

Ecology of the Porcupine caribou herd

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Abstract: Researchers have described general patterns of population regulation that fit most caribou (*Rangifer tarandus*) herds. Nevertheless, specific factors operating on particular populations vary greatly, and efforts to categorize herds according to the general patterns often lead to confusion. It is difficult for biologists to attempt to describe population dynamics in terms of density relationships for wide-ranging arctic caribou such as the Porcupine Herd. In these herds density varies as a function of dispersal and erratic movement patterns and is not simply the number of caribou divided by a fixed range area. Density is also a poor surrogate for resource availability per individual caribou because climatic factors affect forage and/or access to forage independently of caribou numbers. Thus classic signs of nutritional stress such as delayed puberty, reduced productivity, and winter starvation can occur when a population is small as well as large and do not necessarily denote food competition brought on by high density, *per se*. Nutritional stress and exacerbated predation due to adverse weather conditions occasionally cause the Porcupine Herd to decline, and limiting factors such as poor nutrition, predation, harvest, accidents, and disease act in combination to keep herd growth rates low during periods of good weather. Adverse weather setbacks occur frequently, and the herd remains within a fairly restricted range of densities over long time periods. There is no true density dependent regulation and no equilibrium in this system.

Key words: caribou, density, limitation, population dynamics, regulation, *Rangifer tarandus*

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Introduction

Numerous biologists have attempted to identify the factors that determine caribou population dynamics. The Porcupine Herd was put forth as an example of a population regulated by predation when it was stable during the 1970s (Bergerud, 1980). The herd then increased during a period of predominantly mild weather from the late 1970s until about 1989, but rate of increase between censuses declined as the population approached its peak (Table 1). Physiological condition of females declined and the herd is now decreasing, causing some biologists to proclaim regulation by competition for food (Allay-Chan & White, 1992). In this paper I will present some basic natural history data for the Porcupine Herd and try to point out ways in which it does and does not fit these and other hypotheses for population regulation.

The Porcupine Herd and its environment

The Porcupine Herd has numbered between about 100,000 and 180,000 animals over the past 30 years. It is well known for its spectacular aggregations on the arctic coastal plain and its importance to subsistence hunters, and it has been the subject of inten-

sive research for many years. The herd has always occupied the same general area, but annual movements and range use patterns are complex. Generally, the herd winters south of tree line, although much of the winter range is actually alpine tundra, and in some years much of the herd remains on arctic tundra all year. In spring the caribou migrate north to calve and spend the summer on arctic tundra, where they may remain for only a few weeks, or for several months. Mountain habitats are used extensively, and irregular mid-summer movements south to the edge of the taiga occur nearly every year. The herd often penetrates deep into traditional winter ranges during August, only to return north again before making its final fall migration in late September or October.

The Porcupine Herd shares its range with 3 other large ungulate species. Moose (*Alces alces*) occur throughout the Porcupine Herd's range, but average density is low (ca. 0.1/km²; Gasaway *et al.*, 1993). Dall sheep (*Ovis dalli*) are abundant in some mountain ranges but scarce or absent in others. About 500 muskoxen (*Ovibos moschatus*) occur on the arctic coastal plain in Alaska and another 150 in the northern Yukon.

Table 1. Population size and rates of increase of the Porcupine caribou herd, 1972-92.

Year	Population		Increase rate between censuses	
1972	100,000	} (+28,000)		1972-79 = STABLE
1977	105,000			
1979	105,000		r = 0.058	
1982	125,000	}	r = 0.077	} INCREASING 1979-89
1983	135,000			
			r = 0.050	
				r = 0.053
1987	165,000		r = 0.038	
1989	178,000	}		} 1 DECREASING
			r = -0.036	
1992	160,000			

Several large predators capable of taking adult caribou or their calves also inhabit the range of the Porcupine Herd. Wolf (*Canis lupus*) distribution and den site locations are not limited at tree line as reported for the Canadian barren grounds (Weiler & Garner, 1987; Heard & Williams, 1991), and wolves prey on caribou throughout the year. Hibernating brown (*Ursus arctos*) and black bears (*U. americanus*) have no effect on the Porcupine Herd on winter range, but brown bears are effective predators on summer range. Golden eagles (*Aquila chryseatos*) are relatively common near the primary calving areas and are adept at taking young calves (Whitten *et al.*, 1992a). Wolverines (*Gulo gulo*) and lynx (*Lynx canadensis*) occur widely but have little effect on Porcupine caribou. Mountain lions (*Felis concolor*) have shown up on Porcupine Herd range recently, but their predation on caribou is insignificant.

Clearly, the Porcupine Herd shares some characteristics with other large migratory populations, but there are also important differences. For example, the large Canadian herds tend to have far fewer alternate prey options for predators, and they also tend to have fewer effective predator species. The Porcupine Herd occupies primarily montane habitats, while the barren-ground herds inhabit much gentler terrain. As we search for common links in the ecology of caribou herds, we should not forget

that their environmental conditions are often quite different.

Population dynamics of the Porcupine Herd

Limiting factors

By definition, limiting factors reduce the rate of increase of a population. Nutrition certainly limits the Porcupine Herd. Forage production and quality vary both geographically, due to general environmental conditions, and *in situ*, due to annual variation in meteorological conditions that affect plant growth (Jorgenson & Udevitz, 1992). Presumably this contributes to the variability in body condition of adult females after the summer foraging season that occurs both within and between years (Fig. 1). Evidence for relative shortages of forage (i.e., inaccessibility due to deep snow) is also compelling, and caribou are generally in poor shape after severe winters. Poor condition of adult females in the adjacent Central Arctic Herd has been linked to decreased reproductive performance (Cameron *et al.*, 1993). Perinatal calf mortality (occurring within 48 hr of birth) is common in the Porcupine Herd and derives mostly from causes that are consistent with poor nutrition (Roffe, 1990; Whitten *et al.*, 1992a).

Predation also limits the Porcupine Herd. Most of the nonperinatal mortality of calves during the

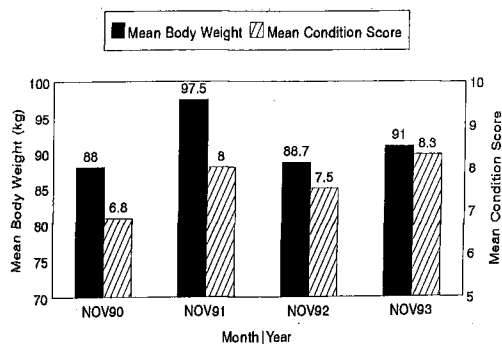


Fig. 1. Mean fall body weight and condition score of Porcupine Herd cows, 1990–93. Condition score is an index of the amount of soft tissue covering bone (5 being high, 1 low) summed for 3 sites: withers, ribs, and hips (Gerhart *et al.*, 1992)

first month after birth is caused by eagles, brown bears, and wolves. Nonperinatal mortality is higher when calving is displaced into foothill and mountain areas than when calving occurs primarily on the coastal plain where predators are scarce (Table 2; Whitten *et al.*, 1992a,b). Predation is also involved in a high proportion of adult deaths.

Human harvest is a minor limiting factor. Hunter kill is typically about 1,000–5,000 caribou and seldom exceeds about 3% of the herd. Subsistence harvest by rural residents within the range of the herd is already essentially *ad libitum*, and significantly increasing nonlocal harvest is not politically feasible. Accidents, disease, and parasites take their toll. Insects and weather cause little direct mortality, but have profound effects on caribou through their influence on habitat use and feeding, which in turn influence nutrition and predation.

Potential regulating factors

Of all these limiting factors, only nutrition and predation have been suggested as regulating the size of the Porcupine Herd. Regulating factors are defined as acting in a density dependent manner to keep a population within normal density ranges (Davis & Valkenburg, 1991; Messier, 1991). Unfortunately, because it is defined as number of animals divided by area used, density becomes a confusing parameter in a large migratory caribou herd.

The problem is that range size of a caribou herd is difficult to quantify objectively. Range use varies seasonally and even within seasons. Density is conventionally based on year-round range, but the same areas are not used every year. Most published accounts list range area for the Porcupine Herd at about 250,000 km² (Bergerud, 1980; Garner & Reynolds, 1986; Russell *et al.*, 1993). Total year-

round range actually occupied during the past 15 years is closer to 340,000 km² (Valkenburg *et al.*, this workshop). Maximum extent of range use occurred in the 1970s and early 1980s when the herd numbered about 100,000 and used virtually all its known range at a density of about 0.3/km². As the population increased, the herd did not expand its range and maintain a constant density. Nor did density increase in proportion to population size, as would have occurred if range size were fixed. Density reached as high as 1.1/km² during several years in the late 1980s when the herd was near its peak population of 180,000 but used only about half the historic range. Thus, density did increase as the population grew, but its peak value resulted as much or more from range restriction as from population growth.

Recent declines in caribou body condition and in yearling recruitment occurred at a time when caribou density was highest. However, other signs of nutritional stress such as delayed puberty and perinatal calf mortality occurred throughout the period of population increase (Tables 2 & 3). There was relatively poor recruitment in the early 1970s when the herd was at relatively low density (Davis, 1977; Fancy *et al.*, 1992), yet recruitment was consistently good during the mid-1980s when the herd was growing and density increasing (Fancy *et al.*,

Table 2. First month calf mortality in the Porcupine caribou herd, 1983–90.

Year	Perinatal Mortality ^a (%)	Nonperinatal Mortality ^b (%)
1983	21.5	13.5
1984	7.5	8.5
1985	21.2	13.8
1986	--	--
1987	9.0	21.0
1988	12.2	16.8
1989	15.0	9.0
1990	10.0	0.0

^a Occurring within 48 hr of birth and deriving mostly from nutritional causes (Whitten *et al.*, 1992a).

^b Occurring >48 hr after birth and caused primarily by predation.

1992). Cows captured and collared in the early 1980s were smaller than those caught a few years later, rather than larger, as would be expected if caribou numbers affected access to food resources in a strictly density dependent manner (Alaska Dep. Fish and Game, unpubl. files). Thus, it is not at all clear that lowered body condition or other signs of nutritional stress in the Porcupine Herd have been caused by increased caribou density. Furthermore, Porcupine Herd density has never approached the K-carrying capacities calculated for other herds (5-14/km²) or at which other herds experienced food related die-offs (19/km²; Bergerud, 1980).

Density dependence has also been suggested for the relationship between caribou and predators. Bergerud (1980) argued that caribou need space to avoid wolves, and he predicted that at densities exceeding about 0.4/km² caribou would encounter wolves frequently and predation rates would rise to stabilize the caribou population. Seip (1991) set the level at which wolf/caribou equilibrium occurs in migratory arctic herds at about 0.6-1.1/km². The Porcupine Herd in recent years has covered this range of densities. Messier (1991) stated that Bergerud's predation regulation hypothesis poses two testable predictions: 1) that predation rate increases with caribou density, and 2) that wolf predation becomes sufficient to stabilize a caribou population before it is stressed by poor nutrition.

The few published accounts of wolf populations on Porcupine Herd range indicate stable numbers (Weiler & Garner, 1987; Stephenson, 1991). Caribou density did not stabilize at 0.4/km², as predicted by Bergerud (1980). Neither early calf mortality nor adult mortality increased measurably even during severe winters at peak population/density levels. Overwinter calf mortality finally did increase in the early 1990s, but only when there was also

food stress (Fancy *et al.*, in press). Thus the predation hypothesis did not stand up to Messier's tests.

Effects of adverse weather on population dynamics

Many biologists have suspected density dependent population regulation in the Porcupine Herd because it has remained within a fairly restricted realm of densities. Yet we've seen that evidence for regulation by either predation or nutrition is weak. If density dependent regulation is not occurring, what does keep the Porcupine Herd within bounds?

In theory, density dependent population regulation occurs through negative feedback loops between animals and their environment. That is, the number of animals per unit area affects other environmental components, and vice versa. The major problem with density theory and arctic caribou is that many factors other than caribou density profoundly affect the environment.

Caughley & Gunn (1993) recently pointed out that important relationships between herbivores and their forage can be missed by focusing on herbivore density alone because forage availability varies with weather and can change independently of herbivore numbers or density. We know there was adverse weather on the Porcupine Herd range in the early 1970s and again in the early 1990s. I believe that nutritional stress occurred then because, even at relatively low caribou densities, adverse weather reduced the availability of forage resources. Functionally, the result was the same as if density suddenly jumped to a much higher level. But the system was not density dependent, it was resource dependent. Caughley & Gunn (1993) suggested that the proper parameters to compare in such weather-driven systems are rate of increase in the animal population and density of forage biomass. For

Table 3. Age-specific parturition of known-age Porcupine caribou herd females.

Cohort ^a	Age (Years)						
	2	3	4	5	6	7	8
1981	0/5 ^b	3/5	5/5	2/2	2/2	2/2	2/2
1982	0/28	18/25	7/14	8/8	7/8	5/5	2/2
1983	1/9	5/6	0/1				
1984	1/9	4/8	1/2	1/1			
1981-1984	2/51 4%	30/44 68%	13/22 59%	11/11 100%	9/10 90%	7/7 100%	4/4 100%

^aBirth year. 1981 females were 22 months at capture. All others were <10 months.

^bNumber parturient/total captured.

migratory caribou I think we need to get stop thinking of caribou/km², and think instead of available resources per caribou.

Unfortunately, it is not a simple task to merely change the label on an x-axis and plot recruitment versus available forage per caribou. The influence of weather is extremely difficult to measure because it can affect resource availability in many ways. Snow can make forage unavailable, or less available, and it affects the energy costs of foraging so that the net nutritional value of forage is variable, and never the same as the gross energy indicated by a bomb calorimeter. Summer weather affects both primary productivity and accumulation of key nutrients. Superimposed on all this are potential feedback loops between caribou and forage. If snowcover concentrates caribou onto small areas, there may be intense grazing pressure and a strong negative effect on forage. In contrast, if crusted snow generally restricts access to all forage, there may be less grazing pressure when food is limited, rather than more. Finally, equivalent weather events can have different effects on forage (i.e., the second year of drought can have a worse effect on plants than the first), and equivalent availability of forage can have different effects on caribou (i.e., a moderate winter after a severe one can have a greater effect on spring body condition than a single moderate winter after a series of mild winters). We should at least try to consider these complicating effects of weather when we investigate interactions between caribou and their range.

The role of predation in a weather-driven system

Weather induced nutritional stress stops population growth in the Porcupine Herd. This does not mean that predation is unimportant in the ecology and population dynamics of the herd. Caribou and wolves affect each other profoundly and the same adverse weather that reduces nutrition can also exacerbate predation, as when deep snow impedes caribou movements, or weakens them to the point where they are more vulnerable to wolves.

Most wolves the Porcupine Herd encounters are in resident packs on year-round range. These wolves thrive when caribou use their territories. Packs from some distance around may converge on a caribou concentration, and well fed wolves may experience a short-term boost in pup production. But when caribou move on they don't just become scarce, they virtually disappear. Caribou shift areas seasonally, but they also abandon parts of their range for years at a time. Whenever caribou shift away from an area, resident wolves must adjust back to resident prey availability. The longer the caribou

stay away, the greater the adjustment wolves must make.

The Porcupine Herd calving and early summer range includes extensive areas of coastal tundra where sedentary ungulate prey are rare. Wolves using these areas must depend on caribou, but on most of the calving grounds caribou do not linger more than a few weeks. Few wolves can raise pups on the coastal plain, and no wolves den in the core calving area in Alaska (Weiler & Garner, 1987). Wolves, brown bears, and golden eagles all hunt primarily the fringes of the calving area.

Thus, the Porcupine Herd spaces away from predators effectively on its calving area. Bergerud's (1980) argument that wolves would stabilize the Porcupine Herd was based on the assumption that resident packs would thrive at times of high caribou density and produce surplus pups. Young migrant wolves would then move to the calving grounds and kill many calves. A few wolves not associated with established packs have indeed been captured near the core calving area, but such wolves did not become more abundant as the herd increased. More importantly, early calf mortality did not increase (Fancy *et al.*, in press). I believe that regular shifts in seasonal distribution of caribou and erratic changes in annual distribution effectively limit the long-term numerical response of predators to the Porcupine Herd.

Summary

Periodic adverse weather temporarily changes forage availability in the range of the Porcupine Herd, and caribou decline because of nutritional stress and the additive effects of predation, harvest, and other limiting factors. Adverse weather may also exacerbate predation. Declines can be rapid because nutritional stress affects the population from both ends—it lowers natality and raises mortality, and there are no biological restraints on mortality (Caughley & Gunn, 1993). Recovery has constraints because calves can only be born and recruited so fast, and predation never goes away.

The Porcupine Herd has effective predator avoidance options, and predation is not regulating. Nevertheless, predation remains a major limiting factor. Net recruitment during the period of mild weather, normal predation, and normal harvest that persisted through most of the 1980s resulted in an increase rate of only about 5% annually and a doubling time of about 14 years. The population would take 28 years to quadruple, which is a very long time to go without experiencing an adverse weather setback in the Arctic. The Porcupine Herd undergoes population fluctuations of variable amplitude and period because weather setbacks come at irre-

gular intervals. Recovery rates under normally prevailing conditions are slow enough and weather setbacks occur frequently enough that the population tends to stay within a fairly narrow range of densities and seldom, if ever, reaches levels where there would be population regulation through food competition if access to forage were never restricted. There is no true equilibrium in this system, and synergism in stochastic events can drive it out of the range we normally see, but that's a rare occurrence.

The mechanism for population regulation I've suggested for the Porcupine Herd differs from what Bergerud (1980) proposed. It also differs from Seip's (1991) model for migratory arctic caribou, because I see no indication that predation or density dependent competition for food, either singly or in combination, stop growth of the herd in the absence of adverse weather. My model incorporates most of what Caughley & Gunn (1993) proposed for kangaroos and caribou in "desert" environments. It also reaches much the same conclusion as Valkenburg *et al.*, (this workshop) and Adams *et al.*, (in press) have for interior Alaska caribou.

This model is essentially a "plurality of factors" approach. In a practical sense, it holds that there is no single, ultimate regulating factor that alone explains the population dynamics of migratory arctic caribou over the range of densities and environmental conditions we normally experience. Finally, we must acknowledge that, although the same functional components may operate on many different caribou populations, those components will differ in magnitude in different times and different places and, therefore, do not inevitably lead to the same results. All caribou herds are not the same. The ecological situation of each is unique, and attempts to categorize herds into types usually lead to confusion (Davis & Valkenburg, 1991). In our search for common ground, we should examine processes. I see no reason to suspect that any single factor regulates all populations, or that any single explanation of population dynamics applies to all herds, or even to all herds of a certain type.

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