

Limiting factors in caribou population ecology.

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Abstract: Caribou and wild reindeer populations fluctuate over time. On this fact there is general agreement. Factors responsible for population limitation and subsequent declines have been examined within the framework of animal population theory. There is, however, little agreement when factors limiting specific populations are generalized to *Rangifer* populations over broad geographic regions. Comparative examinations of wild *Rangifer* populations worldwide disclose that factors that have regulated those populations are highly variable between populations, apparently as a reflection of the differences in environmental variables unique to each population. Examples exist of populations where major regulating factors have been climatic extremes, predation, hunting mortality, food limitation, insects, parasites, disease, interspecific competition, and human developmental impacts or combinations of these factors. This diversity of limiting factors affecting caribou and wild reindeer populations is a reflection of the ecological complexity of the species, a concept that has often been ignored in past efforts to reach management decisions by extrapolation from the limited localized knowledge available on the species.

Keywords: Population dynamics, hunting, predation, food, climatic influence, parasites, diseases, interspecific competition.

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Caribou and wild reindeer populations fluctuate over time in response to a variety of population regulating factors. No single factor is universally responsible for these fluctuations. Each herd has a unique set of environmental constraints with which it interacts. In most cases multiple factors are at play, although at any one time a single factor may dominate in its regulatory effect on the herd. Because of the migratory nature of large herds, their ecosystem relationships are more complex than is the case for nonmigratory wildlife.

Hunting pressure

Hunting has accounted for the limitation of growth and reduction of *Rangifer* populations worldwide. In North America excessive hunting pressure has been implicated in reductions of the Nelchina (Bos 1975), Western Arctic (Davis *et al.* 1980), and Fortymile (Davis *et al.* 1978) herds in Alaska and the Bathurst, Bever-

ly, and Kaminuriak herds in Canada (Calef 1981). Today, in Alaska regulated hunting pressure is a primary factor controlling the Adak, Nelchina, and Delta herds. Hunting accounted for the near extinction of the Svalbard reindeer (Wollebaek 1926), and hunting has been the primary regulating factor of wild reindeer herds in Norway (Reimers *et al.* 1980) and the large Taimyr herd of the Soviet Union (Syroechkovski 1986).

Predation

Predators, primarily wolves, have been associated with population limitation of the Delta Herd (Davis *et al.* 1983) in Alaska and small herds of woodland caribou in Canada (Bergerud 1983). While predation has been invoked as the primary limiting factor on other herds, such as the Nelchina in Alaska (Bergerud and Ballard 1988) and the large caribou herds in northern Canada (Bergerud 1983), opposing viewpoints

cite contrary evidence (VanBallenberghe 1985; LeHénaff and Luttich 1988). Predators clearly interact in an additive or compensatory way with other regulatory factors such as hunting mortality, climatic extremes, and food limitation in their degree of influence on caribou populations.

Food limitation

Constraints on food availability associated with population control of *Rangifer* populations have been most frequently documented in situations where other controlling mechanisms, such as predation, hunting pressure or dispersal were absent or constrained. Island introductions have experienced classic overgrazing and associated population «crashes» or declines (Scheffer 1951; Klein 1968; Leader-Williams 1988). Insular populations in the Arctic have also fluctuated in relation to food abundance and availability; the New Siberian Islands (Kischinskii 1971) and Coats Island in Hudson Bay (Adamczewski *et al.* 1986), being of particular note. West Greenland caribou (Thing 1984) and Norwegian wild reindeer herds (Skogland 1985) have also fluctuated in response to density-food relationships.

In northern North America, where large predator populations have remained intact, food limitation of caribou herds has been poorly documented. The George River Herd in Quebec/Labrador (LeHénaff and Luttich 1988) and the Southern Alaska Peninsula Herd (Pitcher *et al.* 1990) appear to be exceptions where declining body condition, reduced calf production, and increased mortality appear to be tied to constraints on seasonal forage quantity and quality.

Climatic extremes

Climatic extremes may account for increased mortality of caribou, either directly as in the case of loss of newborn calves to hypothermia during windy or wet conditions (Kelsall 1953) or indirectly as when extreme snow depths or icing conditions limited access to forage (Klein 1968; Miller *et al.* 1982). Climatic extremes have been more frequently documented as limiting caribou populations in the High Arctic and on islands than has been the case among the larger continental herds (Parker *et al.* 1975; Kischinskii 1971; Adamczewski *et al.* 1986).

Extinction of the endemic subspecies of caribou in East Greenland at the turn of the last century is believed to have been brought about by a series of winters with extreme snow accumulation (Vibe 1967). The synchrony of population fluctuations of most large caribou herds across North America during the past two decades appears to be most parsimoniously explained on the basis of continent-wide trends in weather patterns. There are, however, inadequate weather records for the regions involved to test this hypothesis.

Insects and parasites

The introduction of the warble fly and nasal bot fly to West Greenland with a shipment of domestic reindeer in 1952 resulted in apparent decreases in body condition and accentuated population lows among the caribou that previously had been free of these parasitic insects Clausen *et al.* 1980). In Svalbard, the absence of insect harassment and parasitic insects is believed to contribute to the population welfare of the endemic subspecies of reindeer (Reimers 1980). Extreme insect harassment and associated parasitism during and unusually warm summer is believed responsible for heavy mortality of calves during the subsequent winter among the Western Arctic Herd (Davis *et al.* 1980).

Caribou have much lower tolerance for infestation by the brain worm than deer that are the principal host species (Dauphiné 1975). It has therefore been speculated that the southern limits of caribou in North America are controlled by the northern distribution of deer (Berge-rud 1983).

Disease

Disease has not been documented as the primary cause of population limitation among wild *Rangifer*, although it has been a contributing mortality factor in a few situations under conditions of high density and apparent food limitation. Colibacillosis has accounted for heavy loss of calves during summer among caribou in West Greenland (Clausen *et al.* 1980) and brucellosis increased substantially among the Western Arctic Herd in Alaska (Neiland *et al.* 1968) and the Taimyr Herd in Siberia (Syroechkovski 1986) under conditions of high density with concurrent reduced reproductive success.

Interspecific competition

Throughout much of the range of distribution of wild *Rangifer* muskoxen are the only other ungulate species present. Seasonal patterns of habitat use by the two species result in limited overlap in diet (Thomas and Edmonds 1984; Klein 1986), although under extreme winter conditions, when forage availability is limited by snow cover, direct competition may occur (Vibe 1967; Klein and Staaland 1984).

Grazing by domestic sheep in eastern Iceland has, over several centuries, altered plant composition, reduced plant biomass, and accelerated erosion in areas occupied by feral reindeer, with concomitant reduction in the «carrying capacity» of the area for the reindeer, however, little direct competition for forage between reindeer and sheep appears to exist at present (Thorisson 1983).

Domestic reindeer and wild reindeer or caribou have a long history of direct competition for forage resources wherever they have occurred together (Klein 1980b). In the Soviet Union official management policy, until the late 1970's, encouraged the elimination of wild reindeer to allow for expansion of reindeer husbandry (Andreev 1975). During the 1980's it was recognized that management for wild reindeer could be far more productive in many areas of the USSR than reindeer herding, and policy was changed accordingly (Syroechkovski 1986).

Human development activities

The effects of human development activities on caribou and wild reindeer population dynamics have been the subject of widespread debate (Klein 1971, 1980a; Bergerud *et al.* 1984; Skogland 1986), often fueled by polarized support from development interests on the one hand and environmental advocates on the other. Behavioral responses of caribou to disturbances, including avoidance and range abandonment, have been documented in association with oil field development and development of transportation corridors, including roads, railroads, pipelines, and icebreaker traffic in rivers (Parovshchikov 1965; Klein and Kuzyakin 1982; Skogland 1986). Population responses to human development activities have not been as well documented, perhaps in some cases because of the lack of background information on the populations prior to development, a long lag time

in population responses, and because of the difficulty in establishing cause and effect relationships for such an ecologically complex species. In Norway, construction of a highway and railroad transportation corridor resulted in obstruction of a traditional migration route for wild reindeer with associated overgrazing on the restricted available range, followed by a precipitous population decline (Skogland 1986). A similar population decline of wild reindeer as a result of railroad construction in northern European Russia has been reported (Parovshchikov 1965). Mountain caribou in the northern Rocky Mountains of the United States and adjacent Canada have suffered deterioration of habitat quality through logging of old growth forests and associated road and highway construction with corresponding population declines (Bloomfield 1979).

Unjustified assumptions and untested hypotheses

1) *Ecosystem relationships in the Arctic and Subarctic are simple:*

Caribou belie this assumption. In contrast to other deer species living at lower latitudes, caribou show more plasticity of diet and habitat use throughout their distribution, and through migration they bridge ecosystems with their associated and unique predator, insect, and forage relationships.

2) *Nature tends toward stability:*

At high latitudes, climatic extremes with interannual variations result in wide fluctuations in plant productivity and availability as forage, as well as having direct effects on survival of young, predator-prey interactions, levels of insect harassment, and energetic costs of locomotion and thermoregulation. Consequently, wide fluctuations in numbers of caribou is common as is also true of many other northern herbivores, such as lemmings, hares, and ptarmigan.

3) *Caribou populations cycle:*

Caribou populations fluctuate widely over long periods of time and the possibility that caribou populations cycle with a periodicity of 65 or more years has been proposed (Meldgaard 1986). Unfortunately, estimates of population numbers of specific herds are reliable only during recent decades, therefore

no adequate data sets exist upon which to test this hypothesis. To be cyclic, fluctuations in numbers must have a common periodicity.

4) *Population dynamics are influenced by exchange of caribou between herds:*

It has been hypothesized that when caribou populations increase to very high numbers large segments of these herds may «spill over» to join adjacent herds that may be at low levels and unable to «escape» from «predator pits» (Haber and Walters 1980). This «seeding» of small herds by large herds has been proposed as the mechanism that allows small herds to escape predator pits. Although cited by some authors (Kelsall 1968; Skoog 1968) as a possible explanation for initial caribou herd increase there is no documentation of exchanges of more than a few animals between herds. The increased frequency of use of radio collars to track caribou movements in recent decades should have provided evidence for large scale transfer of animals between herds if it had occurred.

5) *Migratory caribou do not require lichens:*

This assumption is based on experimental feeding trials in which caribou were able to subsist quite well in the absence of lichens (Bergerud 1974), and observations that some populations of caribou and reindeer in the High Arctic and on islands have existed with virtually no available lichens (Thomas and Edmonds 1983). Thus, while it is true that high arctic populations at very low density, island populations under strong maritime climatic influence, and individual caribou and reindeer do not require lichens, the large migratory herds of the northern portions of North America and Eurasia are dependent upon lichens as the major winter forage resource that sustains their high population levels (Kelsall 1968; Andreev 1975; Holleman *et al.* 1979).

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