributed to unknown large predators, but grizzly bear kills stayed about the same (Table 1).

Wolverines and golden eagles killed 1 and 4 neonates, respectively. The wolverine kill and 3 golden eagle kills occurred in 1985 when snow was deep throughout the study area, resulting in greater losses to these small predators in 1985 than in other years ($\chi^2 = 8.60$, 1 df, $P = 0.003$).

Comparison of Bear- and Wolf-caused Mortality

Daily mortality rates attributed to grizzly bears declined with age (Fig. 2; $G^2 = 30.68$, 1 df, $P < 0.001$), and grizzly bears killed few calves >10 days of age (Fig. 2 and Table 1). Daily wolf-caused mortality rates, on the other hand, showed no declining trend with calf age during

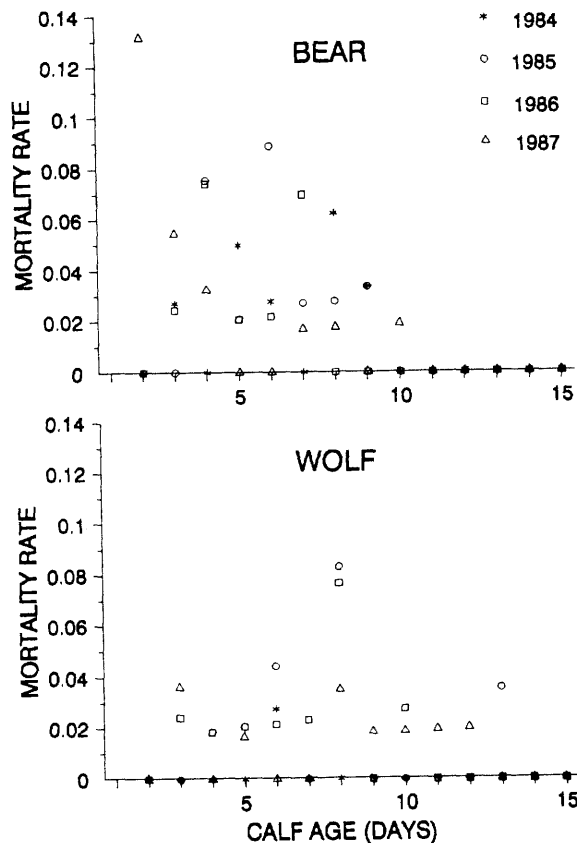


Fig. 2. Age-specific rates of grizzly bear- and wolf-caused mortalities of caribou calves radiocollared in the Denali herd, Alaska, during May 1984-87.

the neonatal period (Fig. 2; $G^2 = 2.33$, 1 df, $P = 0.126$). Losses to wolves, as well as unknown predator kills, decreased after 15 days of age (Table 1). Timing of grizzly bear and wolf kills appeared to differ with grizzly bear mortalities occurring throughout the calving period while most wolf-caused deaths occurred during the middle of the calving period (Fig. 3). Higher losses of peak and late calves in 1985, compared with other years (Fig. 1), were the result of greater losses to wolves ($\chi^2 = 4.38$, 1 df, $P = 0.036$) and grizzly bears ($\chi^2 = 6.78$, 1 df, $P = 0.009$), respectively.

DISCUSSION

Predators killed 43% of the calves we instrumented before 30 days of age. These figures could be low estimates of mortality because some calves may have died prior to any opportunity for inclusion in our radio-collared sample (Ozaga and Clute 1988; Whitten et al. 1992; Adams, unpubl. data).

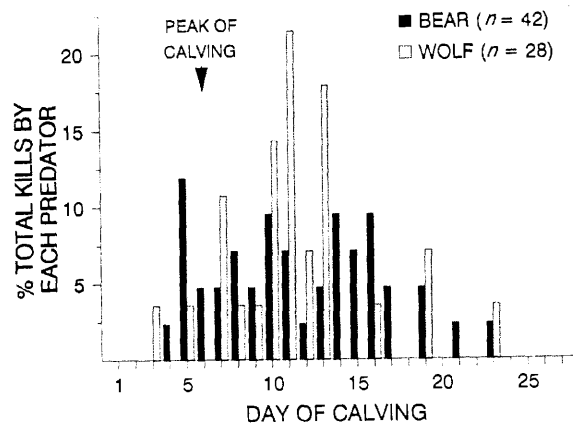


Fig. 3. Timing of grizzly bear and wolf kills of radio-collared neonates (calves ≤ 15 days old) in the Denali Caribou Herd, Alaska, during May 1984-87. Results from each year were aligned on the earliest estimated birthdate for calves in the radio-collared sample.

Factors Influencing Survival

The role of winter snowfall and spring snow-depths in determining the extent of neonatal mortality is unclear. In this study, neonate survival was lower following the high snowfall of winter 1984-85. In that year, the snowpack persisted throughout the calving season, restricting caribou to a few low elevation areas, and the calving grounds were covered with 20 cm of snow shortly after the calving peak. Additional calf deaths in 1985 were attributed to large predators (45 and 33% of calves instrumented in 1985 and other years, respectively) and small predators (7 and 1% in 1985 and other years, respectively). Losses to small predators occurred throughout the calving season, but most losses to grizzly bears and wolves occurred immediately following the mid-calving season snowstorm.

For caribou, calf survival is generally lower in years of late snowmelt (Page 1985, Bergerud and Elliot 1986, Bergerud and Page 1987, Adams et al. 1995). Bergerud and Page (1987) hypothesized that following severe winters, caribou calve at lower elevations because of persistent snow at higher elevations and suffer higher calf losses because they are not able to space themselves from wolves using alternative prey at these lower elevations. Further, caribou cows rely on mottled snow cover to provide crypsis for their newborns and increase the search effort required by predators to find them (Bergerud and Page 1987). Snowpack conditions and the snowstorm following the calving peak on our

study area in 1985 would have negated these predator evasion strategies.

Alternatively, Adams et al. (1995) showed for Denali caribou that calf birth masses declined with increasing winter snowfall during gestation and that neonatal mortality was more strongly correlated with average birth mass than with mean calving elevation. Further, higher losses of calves to small predators is consistent with increased vulnerability of calves and/or poor maternal care (Langenau and Lerg 1976). Unfortunately, we do not know if heavy snowfall in winter 1984–85 resulted in lighter calves because we did not weigh 1985 calves.

In years other than 1985, birthdate influenced neonatal survival with higher survival of peak-born calves over those born either early or late. Two factors may explain poor survival of calves born early: (1) their numbers were insufficient to swamp predators on the calving grounds, and (2) they were first to aggregate into nursery bands, and therefore, more detectable than other calves when the majority of wolf kills occurred. As calving proceeded into the peak period, the number of calves increased and local predators were probably swamped resulting in higher survival of peak-born calves. Late calves experienced poor survival because predators were attracted to areas where caribou were calving, and vulnerable newborn calves were rapidly detected and killed. Therefore, peak-born calves accrued the most benefit from synchronous calving (Estes 1976).

Comparisons of Grizzly Bear and Wolf Predation

Grizzly bears were the most important mortality agent for neonates, with wolves second. Grizzly bear predation declined with calf age (Fig. 2) and occurred throughout the calving period dependent on the abundance of young calves. Wolf predation was not related to calf age up to 15 days old but occurred during a short period a few days after the peak of calving.

Differences in these patterns are related to differences in abundance, distribution, and predatory characteristics of these carnivores. Grizzly bears, because of their solitary nature, overlapping home ranges (Jonkel 1978), and habitat selection patterns (Murie 1981), were distributed throughout habitats available to caribou cows during calving. Grizzly bears occurred at densities of about 30 bears/1,000 km²,

or 20 individuals or family groups/1,000 km² (Dean 1987). Density and distribution of grizzly bears, particularly sows that inhabit relatively small, overlapping home ranges of 100–250 km² (Reynolds and Hechtel 1983, Miller 1987), resulted in rapid detection of calving caribou and continued success in locating young vulnerable calves by many bears within their home ranges. Bear-caused mortality rates declined with calf age indicating vulnerability to grizzly bear predation declined rapidly as calves matured (Lent 1964) and joined larger nursery groups (Bergerud 1974; Adams, unpubl. data).

Caribou calves were probably an important component in the nutrient budget of grizzly bears. Caribou calves were available prior to the emergence of green vegetation and were a source of energy and protein, when other foods were of limited quality and availability. Using methodology from Schwartz and Franzmann (1991: 58), we estimated that the digestible energy content of a single caribou calf provided the energy requirement of an adult female grizzly bear for 1.7–3.3 days. A sow consuming 1 caribou calf/day during the 20 days that young calves were abundant each year could meet 34–66 days of her annual energy requirement from this food source alone. Reynolds and Garner (1987) provided evidence that population density and productivity of grizzly bears in Alaska's Brooks Range were greater where caribou calving occurred than where caribou calves were not available. Similar conclusions have been drawn for black bears preying on moose calves (Schwartz and Franzmann 1991).

The lag between onset of calving and most wolf predation could result from the time required for wolves to detect calving concentrations of caribou. Wolves were approximately 15% as abundant as grizzly bears and only 2–3 wolf packs had caribou concentrated for calving within their territories (Adams et al. 1995). Within these pack territories, caribou selected habitats for calving that were unlikely to be regularly searched by wolves at onset of calving, particularly in years when little snow remained on the calving grounds. If spring snowpack was shallow, caribou calved at higher elevations away from alternative wolf prey (Bergerud and Page 1987, Adams et al. 1995).

Alternatively, for wolves, profitability of hunting caribou calves may be low at onset of calving, relative to other available prey. Ini-

tially, calves were rare and widely scattered. Calves also were a poor quality food source for wolves because of their small size and low energy and protein content/kg compared with older ungulates (Robbins 1983). As calving progressed, however, profitability of hunting calves increased because calves were aggregating in nursery bands and many could be killed at once. Several incidents of multiple kills of caribou calves by wolves have been documented (Murie 1944; Miller and Broughton 1974; Miller et al. 1985, 1988), indicating the vulnerability of calves in larger groups. In this study, ≥ 7 of 28 radiocollared calves killed by wolves were taken in multiple killing events. In addition, on the basis of the average age at death and our growth rate estimate, neonates killed by wolves averaged nearly 50% larger at death than at birth, further increasing their value as wolf prey.

The period of intense wolf predation ended abruptly. Although young calves were still abundant by day 14 of the calving period, 25% of the calves were ≥ 8 days old and that proportion of older calves increased over the ensuing days. The increasing proportion of older calves may have complicated detection or killing of younger, still vulnerable calves within increasingly large nursery bands (Estes 1976). Further, handling time to consume, cache, and/or transport calf remains to dens could limit time available to kill additional calves (Krebs 1978). Finally, moose calves and Dall's sheep lambs began to appear shortly after the peak of caribou calving (Ballard et al. 1991, Rachlow and Bowyer 1991) and may have replaced caribou calves as the most profitable prey for wolves to pursue.

Survival Patterns

The first 8 days following birth were the most crucial period for caribou calves in this study. Combined effects of grizzly bear predation decreasing with age and the preponderance of 8-day-old calves killed by wolves resulted in this threshold of survival at 8 days of age. After the neonatal period, a few calves died during summer but we noted no deaths after September in 1986 and 1987, the only years that calves were monitored beyond midsummer. Similar to this study, 2 other studies of radiocollared calves in Alaska reported winter survival of calves comparable with that of adults (Davis et al. 1988; K. R. Whitten, Alaska Dep. Fish and Game, Fairbanks, pers. commun.). Comparable winter calf survival is also indicated by composition

survey data for the Nelchina Herd (Bergerud and Ballard 1988), as well as Newfoundland caribou (Bergerud 1971). Finally, in recent studies of wolf predation on caribou, calves were not selected preferentially by wolves during winter (Ballard et al. 1987, Ballard 1993, Dale et al. 1995, Mech et al. 1995).

MANAGEMENT IMPLICATIONS

Our study documented the magnitude, timing, and causes of calf mortality in a caribou population that is ecologically similar to many herds throughout northwestern North America. During our study, the DCH occurred at a low density (0.2–0.3/km²). Cows were large bodied and experienced high survival. They were productive and produced large calves (Adams, unpubl. data). More females died as calves within 8 days of birth than died in all age classes throughout the remainder of the year. The herd grew 6% annually in spite of the calf losses described here. Because these numerous neonatal losses, almost entirely the result of grizzly bear and wolf predation, occurred in this low density herd, were restricted to a narrow age span, were affected by differences in calf birthdates of only a few days, and were not related to calf birth masses, we conclude that this mortality was additive and therefore a major limiting factor.

LITERATURE CITED

- ADAMS, L. G., B. W. DALE, AND L. D. MECH. 1995. Wolf predation on caribou calves in Denali National Park, Alaska. Pages in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world: proceedings of the second North American symposium on wolves. Can. Circumpolar Inst., Univ. Alberta, Edmonton. In Press.
- , ———, AND B. SHULTS. 1989. Population status and calf mortality of the Denali Caribou Herd, Denali National Park and Preserve, Alaska—1984–1988. U.S. Natl. Park Serv. Alaska Reg. Nat. Resour. Prog. Rep. AR-89/13, Anchorage. 131pp.
- BALLARD, W. B. 1993. Demographics, movements, and predation rates of wolves in northwest Alaska. Ph.D. Thesis, Univ. Arizona, Tucson. 374pp.
- , A. W. FRANZMANN, K. P. TAYLOR, T. SPRAKER, AND R. O. PETERSON. 1979. Comparisons of techniques utilized to determine moose calf mortality in Alaska. *Alces* 15:363–387.
- , J. S. WHITMAN, AND C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* 98. 53pp.
- , ———, AND D. J. REED. 1991. Population dynamics of moose in south-central Alaska. *Wildl. Monogr.* 114. 49pp.

- BERGERUD, A. T. 1971. The population dynamics of Newfoundland caribou. *Wildl. Monogr.* 25: 55pp.
- . 1974. The role of the environment in the aggregation, movement and disturbance behaviour of caribou. Pages 552–584 in V. Geist and F. Walther, eds. *The behaviour of ungulates and its relation to management*. Int. Union Conserv. Nat. New Ser. Publ. 24, Morges, Switz.
- . 1980. A review of the population dynamics of caribou and wild reindeer in North America. Pages 556–581 in E. Reimers, E. Gaare, and S. Skjenneberg, eds. *Proc. second international reindeer/caribou symposium*. Dir. for Vilt of Ferskvannsfisk, Trondheim, Norway. 799pp.
- , AND W. B. BALLARD. 1988. Wolf predation on caribou: the Nelchina herd case history, a different interpretation. *J. Wildl. Manage.* 52: 344–357.
- , AND J. P. ELLIOT. 1986. Dynamics of caribou and wolves in northern British Columbia. *Can. J. Zool.* 64:1515–1529.
- , AND R. E. PAGE. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Can. J. Zool.* 65:1597–1606.
- BOERTJE, R. D. 1981. Nutritional ecology of the Denali Caribou Herd. M.S. Thesis, Univ. Alaska, Fairbanks. 294pp.
- . 1984. An energy model for adult female caribou of the Denali Herd, Alaska. *J. Range Manage.* 38:468–473.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Ill. 378pp.
- DALE, B. W., L. G. ADAMS, AND R. T. BOWYER. 1995. Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park, Alaska. Pages in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. *Ecology and conservation of wolves in a changing world: proceedings of the second North American symposium on wolves*. Can. Circumpolar Inst., Univ. Alberta, Edmonton. In Press.
- DAVIS, J. L., P. VALKENBURG, AND D. J. REED. 1988. Mortality of the Delta Caribou Herd to 24 months of age. *Proc. third North American caribou workshop*. Alaska Dep. Fish and Game, Juneau, Wildl. Tech. Bull. 8:38–51.
- , ———, AND H. V. REYNOLDS. 1980. Population dynamics of Alaska's Western Arctic Caribou Herd. Pages 595–604 in E. Reimers, E. Gaare, and S. Skjenneberg, eds. *Proc. second international reindeer/caribou symposium*. Dir. for Vilt of Ferskvannsfisk, Trondheim, Norway.
- DEAN, F. C. 1987. Brown bear density, Denali National Park, and sighting efficiency adjustment. *Int. Conf. Bear Res. and Manage.* 7:37–43.
- EBERHARDT, L. L., AND K. W. PITCHER. 1992. A further analysis of the Nelchina caribou and wolf data. *Wildl. Soc. Bull.* 20:385–395.
- ESTES, R. D. 1976. The significance of breeding synchrony in the wildebeest. *East Afr. Wildl. J.* 14:135–152.
- FARNELL, R., AND J. MACDONALD. 1988. The influence of wolf predation on caribou mortality in Yukon's Finlayson Caribou Herd. *Proc. third North American caribou workshop*. Alaska Dep. Fish and Game, Juneau, Wildl. Tech. Bull. 8:52–70.
- FEINBERG, S. E. 1980. The analysis of cross-classified categorical data. Massachusetts Inst. Tech. Press, Cambridge. 198pp.
- GASAWAY, W. C., R. O. STEPHENSON, J. L. DAVIS, P. E. K. SHEPARD, AND O. E. BURRIS. 1983. Interrelationships of wolves, prey and man in interior Alaska. *Wildl. Monogr.* 84. 50pp.
- HAUGEN, A. O., AND D. W. SPEAKE. 1958. Determining age of young fawn white-tailed deer. *J. Wildl. Manage.* 22:319–321.
- JOHNSON, D. E. 1951. Biology of the elk calf, *Cervus canadensis nelsoni*. *J. Wildl. Manage.* 15:396–410.
- JONKEL, C. 1978. Black, brown (grizzly), and polar bears. Pages 227–248 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America: ecology and management*. Stackpole Books, Harrisburg, Pa.
- KLEIN, D. R., AND R. G. WHITE, EDITORS. 1978. Parameters of caribou population ecology in Alaska: proceedings of a symposium and workshop. *Biol. Pap. Univ. Alaska Spec. Rep.* 3, Fairbanks. 49pp.
- KREBS, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23–63 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell Sci. Publ. Oxford, U.K. 494pp.
- LANGENAU, E. E., JR., AND J. M. LERG. 1976. The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. *Appl. Anim. Ethology* 2:207–223.
- LENT, P. C. 1964. Calving and related social behavior in the barren-ground caribou. Ph.D. Thesis, Univ. Alberta, Edmonton. 220pp.
- MAHONEY, S. P., H. ABBOTT, L. H. RUSSELL, AND B. R. PORTER. 1990. Woodland caribou calf mortality in insular Newfoundland. *Int. Congr. Game Biol.* 79:592–599.
- MECH, L. D., T. J. MEIER, J. W. BURCH, AND L. G. ADAMS. 1995. Patterns of prey selection by wolves in Denali National Park. Pages in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. *Ecology and conservation of wolves in a changing world: proceedings of the second North American symposium on wolves*. Can. Circumpolar Inst., Univ. Alberta, Edmonton. In Press.
- MEIER, T. J. 1987. 1986 aerial moose census-Denali National Park and Preserve. U.S. Natl. Park Serv. Alaska Reg. Nat. Resour. Rep. AR-87/10, Anchorage. 15pp.
- MILLER, F. L., AND E. BROUGHTON. 1974. Calf mortality on the calving grounds of Kaminuriak caribou, during 1970. *Can. Wildl. Serv. Rep. Ser.* 26. 26pp.
- , ———, AND A. GUNN. 1988. Mortality of migratory barren-ground caribou on the calving grounds of the Beverly herd, Northwest Territories, 1981–1983. *Can. Wildl. Serv. Occas. Pap.* 66. 26pp.
- , A. GUNN, AND E. BROUGHTON. 1985. Surplus killing as exemplified by wolf predation on newborn caribou. *Can. J. Zool.* 63:295–300.

- MILLER, S. D. 1987. Susitna hydroelectric project final report—big game studies, volume VI: black bear and brown bear. Alaska Dep. Fish and Game, Juneau. 276pp.
- MURIE, A. 1944. The wolves of Mount McKinley. U.S. Natl. Park Serv. Fauna Ser. 5. 238pp.
- . 1981. The grizzlies of Mount McKinley. U.S. Natl. Park Serv. Sci. Monogr. Ser. 14. 251pp.
- NOWOSAD, R. F. 1975. Reindeer survival in the MacKenzie Delta Herd, birth to four months. Pages 199–208 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. first international reindeer and caribou symposium. Biol. Pap. Univ. Alaska Spec. Rep. 1, Fairbanks.
- OZOGA, J. J., AND R. K. CLUTE. 1988. Mortality rates of marked and unmarked fawns. J. Wildl. Manage. 52:549–551.
- PAGE, R. E. 1985. Early caribou calf mortality in northwestern British Columbia. M.S. Thesis, Univ. Victoria, B.C. 143pp.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53:7–15.
- RACHLOW, J. L., AND R. T. BOWYER. 1991. Inter-annual variation in timing and synchrony of parturition in Dall's sheep. J. Mammal. 72:487–492.
- REYNOLDS, H. V., AND G. W. GARNER. 1987. Patterns of grizzly bear predation on caribou in northern Alaska. Int. Conf. Bear Res. and Manage. 7:59–68.
- , AND J. L. HECHTEL. 1983. Population structure, reproductive biology, and movement patterns of grizzly bears in northcentral Alaska. Alaska Dep. Fish and Game Fed. Aid in Wildl. Restoration Prog. Rep., Proj. W-22-1, Juneau. 29pp.
- ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, N.Y. 343pp.
- SCHWARTZ, C. C., AND A. W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr. 113. 58pp.
- SINGER, F. J. 1987. Dynamics of caribou and wolves in Denali National Park. Pages 117–157 in F. J. Singer, ed. Proc. conference on science in the national parks, volume 2: wildlife management and habitats. George Wright Soc. and U.S. Natl. Park Serv., Washington, D.C.
- , AND J. DALLE-MOLLE. 1985. The Denali ungulate-predator system. Alces 21:339–358.
- VALKENBURG, P., AND J. L. DAVIS. 1988. Status, movements, range use patterns, and limiting factors of the Fortymile Caribou Herd. Alaska Dep. Fish and Game Fed. Aid in Wildl. Restoration Prog. Rep., Proj. W-22-6, Juneau. 25pp.
- VAN BALLEMBERGHE, V. 1985. Wolf predation on caribou: the Nelchina herd case history. J. Wildl. Manage. 49:711–720.
- WHITTEN, K. R., G. W. GARNER, F. J. MAUER, AND R. B. HARRIS. 1992. Productivity and early calf survival in the Porcupine Caribou Herd. J. Wildl. Manage. 56:201–212.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 718pp.

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