

Population dynamics of caribou herds in southwestern Alaska

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Abstract: The five naturally occurring and one transplanted caribou (*Rangifer tarandus granti*) herd in southwestern Alaska composed about 20% of Alaska's caribou population in 2001. All five of the naturally occurring herds fluctuated considerably in size between the late 1800s and 2001 and for some herds the data provide an indication of long-term periodic (40–50 year) fluctuations. At the present time, the Unimak (UCH) and Southern Alaska Peninsula (SAP) are recovering from population declines, the Northern Alaska Peninsula Herd (NAP) appears to be nearing the end of a protracted decline, and the Mulchatna Herd (MCH) appears to now be declining after 20 years of rapid growth. The remaining naturally occurring herd (Kilbuck) has virtually disappeared. Nutrition had a significant effect on the size of 4-month-old and 10-month-old calves in the NAP and the Nushagak Peninsula Herd (NPCH) and probably also on population growth in at least 4 (SAP, NAP, NPCH, and MCH) of the six caribou herds in southwestern Alaska. Predation does not appear to be sufficient to keep caribou herds in southwestern Alaska from expanding, probably because rabies is endemic in red foxes (*Vulpes vulpes*) and is periodically transferred to wolves (*Canis lupus*) and other canids. However, we found evidence that pneumonia and hoof rot may result in significant mortality of caribou in southwestern Alaska, whereas there is no evidence that disease is important in the dynamics of Interior herds. Cooperative conservation programs, such as the Kilbuck Caribou Management Plan, can be successful in restraining traditional harvest and promoting growth in caribou herds. In southwestern Alaska we also found evidence that small caribou herds can be swamped and assimilated by large herds, and fidelity to traditional calving areas can be lost.

Key words: *Canis latrans*, *Canis lupus*, coyotes, Kilbuck caribou herd, lichens, Mulchatna caribou herd, Northern Alaska Peninsula caribou herd, Nushagak caribou herd, nutrition, predation, rabies, *Rangifer tarandus granti*, Southern Alaska Peninsula caribou herd, Unimak caribou herd, volcanic ash, wolves.

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Introduction

Five naturally occurring caribou herds and one transplanted herd occur in southwestern Alaska (Valkenburg, 1998) (Fig. 1). Together, these herds composed about 20% of Alaska's statewide caribou population in 2001. Two of these herds (Northern Alaska Peninsula [NAP] and Mulchatna [MCH]) have been particularly important to the subsistence economy of southwestern Alaska and also to the

guiding industry (Sellers, 1999a; Woolington, 2001). In 1995, however, the NAP began to decline in size, and the MCH also appeared to be on the brink of a major decline. Therefore, to better prepare managers and the public for the potential turmoil that inevitably accompanies the population declines of important game species, the Alaska Department of Fish and Game (in cooperation with federal agencies) intensified work on the caribou herds of south-

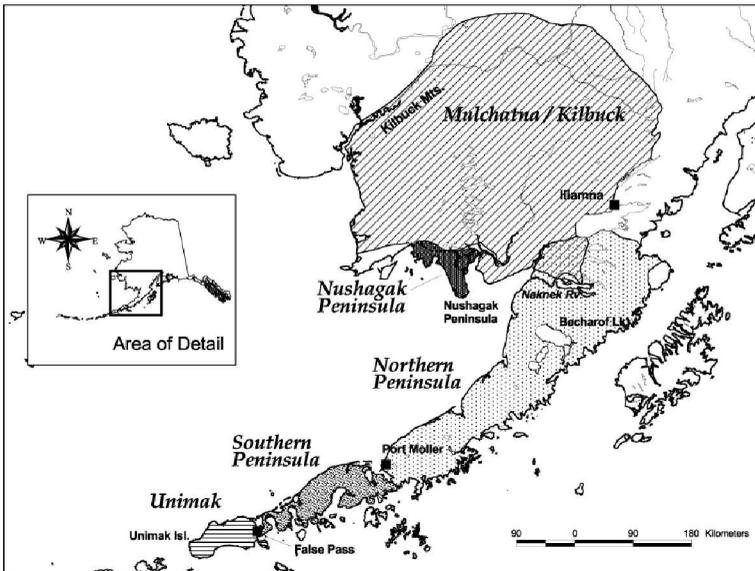


Fig. 1. Location of caribou herds in southwestern Alaska.

western Alaska. We had 2 goals in this work. The first was to review the historical literature (much of it is unpublished) from the late 1800s to the early 1990s to determine if there was a pattern of caribou population fluctuations in southwestern Alaska. We realized that older estimates of population size were undoubtedly less accurate than those done since the 1960s, but it appeared that even the older estimates were sufficient to show major population trends.

Our second goal was to collect basic data on caribou population parameters to determine if limiting and regulating factors were similar to those found in the more thoroughly studied caribou herds of the Alaskan Interior. Because of limited funding, we were not able to collect comprehensive or continuous data from all herds. However, we did begin to collect more frequent data on population size, and annual data on recruitment in 4 of the 5 naturally occurring herds and in the 1 transplanted herd. In addition, we conducted calf mortality studies in the NAP and the Southern Alaska Peninsula (SAP) herds (Sellers et al., 2003, this volume) and also monitored natality and mortality rates of radiocollared females, condition of newborn, 4-month-old, and 10-month-old calves, and began to study nuclear DNA and the prevalence of disease (Valkenburg, 1997; Valkenburg et al., 2000a). In this paper, we present results of our review of the historical literature and also the results of studies of the population dynamics of the caribou herds of southwestern Alaska between 1995 and 2002. We also discuss evidence for density-dependent population regulation, disease, and other possible causes of decline and increase.

Methods

We reviewed the published and unpublished historical literature on the caribou herds in southwestern Alaska. Skoog (1968) reviewed much of the information prior to the early 1960s. Most information collected from the early 1960s through the mid-1990s was previously only reported in agency management reports.

During the mid-1990s we attempted to conduct annual autumn composition counts (in early to mid-October) on all herds except the Kilbuck (KCH). We also increased the numbers of radiocollared caribou in these herds by radiocollaring female calves at 4 and 10

months of age. Because small helicopters were usually not available for charter in southwestern Alaska in spring or autumn, we chartered helicopters from other areas and conducted composition counts, collaring, and collections in as many herds as possible on the same trip. Occasionally, bad weather prevented us from completing fieldwork, especially on the southern Alaska Peninsula and on Unimak Island. During composition counts, caribou were classified as cows, calves, small, medium, or large bulls. In this paper, we report only calf:cow and total bull:cow ratios. We radiocollared only female calves because we were also interested in assessing size and condition of calves relative to calves in other herds, determining age-specific natality, and determining mortality rates of calves, especially during their first winter. For radiocollaring, calves were darted from helicopters with a Palmer Cap-Chur pistol (CO₂) and 1-cc darts with 1 mg of carfentanil citrate (Wildnil®, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) and 33 mg of xylazine HCl (Anased®, Lloyd Laboratories, Shenandoah, Iowa, USA) (Valkenburg et al., 1999). Caribou calves were weighed and measured and these data were compared with other cohorts of calves from the same herd and from other Alaskan herds (Valkenburg et al., 2002). Caribou that were collected for the assessment of condition and prevalence of pneumonia were shot from a helicopter, and the carcasses were delivered to local villages for consumption.

Estimates of population size of the MCH in 1996 and 1999 were from counts of large format aerial photographs (Zeiss RMK-A 9x9 in. camera) with

Table 1. Estimates of herd size, fall calf:cow ratio, and calf weight in the Mulchatna Caribou Herd, 1981–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest ^a	Mean calf weight ^b , s_x , n
1981	18 599	45		280	
1982				1330	
1983	25 416			420	
1984	33 214			2060	
1985	42 945			1980	
1986		37		2500	
1987	45 742	60		2250	
1988	60 328	54		2970	
1989				2700	
1990	70 652			2650	
1991				3270	
1992	110 073			3400	
1993		44	42	4800	
1994	168 351			6000	
1995				7250	50.1(A), 1.4, 10
1996	192 818	34	42	4570	
1997				5100	
1998		34	41	9770	48.3(O), 2.6, 10
1999	175 000 ^c	15	41	9470	
2000		24	39		46.9(A), 1.2, 11 51.2(O), 1.8, 10
2001		25	25		49.8(A), 0.9, 13
2002		28	26		49.5(A), 0.8, 22 50.4(O), 2.1, 10

^a Harvest estimates combined the reported harvest from Harvest Ticket Report Cards and an estimate by the Area Biologist of unreported harvest for nonresident, nonlocal resident, and local resident hunters. Harvest was estimated to be about two-thirds males and one-third females.

^b Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

^c Actual count was 149 012. Estimate was derived by extrapolation for missing radio collars.

extrapolation for missing radio collars (Woolington, 2001). Population estimates for the other herds were from complete visual counts and counts from 35-mm photographs.

Mulchatna Herd (MCH)

Skoog (1968) exhaustively reviewed historical records of caribou in southwestern Alaska and concluded there was a “very large caribou population along the Bering Sea coast from Bristol Bay to Norton Sound.” Numbers apparently peaked in the 1860s but by the 1880s the herd was very low (Skoog, 1968). The population increased during the 1930s, but was very low again by the time the first aerial surveys were flown in 1949, and only about 1000 caribou were counted (Taylor, 1981). By 1965 the population had increased to about 5000, and

when the Alaska Department of Fish and Game (ADF&G) conducted the first systematic aerial census in 1974, just over 13 000 caribou were found (Taylor, 1981). The herd apparently was stable or declining during the late 1970s, but then it increased steadily from 1981 to about 1994 ($\lambda = 1.19$) (Taylor, 1983; Van Daele, 1995). In 1999 the MCH was the second largest caribou herd in Alaska, with 175 000 caribou, but there were indications (declining bull:cow and calf:cow ratios) that population growth was slowing or that the herd had begun to decline (Valkenburg, 1998; Woolington, 2001) (Table 1).

The MCH expanded its range rapidly during the 1980s, especially to the southeast, north, northwest, and west, although total density remained exceptionally high ($>2/\text{km}^2$). By the early 1990s, besides supplying a significant amount of meat to local resi-

dents, the MCH had become a favorite destination for nonresident hunters from the United States, Mexico, and Europe, and harvest increased to over 5000 caribou annually by 1993 (about 5–10% of herd size) (Van Daele, 1995) (Table 1). Mulchatna caribou became noted for their large antler size, and several new world record caribou were taken from the herd during the 1980s and 1990s (Boone and Crockett Club, 2000).

During its rapid expansion from 1980 to the mid-1990s the MCH began to interact with the adjacent KCH and the NAP. In 1986 about 10 000 caribou from the NAP moved north of the Naknek River and began using winter range between the Naknek River and Lake Iliamna (Sellers, 1993). At about the same time, approximately 50 000 caribou from the MCH also began using the same area (Sellers, 1997). This area (approximately 10 000 km²) was one of the most spectacular lichen ranges in Alaska but by the mid-1990s casual aerial observations indicated that lichen biomass was reduced. Use of the area by the MCH became sporadic, and many MCH caribou began searching to the north and northwest for new winter ranges. During 2001–2002 and 2002–2003, about two-thirds of the MCH continued to winter east and southeast of the Nushagak River as far as the Naknek River.

We began more intensive work on the MCH in 1995 by collecting 10-month-old female caribou calves to assess body condition and by increasing the frequency of recruitment and population estimates. Mean weights of cohorts of 10-month-old calves was low compared to weights of calves in Interior Alaska and calves in the adjacent Nushagak Herd (NPCH) (Valkenburg et al., 2000b). However, the calves were relatively fat and appeared to be in good condition (Valkenburg, 1997). However, after 1995, fall calf:cow and bull:cow ratios in the MCH began to decline and we noticed fewer trophy class bulls while conducting autumn composition counts (Woolington, 2001). The autumn 1999 calf:cow ratio was the lowest on record for the herd (Table 1). In autumn 2000, although mean weight of calves was still relatively heavy for the MCH, individual weights were variable, and 6 of 10 calves we collected had moderate to severe bacterial pneumonia. In summer 1998 there was a major outbreak of hoof rot (*Spherophorus necrophorus*) in the herd, and during autumn composition counts, about 1 caribou out of 20 was limping noticeably. Hunters continued to observe symptoms consistent with hoofrot through December. During 1997–2000 it also appeared that mortality of radiocollared caribou increased (Woolington, 2001). At present it appears the MCH is declining from the combination of lower recruitment and higher mor-

tality because autumn calf:cow ratios have been declining and more radiocollared caribou may be dying. Predation is probably not a major mortality factor because of the relatively low wolf population in much of the herd's range and the migratory nature of MCH caribou. A population census conducted in 2002 confirmed the decline in herd size.

Northern Alaska Peninsula Herd (NAP)

The NAP occupies the Alaska Peninsula from Lake Iliamna south to Port Moller. Previously, all caribou on the Alaska Peninsula south to, and including, Unimak Island were considered 1 herd, but by the early 1960s, Skoog (1968) considered them to be divided into 3 populations. However, ADF&G continued to consider all the caribou on the Alaska Peninsula as 1 herd until about 1980 (Smith, 1981). During the early 1980s, ADF&G began differentiating between the caribou living north of Port Moller and those occupying the Alaska Peninsula and Unimak Island south of Port Moller, and since the mid-1990s, the caribou on Unimak Island have been considered a separate herd because of their geographic isolation and lack of interaction with SAP caribou.

Caribou numbers on the Alaska Peninsula have fluctuated between 2000 and 20 000 since the late 1800s (Skoog, 1968; Sellers, 1999a, 2001a). Population highs were reached in the late 1880s and again in the late 1930s. The NAP declined to a low level during the 1940s but then increased between the 1950s and early 1980s. From 1980 to 1993 there was a sustained population of >16 000 in the NAP, and this may be one of the more protracted population highs for the herd (Table 2). During this period, harvest was substantial and hunters often killed at least 10% of the herd each year (Table 2).

Historically (1880–1990), although there is no direct evidence, occasional volcanic eruptions from Mount Iliamna, Mount Spurr, Mount Vemiaminof, Mount Shishaldin, Mount Saint Augustine, and the Pavlov Sisters may also have played a role in caribou distribution and perhaps in numbers because of the extensive and deep ash falls that have occurred (Skoog, 1968). Icing during winter has also been recorded, particularly during the 1930s when up to 50% of the caribou in some local areas were estimated to have died in some years (Skoog, 1968).

The Alaska Peninsula is known for its dearth of lichens, and caribou apparently have existed for long periods on a diet composed primarily of sedges in winter (Skoog, 1968). The only extensive high-biomass lichen ranges on the Peninsula were found north of Becharof Lake and that area has historically

Table 2. Estimates of herd size, fall calf:cow ratio, and calf weight in the Northern Alaska Peninsula Caribou Herd, 1975–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest ^a	Mean calf weight ^b , \bar{x} , n
1975	10 340	45	33	1500	
1976	11 368			1000	
1977				2100	
1978		55	48	1600	
1979				1800	
1980		56	53	1900	
1981	16 600	39	34	2000	
1982	18 000	52	43	1500	
1983	19 000	27	39	1795	
1984	20 000	39	39	1940	
1985	19 000			1951	
1986	17 000	34	51	1908	
1987	17 000	51	54	2300	
1988	20 000	48	49	2400	
1989	20 000			2300	
1990	17 000	29	41	2000	
1991	17 000	47	42	2000	
1992	17 500	44	40	2300	
1993	16 000	39	44	2800	
1994	12 500	34	34	1725	
1995	12 000	24	41	1550	51.4(A), 1.3, 19 44.7(O), 1.6, 10
1996	12 000	38	48	1650	46.0(O), 2.4, 10
1997	10 000	27	47	1350	48.4(A), 2.1, 10 48.3(O), 1.4, 14
1998	9 200	30	31	1000	49.4(O), 1.3, 29
1999	8 000	21	40	200	51.9(O), 1.3, 11
2000	7 200	18	38	200	
2001	7 000	28	49	200	54.3(A), 0.9, 21
2002	6 800	24	46		

^a Harvest estimates combined the reported harvest from Harvest Ticket Report Cards and an estimate by the Area Biologist of unreported harvest for nonresident, nonlocal resident, and local resident hunters. Prior to 1998 the harvest was estimated to be about two-thirds males and one-third females, but from 1998 to 2001 harvest was restricted to bulls only and was estimated to be about 95% males.

^b Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

been the NAP's main winter range (Skoog, 1968; Sellers, 1997). During the mid-1980s, biologists became concerned that the NAP had depleted its winter range between Becharof Lake and the Naknek River (Sellers, 1997). Subsequently, in 1986 the herd began using the abundant lichen forage to the north, between the Naknek River and Lake Iliamna west to the Kvichak River (Sellers, 1989). By the mid-1990s, however, increasing numbers of MCH caribou had also obviously depleted this area of lichens although from aerial observation, it appeared that

lichen biomass was still relatively good (Sellers, 1997).

As in the MCH, we began more intensive work on the NAP in 1995. Weights of female calves that we captured for radiocollaring or collected to determine condition were low relative to Interior caribou and to those of the adjacent MCH and NPCH (Tables 1, 2, and 4). In addition, natality of females also appeared to be relatively low and calf:cow ratios in autumn were declining (Sellers, 1999a) (Table 2). The bull:cow ratio also declined and many calves collected for assessment of body condition had lesions on

their lungs that were consistent with lungworm infection or pneumonia (Sellers, 1999a). By 2000 the herd had declined to about 7000 or about one-third of its size during the previous high (Table 2).

Southern Alaska Peninsula Herd (SAP)

During the early 1900s, caribou became numerous on the Alaska Peninsula south of Port Moller and Murie (1959) recorded 5000 there in 1925. However, the icing conditions of the 1930s apparently were associated with a major decline with a probable low point in the early 1940s. In 1949 only 500 caribou were in the range of the SAP and in 1960 there were about 1000 (Skoog, 1968). By 1983 the herd had peaked again at about 10 200 (Sellers, 1999b). Population size, recruitment estimates, and harvest records have been regularly kept since then (Sellers, 1999b) (Table 3). The herd declined during the mid to late 1980s. During the decline, natality was low, mortality of radiocollared cows was high (40%), and newborn calves were light (Pitcher, 1991). Post & Klein (1999) concluded that summer and winter range conditions were still limiting herd productivity during the early 1990s. During the late 1990s, natality improved, and calf weights (newborn and 4-month-olds) were comparatively high (Sellers, 1999b, 2001b) (Table 3). Recruitment also improved and we observed many trophy class bulls during the autumn composition counts in 1998. During the decline and the population low, hunters had remarked on the lack of large bulls in the herd (R. Gunlogson, pers. comm.). By the time we began increasing data collection from the SAP, the population had increased significantly, calves were in excellent condition, and many large, magnificent bulls were again present (Table 3).

Unimak Caribou Herd (UCH)

Unimak Island is the only island in the Aleutian chain to have native caribou. It is separated from the Alaska Peninsula by a narrow (1 km) ocean passage (Isanotski Strait) that has strong tidal currents. During 1900–1925 caribou were occasionally observed swimming across Isanotski Strait, but there have been no records of more than a few animals making the movement more recently, except perhaps for 1976 (Skoog, 1968; Sellers, 1999b). Biologists now consider the caribou on Unimak Island a separate herd.

Caribou were numerous on Unimak Island during the early 1900s, and they probably reached a population high of at least 7000 in 1925 (Murie, 1959). By the 1940s, caribou had declined, and during the

first aerial survey of Unimak Island in November 1949, no caribou were observed (Skoog, 1968). In a 1953 survey, again no caribou were found on Unimak, but by 1960, almost 1000 were present (Skoog, 1968). In 1975, Irvine (1976) counted 3334 caribou and estimated there were about 5000 on the island. After the mid-1970s the population declined, and during most of the 1980s and early 1990s only about 300 caribou could be found. Recently, the population has expanded again, and in 2000, a hunting guide counted 981 caribou and estimated a population of at least 1100 on the island (Schuh, pers. comm.).

During the last few decades, at least, hunting has been a minor influence on the population size of caribou in the UCH. The island is remote, there are no light commercial aircraft for hire nearby, the weather is notoriously bad, and the interior of the island was closed to aircraft access from the late 1970s until the mid-1990s. Most of the island is also closed to the use of ground vehicles. During the 1970s when the population was high, only about 40 caribou were taken per year.

Unimak Island is so remote, and the weather so consistently poor that we were unable to collect extensive or continuous data there during the late 1990s. However, we were able to weigh and measure 12 female caribou calves there in 1999, and we found them to be relatively heavy (\bar{x} = 56.0 kg) and in excellent condition, judging from condition scores (Gerhart et al., 1996) and their visible appearance. Several calves had forked or 3-point antlers, and several had already shed the velvet from their antlers. During composition counts in October 2000, we found 21 calves:100 cows and 40 bulls:100 cows, including many trophy-class bulls.

Kilbuck Herd (KCH)

During the early 1980s, biologists noticed about 200 calving caribou in the Kisaralik drainage of the Kilbuck Mountains (Machida, 1984). At the time, hunting pressure was heavy, there was debate about the origin of the animals, and some people suggested they were feral reindeer. Surveys in the mid-1980s confirmed the animals were caribou (late calving date and appearance) and determined there were only about 60–70 remaining (Patten, 1987). Subsequently, a cooperative management plan was written, local people agreed to stop hunting, and the herd increased to about 685 caribou in 1987–1988 (Kacyon, 1995). By 1991 the KCH numbered over 2584 (Kacyon, 1995). In October 1994, about 35 000 MCH began using the Kilbuck Mountains as winter range, and over the next few years, MCH cari-

Table 3. Estimates of herd size, fall calf:cow ratio, and calf weight in the Southern Alaska Peninsula Caribou Herd, 1975–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest ^a	Mean calf weight ^b , \bar{x} , n
1975	3000				
1980	6500			700	
1983	10200			900	
1984	7500			1000	
1985	4000			650	
1986	4500	20	32	200	
1987	4700	26	36	230	
1988	3500	19	41	200	
1989	3500			200	
1990	3400	12	19	100	
1991	2500	19	28	75	
1992	2500	22	22	65	
1993	2000	24	30	no hunting	
1994	2000	28	29	no hunting	
1995	1500			no hunting	
1996	1500			no hunting	
1997	1800	19	42	53	48.9(A), 1.0, 13
1998		35	32	38	52.2(O), 1.2, 13
1999	3600	25	51	50	
2000	2860	37	42	40	
2001		38	57	40	
2002		16	38	40	

^a Harvest estimates combined the reported harvest from Harvest Ticket Report Cards and an estimate by the Area Biologist of unreported harvest for nonresident, nonlocal resident, and local resident hunters. Prior to 1991 harvest was estimated to be about 50% males and 50% females. From 1991 to 2001, harvest was estimated to be about 95% males.

^b Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

bou invaded the entire range of the KCH during summer, autumn, and winter. Radiocollared KCH caribou that had previously used only the KCH calving area began using calving areas of the MCH. By the late 1990s the MCH had almost completely assimilated the KCH, and the 2 herds were no longer distinguishable (Seavoy, 1997). In early June 2000 we surveyed the entire previous calving area of the KCH and surrounding areas (i.e., virtually the entire Kilbuck Mountains) after the MCH had moved eastward to its calving area, and we found <50 adult female caribou with newborn calves. Therefore, although there is little calving in the Kilbuck Mountains today, the calving tradition is still being maintained by a small number of caribou, and the KCH could re-emerge.

Nushagak Peninsula Herd (NPCH)

In 1988, caribou were translocated from the NAP to previously ungrazed range on the Nushagak

Peninsula southwest of Dillingham (Hinkes & Van Daele, 1996; Valkenburg et al., 2000b). The population grew rapidly (annual finite rate of population growth $\lambda = 1.38$) and reached about 1200 by the mid-1990s (Table 4). During the first few years after the transplant, population growth exceeded the theoretical maximum for caribou because of the preponderance of females. Caribou in the NPCH were on a high plane of nutrition and 10-month-old calves were the heaviest recorded for caribou in southwestern Alaska (Table 4). All radiocollared 2-year-old females produced calves, and survival of calves and adults was initially high (Hinkes & Van Daele, 1996). During 1996–2001 herd growth slowed for largely unknown reasons, although unreported harvest may have equaled or exceeded reported harvest. So far, there has been no documented dispersal of radiocollared Nushagak females to the MCH, and MCH caribou have not begun using the primary range of the NPCH.

Discussion

Population trajectories and data on natality rate and body weight of newborn, 4-month-old, and 10-month-old calves in the MCH, NAP, and the SAP provide strong evidence that density-dependent limiting factors significantly affect caribou herds in southwestern Alaska. For the caribou herds on the Alaska Peninsula and Unimak Island, there is evidence for periodic population fluctuations with population highs occurring every 40–50 years (Fig. 2). During the early 1900s, and also recently, population highs progressed from south to north, with the UCH peaking first, followed by the SAP and the NAP thereafter. Without the recent high harvests of NAP caribou during the high population from the late 1970s to the late 1990s, the herd probably would have increased to higher levels and perhaps declined sooner. The decline of the NAP, when it finally did occur, was clearly related to nutrition and perhaps to disease. Both poor nutrition and disease were likely related to the high densities of caribou. Pneumonia was prevalent in calves during the decline, but it probably was facilitated by the high population density and relatively poor condition of the caribou. Ten years prior to the decline, biologists had already been concerned about depleted winter range, a problem that was exacerbated by an influx of caribou from the MCH (Sellers, 1987). However, it is also likely that summer range is limiting in the NAP because natality in June, and weight and condition of calves in October has also been low, and these factors are generally considered to be more affected by summer nutrition than by winter nutrition (cf. Skogland, 1984; Reimers, 1997).

The transplant of caribou to the Nushagak Peninsula also has provided evidence for a nutrition-related population response in caribou in southwestern Alaska. Although the caribou were transplanted from a high-density population (the NAP), body size of 4-, and 10-month-old calves increased and the herd reached maximum productivity (Hinkes & Van Daele, 1996; Valkenburg et al., 2000b).

Predation is also a significant factor that strongly limits caribou on the Alaska Peninsula, but it apparently does not keep caribou population low for extended periods as it does in some Interior herds in Alaska (Mech et al., 1998; Boudreau, 1999; Gardner, 1999). Although brown bears (*Ursus arctos*) are abundant on the Alaska Peninsula (density about 200 bears/1000 km², Miller et al., 1997), and wolves (*Canis lupus*) probably fluctuate around a density of about 4/1000 km² (similar to many areas of Interior Alaska), patterns of neonatal calf mortality on the Alaska Peninsula differed significantly from those in

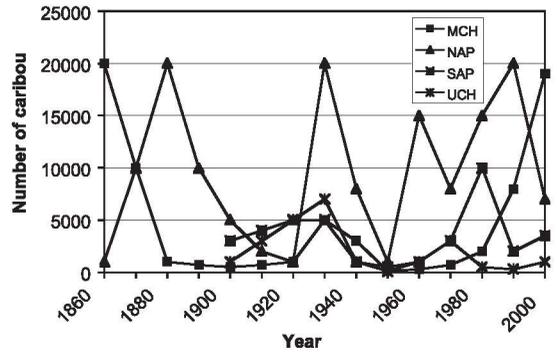


Fig. 2. Population trajectory of caribou herds in southwestern Alaska (MCH = Mulchatna Herd, NAP = Northern Alaska Peninsula Herd, SAP = Southern Alaska Peninsula Herd, and UCH = Unimak Herd). Population size of Mulchatna Herd is divided by 10.

the Interior (Adams et al., 1995; Valkenburg, 1998; Sellers, 2000; Boertje & Gardner, 2001; Sellers et al., 2003, this volume). Alternate prey for wolves are also more limited on the Alaska Peninsula than in Interior Alaska because moose (*Alces alces*) are confined to local areas with sufficient willow (*Salix* spp.), and Dall sheep (*Ovis dalli*) and other ungulates are absent. Tundra hares (*Lepus othus*) have been recorded, but most of the area probably has not sustained a breeding population in recent times. In addition, wolf numbers on the Alaska Peninsula seldom remain high for long because, during winters with persistent snow cover, they are heavily hunted, and they are probably also periodically reduced by rabies. Rabies is prevalent in red foxes and likely is transferred to wolves (cf. Ballard et al., 1997). In 1998 we also found a dead coyote (*Canis latrans*) near Port Heiden, that was positive for rabies.

Previously, biologists have commented on the lack of lichens on the Alaska Peninsula and the ability of caribou there to thrive on a winter diet composed primarily of sedges (cf. Skoog, 1968). To the casual observer, lichens do appear to be scarce. However, in 3 fecal samples collected in the range of the NAP in late winter 1995, lichens composed 38–55% and sedges composed 9–35% of discerned plant fragments. We believe the primary reason for the obvious lack of lichens on the Alaska Peninsula is the virtually continuous grazing pressure to which the area has been subjected. Around the settlement of King Salmon, where caribou are excluded by human activity, lichens are abundant. In addition, lichens are widespread on the uplands south of Port Moller

Table 4. Estimates of herd size, fall calf:cow ratio, and calf weight in the Nushagak Peninsula Caribou Herd, 1988–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest ^a	Mean calf weight ^b , \bar{x} , n
1988 ^c	146		12	no hunting	
1988	202			no hunting	
1989	268			no hunting	
1990	383			no hunting	
1991	561			no hunting	
1992	734	72	60	no hunting	
1993	1007			no hunting	
1994		65	71	no hunting	
1995				81	57.1(A), 1.3, 15
1996	1304			110	
1997	1429	62	64	44	50.9(A), 1.9, 10
1998	1381	63	57	133	55.8(O), 1.6, 5
1999		53	48	106	
2000	1037	38	52	136	49.2(A), 0.7, 10
2001		35	46		51.3(A), 1.6, 10
2002	900	36	43		49.1(A), 1.0, 10

^a Actual harvest was estimated to be at least twice the reported harvest during 1995–2002.

^b Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

^c Herd was introduced in February.

although they grow primarily between sedge tussocks, their biomass is low, and they are not readily apparent from the air. During the recent population low in the SAP, lichens became more noticeable than they were during and shortly after the population decline. The moist climate, high winds, and new soils provide ideal growing conditions for lichens in the uplands of the Alaska Peninsula.

During the last several decades we are not aware of icing conditions that may have contributed to population declines of caribou on the Alaska Peninsula. There have been significant ash falls, however, and in April 1998, many of the caribou calves we handled in the range of the SAP had incisors worn to the gum line. We only observed these extremely worn incisors in one year, and these calves were still in moderately good condition. Whether this single event of extreme tooth wear in calves had an effect on mortality is unknown, but ash falls are a stochastic event that would only occasionally be of significance to the populations.

The MCH is much larger than the Alaska Peninsula herds and has many more options for range expansion, but it too appears to be strongly limited by nutrition. Brown bears are abundant, and wolves are common in some areas within the range of the MCH, but predation obviously was not a severe-

ly limiting factor during the period of rapid population growth from 1980 to 1995. Hunting pressure on the MCH has been lighter than on the NAP and apparently was not a major restraint to herd growth during the 1980s and 1990s. However, during the late 1990s, as recruitment declined and the harvest of bulls remained high, the bull:cow ratio in the MCH declined. The recent severe outbreak of hoof rot and the prevalence of pneumonia in the MCH indicate that disease could be a limiting factor, although we have not been able to quantify the effects of these diseases on recruitment and survival.

The increase and subsequent decline of the KCH is interesting because it demonstrates the effectiveness of cooperative management programs in restraining harvest and promoting conservation of caribou. Additionally, as far as we are aware, it is only the second documented instance in which a caribou herd has been assimilated by a larger, expanding herd. This was previously documented with the Delta and Yanert herds in the central Alaska Range (Davis et al., 1991).

Conclusions

1 Nutrition had a significant effect on the size of 4-month-old and 10-month-old calves in the NAP

- and the NPCH and probably also on population growth in at least 4 (SAP, NAP, NPCH, and MCH) of the 6 caribou herds in southwestern Alaska. Data were insufficient to determine the influence of nutrition in the remaining 2 herds.
- 2 There is evidence for long-term periodic (i.e., 40–50 year) population fluctuations in the UCH, NAP, and SAP caribou herds.
 - 3 Predation does not appear to be sufficient to keep caribou herds in southwestern Alaska from expanding, probably because rabies is endemic in arctic foxes and is periodically transferred to wolves and other canids.
 - 4 Pneumonia and hoof rot may result in significant mortality of caribou in southwestern Alaska.
 - 5 Cooperative conservation programs, such as the Kilbuck Caribou Management Plan, can be successful in restraining traditional harvest and promoting growth in small caribou herds.
 - 6 Small caribou herds can be swamped and assimilated by large herds, and fidelity to traditional calving areas can be lost.

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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., Krausman, P. R., Reed, D. J. & Fancy, S. G. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. – *Wildl. Monographs* 35: 1-47.
- Boertje, R. D. & Gardner, C. L. 2000. The Fortymile caribou herd: novel proposed management and relevant biology, 1992-1997. – *Rangifer Special Issue No. 12*: 17-37.
- Boone and Crockett Club. 2000. Records of North American big game. Boone and Crockett Club, Alexandria, Virginia.
- Boudreau, T. A. 1999. Beaver Mountains, Big River–Farewell, Kilbuck Mountains, Kuskokwim Mountains, Rainy Pass, Sunshine Mountain, and Tonzona caribou herds management progress report of survey–inventory activities. – In: M. V. Hicks (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-5 through W-27-1. Study 3.0. Juneau, Alaska, pp. 105-115.
- Davis, J. L., Valkenburg, P., McNay, M. E., Beasley, R. M. & Tutterrow, V. L. 1991. Demography of the Delta caribou herd under varying rates of natural mortality and human harvest and assessment of field techniques for acquiring demographic data. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Final Report. Grants W-22-5 through W-23-3. Study 3.33. Juneau, Alaska. 112pp.
- Gardner, C. L. 1999. Chisana 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. Grants W-24-5 through W-27-1. Study 3.0. Juneau, Alaska, pp. 55-66.
- Gerhart, K. L., White, R. G., Cameron, R. D. & Russell, D. E. 1996. Estimating fat content of caribou from body condition scores. – *J. Wildl. Manage.* 60: 713–718.
- Hinkes, M. T. & Van Daele, L. J. 1996. Population growth and status of the Nushagak Peninsula caribou herd in southwest Alaska following reintroduction, 1988–1993. – *Rangifer Special Issue No. 9*: 301-309.
- Irvine, C. 1976. Population size of the Alaska Peninsula caribou herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Final Report. Grants W-17-7 and W-17-8. Study 3.17R. Juneau, Alaska. 10pp.
- Kacyon, R. H. 1995. Kilbuck and Andreafsky Mountains caribou management progress report of survey–inventory activities. – In: M. V. Hicks (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-2 and W-24-3. Study 3.0. Juneau, Alaska. pp. 92-101.
- Machida, S. 1984. Andreafsky Mountain and Kilbuck Mountain caribou management progress report of survey–inventory activities. – In: J. A. Barnett (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-22-2. Study 3.0. Juneau, Alaska. pp. 24-25.
- Mech, L. D., Adams, L. G., Meier, T. J., Burch, J. W. & Dale, B. W. 1998. The wolves of Denali. University of Minnesota Press. Minneapolis, Minnesota. 225pp.
- 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 replicate mark-resight techniques. – *Wildl. Monographs* 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.
- Patten, S. 1987. Kilbuck Mountains and Andreasfky Mountains caribou management progress report of survey–inventory activities. – In: B. Townsend (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-22-5. Study 3.0. Juneau, Alaska. pp. 24–29.
- Pitcher, K. W. 1991. Nutritional status of the Southern Alaska Peninsula, Nelchina, and other Southcentral Alaska 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.
- 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.
- Seavoy, R. 1997. Kilbuck Mountain and Mulchatna caribou herds management progress report of survey–inventory activities. – In: M. V. Hicks (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-3 through W-24-4. Study 3.0. Juneau, Alaska. pp. 98–107.
- Sellers, R. A. 1987. Northern Alaska Peninsula caribou herd management progress report of survey–inventory activities. – In: B. Townsend (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-22-5. Study 3.0. Juneau, Alaska, pp. 6-7.
- Sellers, R. A. 1989. Northern Alaska Peninsula caribou herd management progress report of survey–inventory activities. – In: S. O. Morgan (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-23-1. Study 3.0. Juneau, Alaska, pp. 17-24.
- Sellers, R. A. 1993. Northern Alaska Peninsula Caribou Herd management progress report of survey–inventory activities. – In: S. M. Abbott (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-23-5 through W-24-1. Study 3.0. Juneau, Alaska, pp. 28-34.
- Sellers, R. A. 1997. 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. Grants W-24-3 through W-24-4. Study 3.0. Juneau, Alaska, pp. 37-48.
- Sellers, R. A. 1999a. 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. Grants W-24-5 through W-27-1. Study 3.0. Juneau, Alaska, pp. 35-46.
- Sellers, R. A. 1999b. Southern 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. Grants W-24-5 through W-27-1. Study 3.0. Juneau, Alaska, pp. 47-54.
- Sellers, R. A. 2000. Wolf management progress report of survey–inventory activities for Game Management Units 9 and 10. – In: M.V. Hicks (ed.). Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration. Grants W-24-5, W-27-1, and W-27-2. Juneau, Alaska, pp. 57-60.
- Sellers, R. A. 2001a. Northern Alaska Peninsula caribou herd management progress report of survey–inventory activities. – In: C. Healy (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-27-2 and W-27-3. Project 3.0. Juneau, Alaska, pp. 39-49.
- Sellers, R. A. 2001b. Southern Alaska Peninsula caribou herd management progress report of survey–inventory activities. – In: C. Healy (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-27-2 and W-27-3. Project 3.0. Juneau, Alaska, pp. 50-58.
- Sellers, R. A., Valkenburg, P., Squibb, R. C., Dale, B. W. & Zarnke, R. L. 2003. Natalivity and early calf mortality in the Northern Alaska Peninsula and Southern Alaska Peninsula caribou herds. – *Rangifer Special Issue* No. 14.
- Skogland, T. 1984. The effects of food and maternal conditions on fetal growth and size in wild reindeer. – *Rangifer* 4 (2): 39–46.
- Skoog, R. O. 1968. Ecology of caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Thesis, University of California, Berkeley, California. 699pp.
- Smith, C. A. 1981. Northern Alaska Peninsula caribou herd management progress report of survey–inventory activities. – In: R. A. Hinman (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-17-12. Study 3.0. Juneau, Alaska, pp. 12-13.
- Taylor, K. P. 1981. Mulchatna Caribou Herd management progress report of survey–inventory activities. – In: R. A. Hinman (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-17-12. Study 3.0. Juneau, Alaska, pp. 14-17.
- Taylor, K. P. 1983. Mulchatna caribou herd management progress report of survey–inventory activities. – In: J. A. Barnette (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grant W-22-1. Study 3.0. Juneau, Alaska, pp. 7-8.
- 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. Research Final Report. Grants W-23-5 through W-24-4. Study 3.37. Juneau, Alaska. 45pp.

- Valkenburg, P. 1998. Herd size, distribution, harvest, management issues, and research priorities relevant to caribou herds in Alaska. – Rangifer Special Issue No. 10: 125-130.
- Valkenburg, P., R. W. Tobey, & D. Kirk. 1999. Velocity of tranquilizer darts and capture mortality of caribou calves. – Wildl. Soc. Bull. 27: 894-896.
- Valkenburg, P., Dale, B. W., Tobey, R. W. & Sellers, R. A. 2000a. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Progress Report. Grant W-27-3. Study 3.42. Juneau, Alaska.
- Valkenburg, P., Keech, M. A., Sellers, R. A., Tobey, R. W. & Dale, B. D. 2002. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-5 and W-27-1, through W-27-5. Project 3.42. Juneau, Alaska, 98pp.
- Valkenburg, P., Spraker, T. H., Hinkes, M. T., Van Daele, L. H., Tobey, R. W. & Sellers, R. A. 2000b. Increases in body weight and nutritional status of transplanted Alaskan caribou. – Rangifer Special Issue No. 12: 133-138.
- Van Daele, L. J. 1995. Mulchatna 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. Grants W-24-1 and W-24-2. Study 3.0. Juneau, Alaska, pp. 22-37.
- Woolington, J. D. 2001. Mulchatna caribou herd management progress report of survey–inventory activities. – In: C. Healy (ed.). Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-27-2 and W-27-3. Project 3.0. Juneau, Alaska, pp. 23-38.