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Natality and calf mortality of the Northern Alaska Peninsula and Southern Alaska Peninsula caribou herds

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Abstract: We studied natality in the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou (*Rangifer tarandus granti*) herds during 1996–1999, and mortality and weights of calves during 1998 and 1999. Natality was lower in the NAP than the SAP primarily because most 3-year-old females did not produce calves in the NAP. Patterns of calf mortality in the NAP and SAP differed from those in Interior Alaska primarily because neonatal (*i.e.*, during the first 2 weeks of life) mortality was relatively low, but mortality continued to be significant through August in both herds, and aggregate annual mortality was extreme (86%) in the NAP. Predators probably killed more neonatal calves in the SAP, primarily because a wolf den (*Canis lupus*) was located on the calving area. Despite the relatively high density of brown bears (*Ursus arctos*) and bald eagles (*Haliaeetus leucocephalus*), these predators killed surprisingly few calves. Golden eagles (*Aquila chrysaetos*) were uncommon on the Alaska Peninsula. At least 2 calves apparently died from pneumonia in the range of the NAP but none were suspected to have died from disease in the range of the SAP. Heavy scavenging by bald eagles complicated determining cause of death of calves in both the NAP and SAP.

Key words: *Aquila chrysaetos*, bald eagle, *Canis lupus*, coyote, golden eagle, grizzly bear, *Haliaeetus leucocephalus*, pneumonia, predation, *Rangifer tarandus granti*, *Ursus arctos*, wolf.

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Introduction

The Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou (*Rangifer tarandus granti*) herds have been important to local subsistence hunters for centuries and to guides and recreational hunters since the 1950s (Murie, 1959; Skoog, 1968; Sellers, 1999). Caribou from these 2 herds are widely known for their large antlers and have attracted hunters from all over the world (Boone & Crockett Club, 2000). However, these herds have fluctuated in size, and recent population declines have caused economic hardships for local residents and guides.

The SAP reached a peak population size of 10 200 in 1982 and then declined continuously to about

1500–2000 by 1995 (Valkenburg *et al.*, 2003a). Hunting was gradually restricted during the late 1980s and all hunting was closed in 1993. The NAP reached a peak population size of 20 000 caribou during the early 1980s but remained relatively stable between 16 000–20 000 during 1981–1994 when it began declining (Valkenburg *et al.*, 2003a). Hunting by nonresidents was severely restricted in 1998 and a year later only 600 permits were issued to subsistence hunters.

There has been considerable speculation about the causes of declines in caribou on the Alaska Peninsula, including predation, disease, icing of winter ranges, and emigration (Skoog, 1968; Valkenburg *et al.*, 2003a). Because the adjacent NAP and SAP caribou

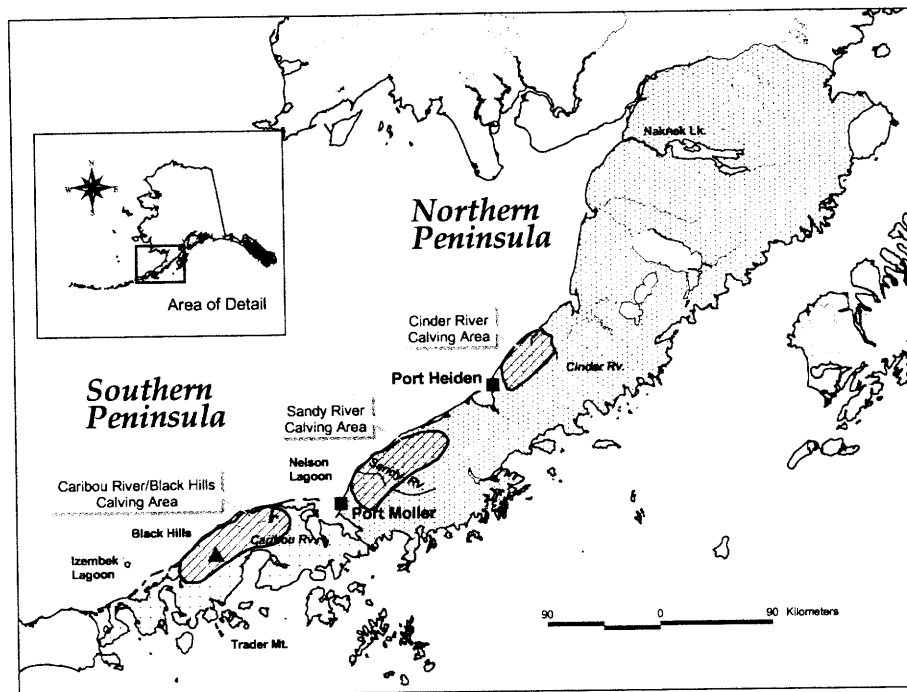


Fig. 1. Location of calving areas and annual ranges of the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou herds.

herds were in different phases of population fluctuation, we investigated natality and mortality to evaluate how differences in these factors might be responsible for differences in population growth rates. Therefore, in 1995 we increased the intensity of annual surveys and began collecting female calves to assess body condition and the prevalence of disease. We also began radiocollaring female calves to determine age-specific natality rates and mortality rates. In addition, we conducted calf mortality studies in the NAP in 1998 and the SAP in 1999. In this paper, we report results of the calf mortality studies and compare mortality and natality patterns in the NAP and SAP with patterns in other Alaskan herds.

Study areas and populations

NAP

The NAP ranges throughout the Alaska Peninsula from Naknek Lake to Port Moller (Fig. 1). Caribou calve primarily on the flat, poorly drained coastal plain of the Bristol Bay side of the Alaska Peninsula from Port Moller to Cinder River Flats north of Port Heiden, and some scattered calving occurs throughout the Aleutian Mountain Range. Most caribou spend the summer south of the Ugashik River but migrate north in autumn to spend the winter between the Ugashik drainage and Lake Iliamna on lichen ranges in tundra and open spruce (*Picea* spp.) woodlands.

Grizzly bears (*Ursus arctos*) are abundant on the

Alaska Peninsula (estimated at 191 bears/1000 km² near the center of the NAP's range, Miller *et al.*, 1997) and wolves (*Canis lupus*) are periodically abundant but susceptible to rabies that is endemic in red foxes (*Vulpes vulpes*) (Ballard *et al.*, 1997; Sellers, 2000). Bald eagles (*Haliaeetus leucocephalus*) are also abundant, but golden eagles (*Aquila chrysaetos*) are uncommon. Wolverines (*Gulo gulo*) occur throughout the ranges of both herds. We detected no denning activity by wolves on the calving area of the NAP.

During the mid-1990s, as the population began to decline, there were indications that NAP caribou were chronically under-

nourished, their winter ranges shifted, and the caribou were probably more vulnerable to parasitism, disease, and predation (Sellers, 1999). During 1996-1998, 14 of 30 4-month-old calves that were collected to assess body condition had lesions on their lungs consistent with lungworm (*Dictyocaulus* spp.) infestation or pneumonia (Sellers, 1999).

SAP

Unlike the NAP, the SAP now appears to be recovering from a population low, and body condition and weights of calves captured in autumn 1998 were excellent (Valkenburg *et al.*, 2002).

Southern Alaska Peninsula females calve on low-lying sedge flats in the Caribou River drainage southeast of Nelson Lagoon and on uplands in the Trader Mountain/Black Hills area (Fig. 1). Caribou remain on and around the calving areas for the summer, but most move south in October to winter in the vicinity of Cold Bay and Izembek Lagoon. Unlike the range of the NAP, there are no native trees in the range of the SAP, and caribou winter primarily on sedge flats and heath-covered uplands (Post & Klein, 1999). Lichens are present in the uplands but have never been described as abundant (Skoog, 1968; Post & Klein, 1999). Fauna of the SAP range is similar to the NAP range, but we discovered an active wolf den with at least 5 adult and yearling wolves located along the Caribou River in the calving area of the SAP. In the ranges of both the NAP and the SAP, severe weather is common at all

Table 1. Natality of females surveyed on the calving areas of the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) herds in 1998 and 1999.

Herd and area	Year	Number parturient (%)	Total females surveyed
NAP — Cinder River	1998	95 (69)	137
NAP — South of Port Heiden	1998	402 (84)	480
NAP — Cinder River	1999	275 (68)	405
NAP — South of Port Heiden	1999	395 (86)	461
Total NAP — 1998 and 1999		1167 (79)	1483
SAP — Caribou River Flats	1999	129 (88)	146
SAP — Black Hill/Trader Mountain	1999	189 (96)	196
Total SAP — 1999		318 (93)	342

times of the year and high winds, low clouds, and intense snowstorms make flying difficult.

Methods

During late May 1997-1999, we observed 35 radiocollared, known-aged, NAP females from fixed-wing aircraft or a Robinson (R-44) helicopter to determine age-specific natality rates (Bergerud, 1964; Whitten, 1995). The females were captured as 4-month-old or 10-month-old calves beginning in 1995. On the Bristol Bay side of the Alaska Peninsula we monitored pregnant radiocollared females daily during 1998 to determine birth dates and locations. Also in 1998, from 30 May to 9 June we radiocollared and weighed 39 1- to 2-day-old calves. Calves were caught by hand after a close approach with the helicopter (*cf.* Adams *et al.*, 1995). To reduce chances of abandonment, we generally only caught calves that were dry (*i.e.*, at least several hours old), and ones that were not in groups with other caribou. We monitored calves daily through 12 June to deter-

Table 2. Mean kg weights (with standard error of the mean) of newborn caribou calves of the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou herds, during 1998 and 1999.

Herd and year	Males (\bar{x} , n)	Females (\bar{x} , n)
NAP 1998	8.44 (0.24, 19)	7.17 (0.30, 20)
NAP 1999	8.35 (0.25, 22)	7.41 (0.24, 22)
SAP 1989	6.67 (0.67, 8)	5.44 (0.57, 9)
SAP 1999	7.70 (0.28, 25)	7.14 (0.16, 29)

mine timing and causes of mortality. We also recorded observations of predators on the calving area and surveyed caribou to determine the proportion of parturient females in the herd. To assess the prevalence of lungworm and pneumonia, we collected samples of lung and liver from calves that were found dead during the calf mortality study. In addition, 30 fresh fecal samples from caribou older than calves were

collected from the calving area to assess prevalence of lungworm in the herd. Follow-up telemetry flights were made on 19 June, 25-28 June, 3-8 August and 30 September 1998. On 30 June a Robinson R-22 helicopter was used to investigate deaths of calves that occurred after 15 June and to collect 2 unmarked calves that were debilitated. The carcasses of these 2 calves and an intact collared calf were sent to the Washington Animal Disease Diagnostic Laboratory in Pullman, Washington for complete necropsy. In October 1998, we collared 19 additional female calves with adult-sized radio collars and monitored their mortality through June 1999.

In 1999 we conducted a similar study on caribou in SAP, and we also captured and weighed (but did not collar) calves in the NAP to compare their weights with the previous year and with weights of SAP calves. Capture and monitoring methods were identical except we collared 52 calves in the SAP during 3-12 June and continued daily monitoring through 18 June. Follow-up flights were made on 26-29 June and on 23 August. We compared natality rates of radiocollared caribou using chi-square (χ^2) tests, and we used t-tests to compare weights of newborn calves. We compared ratios of uncollared parturient to nonparturient cows on the calving areas of the NAP and the SAP by calculating binomial confidence intervals for the ratios. For these comparisons, we report only the P-value. For calculating mortality rates of calves from late June to late September in both the NAP and the SAP, and for calculating total annual mortality rates, we used Kaplan-Meier survival estimates because it was necessary to account for censored caribou that were not found during incomplete survey flights (Pollock *et al.*, 1989).

Table 3. Causes and timing of mortality of caribou calves that were radiocollared as newborns in the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) herds in 1998 and 1999 respectively.

Herd and year	Number of calves collared as newborns that died through 28 June							Total dying (%)
	Brown bear	Wolf	Eagle	Wolverine	Drowning	Disease (pneumonia) ¹	Unknown	
NAP 1998	3 ²	none ²	1	none	1	2	6 ²	13/37 (35)
SAP 1999	3	6	1	1	2	none	9	22/49 (45)

¹ Two calves were found dead in late June. There were no visible subcutaneous marks on them. Carcasses were sent to Washington Animal Disease Diagnostic Laboratory and pneumonia was diagnosed.

² Two calves included as unknown were killed either by bears or wolves.

Results

Natality

There was no difference ($P=0.20$) in natality rates of uncollared females surveyed in 1998 and 1999 in the NAP. We therefore lumped these data and compared them with similar data from the SAP for 1999. In aggregate, females surveyed on the calving areas of the NAP were significantly less fecund than those surveyed on the calving areas of the SAP (79% vs. 93%, $P<0.01$) (Table 1).

Radiocollared 3-year-old females in the NAP were also significantly less fecund than those in the SAP ($\chi^2=9.9$, $P=0.002$, $df=1$). Six of 18 3-year-olds were parturient in the NAP, whereas 8 of 8 were parturient in the SAP. We suspect that natality in older radiocollared females was similar between herds, but sample sizes were too small for meaningful comparison (14/17 in the NAP and 4/5 in the SAP). No 2-year old females were parturient in either herd ($n=25$ for the NAP, and $n=12$ for the SAP).

Weights of newborn calves

There was no difference in weights of NAP calves in 1998 and 1999 (for males, $t=0.27$, $P=0.79$, $df=39$; for females, $t=0.64$, $P=0.52$, $df=40$). We therefore lumped NAP data from 1998 and 1999 for comparison with the SAP data from 1999. Male NAP calves were somewhat heavier than male SAP calves ($t=2.25$, $P=0.03$, $df=64$) (Table 2). There was no difference in weights between herds for females ($t=0.57$, $P=0.57$, $df=69$). Weights of calves from the SAP were significantly heavier (for males, $t=1.70$, $P=0.09$, $df=31$; for females, $t=2.72$, $P=0.01$, $df=36$) in 1999 than recorded by Pitcher (1991) in 1989 (Table 2).

Calf mortality in the NAP

In 1998, of 39 newborn calves collared, 2 did not reunite with their mothers and were censored from the study, and 13 of the remaining 37 died by 28

June (35% mortality) (Table 3). During the first 2 weeks of life, 19% (7/37) of the radiocollared calves died; during 12-19 June only 1 calf died; and during the following week, 5 of the remaining 29 calves died. Two of the calves that died in late June had no subcutaneous marks and apparently died of pneumonia. One of these was diagnosed with bacterial pneumonia. No lungworm eggs were found in the fecal samples collected from the calving area, and lungworm did not appear to be prevalent in the NAP.

Follow up flights in August and September 1998 were less intense and status was determined by the radio collar mortality sensor. Coverage of the caribou range was incomplete and 9 of 24 calves known to be alive in late June were not located and thus were censored. In early August, 13 live and 2 dead calves were found. On 30 September only 7 live and 1 dead calf were located. Therefore, the Kaplan-Meier survival estimate from birth through 30 September was 49.5% (50.5% mortality). The mortality rate of 19 calves collared in October 1998 was 71% by June 1999, but causes of death were not determined. Thus the total annual calf mortality rate was 86% in the NAP during 1998-1999.

Sample size was too small to determine the relative importance of individual predators or disease in the NAP calves, but brown bears killed the most collared neonatal calves. During 29 May-12 June, we observed 88 brown bears on the calving areas of the NAP. Brown bears were not likely involved in the high overwinter mortality.

Calf mortality in SAP

Of the 52 newborn calves collared in the SAP in 1999, 4 did not reunite with their mother and were censored from the study. Also, we discovered 1 calf the day after capture in a steep-sided stream with its mother nearby. We rescued the calf, considered it a mortality for the purposes of the study, and reentered it as a new calf. Therefore, there were 49 calves in the

study. Of these, 45% were dead by late June, and 66% were dead by late August. Brown bears and wolves killed most calves that died, but sample size was inadequate to distinguish which of these predators was most important to herd mortality (Table 3). As in the NAP study in 1998, a high proportion (61%) of deaths occurred late in the calving period (*i.e.*, after 18 June). Because of the high cost of keeping the helicopter available to determine cause of death of calves, we were only able to determine the cause of death of the 11 calves that died before 18 June (Table 3). Eleven more died by 26 June and eagles scavenged 9 of them so much that cause of death could not be determined. Wolves killed the other 2. We could not determine cause of death of the 10 that died between 26 June and 23 August. Of 13 calves collared in October 1998, only 1 died by June 1999. Therefore, total annual mortality rate for SAP calves was at least 69%.

Discussion

Natality

Natality of female caribou in the SAP was higher than in the NAP primarily because most 3-year-old females did not produce calves in the NAP. Similar differences in natality have been shown for Interior caribou herds where summer nutrition (*i.e.*, weight gain of calves over summer) varies (Valkenburg *et al.*, 2003b). In the NAP, survival of calves to 1 year was low during the mid- to late 1990s and, therefore, there were few 1-, 2-, and 3-year-olds in the population.

Weights of newborn calves

Weights of newborn male NAP and SAP calves during this study were similar to weights of newborn calves from other herds in Alaska (except the Porcupine herd and SAP in 1989) in most years (Whitten *et al.*, 1992; Whitten, 1995; Valkenburg *et al.*, 2002). Southern Alaska Peninsula calves were exceptionally light in 1989 (Table 2) during the precipitous population decline, when they were lighter than any other calves weighed in Alaska (Pitcher, 1991; Valkenburg *et al.*, 2002). The relatively low weight of SAP males compared with NAP males in 1998 and 1999 may indicate that SAP caribou are more limited by winter nutrition than NAP caribou (*cf.* Reimers, 1997). In contrast, summer nutrition appears better in the SAP than the NAP judging from the higher natality rates in 3-year-old females (see *Natality*), and the slightly higher weights of female calves in autumn in the SAP (Valkenburg *et al.*, 2002).

Calf mortality

Although neonatal calf mortality did not differ between the NAP and the SAP ($\chi^2=0.83$, $P=0.36$, $df=1$), it appeared that predation was a more significant factor in the SAP than in the NAP. This may primarily have been because a wolf den was located within the calving area of the SAP, and no den was present on the calving area of the NAP. It may also be significant that 2 neonates died from pneumonia in the NAP, particular because pneumonia was also found to be prevalent in 3 collections of 4-month-old female calves during autumn 1996-1998. We hypothesize that NAP calves were in generally poor condition during the mid- to late 1990s, and that diseases became more prevalent.

In contrast to mortality patterns in other herds that have been studied in Alaska, in both the NAP and the SAP high mortality continued through August, and golden eagles were rare and were not major predators of caribou calves (Adams *et al.*, 1995; Boertje & Gardner, 2000; Valkenburg *et al.*, 2002). Also, despite their high density (mean density of about 180 bears per 1000 km² within the range of both herds, ADF&G unpublished data), brown bears killed surprisingly few calves in the NAP and SAP compared with other studies on newborn moose and caribou in Interior Alaska (Adams *et al.*, 1995; Miller *et al.*, 1997; Boertje & Gardner, 2000; Bertram & Vivion, 2002; Valkenburg *et al.*, 2002). Also, despite the high density of bald eagles on the calving area, they were not significant predators of calves. In contrast to golden eagles, bald eagles appeared to primarily be scavengers. The extensive scavenging of carrion by bald eagles did make documenting cause of death more difficult on both the NAP and the SAP.

Although neonatal and summer mortality of caribou calves was similar in both herds (albeit for different reasons), the extreme winter mortality in the NAP caused recruitment in that herd to be low and insufficient to prevent the population from declining.

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References

- Adams, L. G., Singer, F. G. & Dale, B. W. 1995. Caribou calf mortality in Denali National Park, Alaska. – *J. Wildl. Manage.* 59: 584-594.
- Ballard, W. B., Ayers, L. A., Krauseman, P. R., Reed, D. J. & Fancy, S. G. 1997. *Ecology of wolves in relation to a migratory caribou herd in northwest Alaska.* – *Wildl. Monogr.* 35: 1-47.
- Bergerud, A. T. 1964. A field method to determine annual parturition rates for Newfoundland caribou. – *J. Wildl. Manage.* 28: 477-480.
- Bertram, M. R. & Vivion, M. T. 2002. Moose mortality in eastern interior Alaska. – *J. Wildl. Manage.* 6: 747-756.
- Boertje, R. D. & Gardner, C. L. 2000. *Reducing mortality on the Fortymile caribou herd.* Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Progress Report. Grant W-27-3. Study 3.43. Juneau, Alaska.
- Boone and Crockett Club. 2000. *Records of North American big game.* Boone and Crockett Club, Alexandria, Virginia.
- Miller, S. D., White, G. C., Sellers, R. A., Reynolds, H. V., Schoen, J. W., Titus, K., Barnes, V. G., Smith, R. B., Nelson, R. R., Ballard, W. B. & Schwartz, C. C. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. – *Wildl. Monogr.* 133: 1-55.
- Murie, O. J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. United States Bureau of Biological Survey. – *N. Am. Fauna* 61: 1-406.
- Pitcher, K. W. 1991. *Nutritional status of the Southern Alaska Peninsula, Nelchina, and other Southcentral Alaska caribou herds.* Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Progress Report. Grant W-23-4. Study 3.36. Juneau, Alaska. 42pp.
- Pollock, K. H., Winterstein, S. R. & Bunck, C. M. 1989. Survival analysis in telemetry studies: the staggered entry design. – *J. Wildl. Manage.* 53: 7-15.
- Post, E. S. & Klein, D. R. 1999. Caribou calf production and seasonal range quality during a population decline. – *J. Wildl. Manage.* 63: 335-345.
- Reimers, E. 1997. *Rangifer* population ecology: a Scandinavian perspective. – *Rangifer* 17: 105-118.
- Sellers, R. A. 1999. Northern Alaska Peninsula caribou herd management progress report of survey–inventory activities. – In: M. V. Hicks (ed.). *Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration*, pp. 35-46. Grants W-24-5 and W-27-1. Study 3.0. Juneau, Alaska.
- Sellers, R. A. 2000. Units 9 and 10 wolf management progress report of survey–inventory activities. – In: M. V. Hicks (ed.). *Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration*, pp. 57-66. Grants W-24-5 and W-27-1. Study 14.0. Juneau, Alaska.
- Skoog, R. O. 1968. *Ecology of caribou (Rangifer tarandus granti) in Alaska.* Ph.D. Thesis, University of California, Berkeley, California. 699pp.
- Valkenburg, P., Keech, M. A., Sellers, R. A., Tobey, R. W. & Dale, B. W. 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. 99pp.
- Valkenburg, P., Sellers, R. A., Squibb, R. C., Woolington, J. D. & Dale, B. W. 2003a. Population dynamics of caribou herds in southwestern Alaska. – *Rangifer* Special Issue No. 14.
- Valkenburg, P., Tobey, R. W., Dale, B. W., Scotton, B. D. & Ver Hoef, J. M. 2003b. Body weight of female calves and natality rate of adults as indicators of summer and winter limitation in two Alaskan caribou herds. – *Rangifer* Special Issue No. 14.
- Whitten, K. R. 1995. Antler loss and udder distension in relation to parturition in caribou. – *J. Wildl. Manage.* 59 (2): 273-277.
- Whitten, K. R., Garner, G. W., Mauer, F. J. & Harris, R. B. 1992. Productivity and early survival in the Porcupine caribou herd. – *J. Wildl. Manage.* 56: 201-212.