

Arctic Tundra Caribou and Climatic Change: Questions of Temporal and Spatial Scales

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Article abstract

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Subspeciation of *Rangifer tarandus* hypothetical¹ occurred during the Wisconsin glaciation. Recent genetic analyses support the current classification of subspecies, except that Baffin Island caribou may be distinct from barren-ground caribou, *R. t. groenlandicus*, on mainland Northwest Territories. Baffin caribou may have originated from a small ancestral population in a refugium on Baffin Island during the Wisconsin glaciation; or, they may have originated from immigrants after the Wisconsin glaciation, later experiencing a severe population bottleneck.

On a shorter time scale, recent research has suggested that density-independent climatic events occurring over a single winter have caused at least one major population decline among Peary caribou on the Queen Elizabeth Islands. Dramatic fluctuations of Greenland populations over the past 200 years have been attributed to climatic changes. However, the onset of some population changes on western Greenland have been inconsistent with the timing of climatic changes. Inuit knowledge of Baffin caribou and studies of tundra caribou on Svalbard, Coats and Southampton islands, South Georgia, and Norway suggest that caribou populations are affected primarily by density-dependent grazing impacts on forage that can last several decades. The discrepancy between these views may be caused by differences in the temporal and spatial scales over which scientific investigations have been conducted, and the measurement of only some ecological factors. Arctic ecological studies require extensive spatial and temporal data before impacts of anthropogenic climate change can be assessed. This will require a long-term interdisciplinary study integrating scientific data from several disciplines, as well as Inuit knowledge.



Arctic Tundra Caribou and Climatic Change: Questions of Temporal and Spatial Scales

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SUMMARY

Climatic changes have affected populations of caribou and reindeer (*Rangifer tarandus*) at scales ranging from a single winter to tens of thousands of years, and from micro-habitats to entire continents. Individuals, populations and the species have adapted to these climatic changes, however, producing complex evolutionary and ecological issues requiring multi-scale, interdisciplinary research. Caribou populations wintering on arctic tundra may be most susceptible to the impacts of anthropogenic climatic change, given the low productivity of their forage, the severity and duration of the winters, and the physical barriers that limit dispersal.

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a single winter have caused at least one major population decline among Peary caribou on the Queen Elizabeth Islands. Dramatic fluctuations of Greenland populations over the past 200 years have been attributed to climatic changes. However, the onset of some population changes on western Greenland have been inconsistent with the timing of climatic changes. Inuit knowledge of Baffin caribou and studies of tundra caribou on Svalbard, Coats and Southampton islands, South Georgia, and Norway suggest that caribou populations are affected primarily by density-dependent grazing impacts on forage that can last several decades. The discrepancy between these views may be caused by differences in the temporal and spatial scales over which scientific investigations have been conducted, and the measurement of only some ecological factors. Arctic ecological studies require extensive spatial and temporal data before impacts of anthropogenic climate change can be assessed. This will require a long-term interdisciplinary study integrating scientific data from several disciplines, as well as Inuit knowledge.

RÉSUMÉ

Les changements climatiques ont eu des répercussions à diverses échelles sur les populations de caribous et de rennes (*Rangifer tarandus*) ; des variations allant d'un seul hiver jusqu'à des dizaines de milliers d'années, s'étendant du micro-habitat jusqu'au continent entier. Les individus, les populations et les espèces se sont adaptées à ces changements climatiques et, l'étude des phénomènes complexes sur l'écologie et évolution que cela a entraînée supposent la réalisation d'études pluridisciplinaires à plusieurs échelles. Les populations de caribous hivernant dans la toundra arctique sont peut-être très sensibles aux changements anthropogéniques, compte tenu de la faible productivité de fourrage de ce milieu, de la rigueur et de la longueur de l'hiver et, de l'existence de barrières physiques limitant les possibilités de dispersion.

L'apparition de la sous-espèce *Rangifer tarandus* s'est produite durant la glaciation du Wisconsin. Les analyses génétiques récentes confirment la classification actuelle des sous-espèces, mais il est possible que le caribou de l'île de Baffin soit différent du caribou des landes (*R. t. groenlandicus*) de la partie continentale des Territoires du Nord-Ouest. Il

est possible que le caribou de l'île de Baffin descende d'ancêtres ayant formés une petite population dans un refuge de l'île de Baffin durant la glaciation wisconsinienne ; il est également possible qu'ils soient des descendants ayant émigrés après la glaciation du Wisconsin, leur population ayant subi une diminution draconienne par la suite.

Sur une échelle de temps plus courte, les résultats d'études récentes indiquent que des événements climatiques indépendants de la densité de la population et se déroulant sur la période d'un seul hiver ont provoqué une importante réduction de la population des caribous de Peary sur les îles de la Reine Élisabeth. Les grandes fluctuations des populations de caribou du Groenland qui ont eu lieu au cours des 200 dernières années ont été attribuées à des changements climatiques. Cependant, certains changements de population ayant débuté dans l'ouest du Groenland ne correspondent pas avec la suite des changements climatiques observés. Selon les connaissances inuites des caribous de l'île de Baffin et d'après des études des caribous de la toundra des îles du Svalbard, de Coats et de Southampton, de Georgie du Sud et de Norvège, les variations des populations de caribous sont principalement reliées à des facteurs qui sont dépendants de la densité de population, qui ont des répercussions sur la paisance et qui peuvent s'étendre sur plusieurs décennies. Les divergences entre ces deux points de vue peuvent être dues à des différences entre les échelles temporelles et spatiales des différentes études scientifiques, et à la mesure d'un trop petit nombre de paramètres écologiques. Les études sur l'écologie arctique doivent d'abord produire un grand nombre de données spatiales et temporelles sur les milieux arctiques avant que l'on puisse évaluer les répercussions climatiques de changements anthropogéniques. Cela signifie qu'il faudra réaliser une étude pluridisciplinaire de longue durée intégrant à la fois les données scientifiques de plusieurs disciplines et les connaissances inuites en la matière.

INTRODUCTION

Questions regarding the effects of anthropogenic climate change on wildlife populations give new urgency to issues debated by northern ecologists throughout this century. Elton (1924) suggested that climatic cycles with a periodicity of

3.5 years caused numeric fluctuations and genetic changes in northern animal populations. Elton suggested that periodic climate change was the only factor that could synchronize population cycles over wide areas. His hypotheses shaped much of the subsequent ecological research into the proximal factors causing fluctuations in wildlife populations. Others have suggested that the impact of herbivores on their forage can be the dominant force in population cycles, however. For example, Keith (1974) suggested that density-dependent interactions between snowshoe hares (*Lepus americanus*), their forage and their predators were responsible for the 10-year population cycles of these species. Further, Windberg and Keith (1976) and Keith *et al.* (1984) suggested that dispersal of snowshoe hares during years of food shortage is sufficient to explain synchrony of population cycles over wide areas. To predict the impacts of anthropogenic climate change, caribou ecologists must elucidate the roles of density-independent (*e.g.*, climate) and density-dependent (*e.g.*, forage, predators) factors that may cause fluctuations in caribou (*Rangifer tarandus*) populations.

The difficulty of this task becomes obvious when one considers the variety of ecological situations that caribou occupy and the complexity of each of those situations. Habitats are aggregated spatially into "patches" of varying sizes (Arditi and Decoronga, 1988). At a fine spatial scale, frost and snow affect the structures of terrestrial micro-habitats used by arctic herbivores (Sigafos, 1952; Zoltai and Tarnocai, 1981; Walker *et al.*, 1993). As spatial scale increases, habitat patches are, in turn, assembled into larger and larger clusters (Kotliar and Wiens, 1990) as they become aggregated by elevation, aspect, ruggedness, marine influences, and other factors. Animals organize their behaviors into temporal aggregations or "bouts" that may last minutes or hours (Slater, 1974). These bouts are subsequently assembled into larger temporal clusters, such as circadian rhythms, seasonal migrations and inter-annual emigration. The current distribution and adaptive capacity of any population has been shaped by the ecological circumstances experienced over past weeks, years, decades, centuries and millennia. Despite this obvious multiscale ecological organization, ecologists rarely consider how the scale at which their studies occur may affect the applicability of

the results at other scales (Wiens, 1989).

Few ecological studies of arctic herbivores have implemented research approaches that allow them to apply their results across several scales. Schaeffer (1995) used a multiscale approach to study the interactions between habitat structure and habitat selection by muskoxen (*Ovibos moschatus*). Although this 3-year study assesses muskox foraging ecology across various spatial scales, such short-term studies may prove inadequate to effectively predict the potential consequences of long-term temporal processes, including climate change.

Scientific ecological data in the Canadian Arctic is limited historically, making it difficult for Arctic ecologists to build and subsequently test models that predict processes occurring over several decades, centuries or millennia. As a result, ecologists face a formidable task in studying the ecology of adaptable arctic herbivores within the reality of both multiscale spatial structures and multiscale temporal processes. This paper attempts to synthesize a variety of evolutionary and ecological issues associated with the potential impacts of climatic change on caribou. I will examine some hypotheses about climatic changes that may be responsible for genetic differences between caribou on Baffin Island and currently recognized sub-species, describe the ecological rationale that makes multiscale research a necessity, and review

some studies and hypotheses on the effects of climate on Arctic tundra caribou. To encourage future interdisciplinary research, I will identify some information sources that caribou ecologists can consult to develop predictions pertinent to climatic change.

THE GENETIC IDENTITY OF CARIBOU IN THE EASTERN CANADIAN ARCTIC

Evidence suggests that at the height of the Wisconsin glaciation, *Rangifer tarandus* occurred in a tundra belt across the southern edges of continental ice-sheets and in the unglaciated Beringia refugium in Alaska-Yukon (Banfield 1961). Genetic evidence suggests that woodland caribou, *R. t. caribou*, have been isolated from Canadian barren-ground caribou, *R. t. groenlandicus*, to the north both in recent time and during their phylogenetic evolution (Røed *et al.*, 1991).

Caribou Origins

Ancestors of Peary caribou, *Rangifer tarandus pearyi*, and the now extinct East Greenland caribou, *R. t. eogroenlandicus*, may have survived the late Wisconsin glaciation in high arctic refugia in Arctic Canada or northern Greenland (Banfield 1961). The Svalbard reindeer, *R. t. platyrhynchus*, may have also originated from the same ancestors (Røed, 1985; Røed *et al.*, 1986). A caribou antler from northern Greenland, radiocarbon-dated

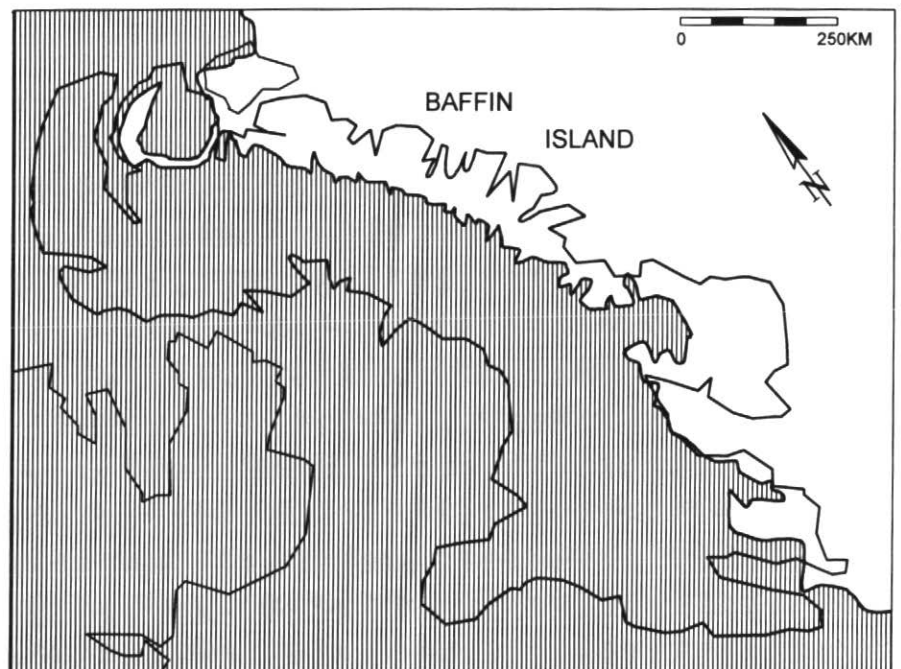


Figure 1 Maximum extent of the Laurentide Ice Sheet on Baffin Island during the late Wisconsin glaciation, 18000 BP (Dyke and Prest, 1986).

at >40,000 BP (Meldgaard and Bennike, 1989), suggests that caribou occurred there when most of northern Eurasia and America was covered with ice. However, a high arctic refugium may not have supported caribou populations sufficiently long for them to become the ancestors of today's Peary caribou and Svalbard reindeer (Degerbøl, 1957; Meldgaard, 1986; Røed, 1985). The genetic similarities between barren-ground and Peary caribou are much greater than between barren-ground and woodland caribou (Røed *et al.*, 1991). This suggests that Peary caribou may have survived parts of the Wisconsin glaciation in areas south of the high arctic refugia, perhaps in more marginal parts of the Beringia refugium (Meldgaard, 1986). In this scenario, ancestors of Peary caribou and Svalbard reindeer may have been only partly isolated from ancestors of barren-ground caribou during the Wisconsin glaciation.

Although animal size can vary with nutrition, Røed (1987) has shown significant correlations between size and genetic variation in *Rangifer tarandus*. Banfield (1961) determined the current sub-species of *R. tarandus* using size differences in skull measurements. Banfield (1961) identified five demes of *R. t. groenlandicus* that showed a mosaic type of variation. Baffin caribou were much smaller than those on the mainland of the Northwest Territories (NWT). Banfield's (1961) size differences between Baffin and mainland caribou are consistent with those reported by Inuit familiar with both animal groups. Baffin

caribou have lighter coat color in all seasons, are about 25% smaller in size, and have smaller antlers (T. Ikummaq, Igloodik, pers. comm., 1989). Baffin caribou showed no sign of a *R. t. pearyi* influence, even though the larger northwest mainland deme did (Banfield, 1961). Banfield (1961) may have ignored size differences between Baffin and mainland caribou in order to accept his hypothesis that the "relatively large" Greenland caribou originated from mainland NWT caribou that supposedly crossed Baffin Island and then Davis Strait. Meldgaard (1986) has since questioned whether caribou could survive this "sweepstakes route" of at least 350 km across Davis Strait.

At the genetic level, transferrin allele frequencies in Baffin Island caribou revealed surprisingly great genetic differences from all other *Rangifer* subspecies (Røed *et al.*, 1991). Tf¹², the dominant allele among Baffin caribou (52%), was absent from all other subspecies, except *Rangifer tarandus caribou* (1%) and *R. t. groenlandicus* (1%), suggesting little genetic exchange between Baffin caribou and any other population. The level of genetic difference from the other subspecies was even greater than between woodland and barren-ground caribou, which apparently had different ancestral origins during the Wisconsin glaciation.

Climatic Influences

Portions of eastern Baffin Island (Fig. 1) have been ice-free for at least the last 70,000-150,000 years (Miller *et al.*,

1977b), and some areas show no evidence of ever being glaciated (Mode, 1981). At the maximum extent of the Laurentide Ice Sheet, which covered almost all of Canada about 18,000 BP, portions of northern and eastern Baffin Island remained ice free (Dyke and Prest, 1986, 1987). This area remained separated from continental North America by the Laurentide Ice Sheet until 8000-7000 BP (Dyke and Prest, 1987). Ancestors of Baffin caribou may have survived the late Wisconsin glaciation in an isolated refugium on northern and eastern Baffin Island, explaining the genetic difference between Baffin caribou and all subspecies of *Rangifer tarandus*.

The climate of northern and eastern Baffin Island during 18,000-11,000 BP was probably characterized by relatively strong, dry surface winds, cold temperatures, minimum snow cover, and presumably long winters with mid-winter thaws being unlikely (G.H. Miller, pers. comm., 1989). The oldest pollen record from northern Baffin Island, C¹⁴-dated to over 16,000 BP, is dominated throughout by *Salix* spp., Cyperaceae and Gramineae (Short and Andrews, 1988). *Betula* pollen, often used to distinguish between low arctic and high arctic conditions (Andrews *et al.*, 1980), appeared in this northern Baffin record at about 16,000 and 14,000 BP and then more frequently after 8000 BP. The northern limit of *Betula* is currently about 1000 km to the southeast on Cumberland Peninsula (Andrews *et al.*, 1980). Short and Andrews (1988) concluded that there was probably a regional source for *Betula* pollen on northern Baffin Island between 16,000 BP and 12,000 BP. Short *et al.* (1985) and Short and Andrews (1988) show that vegetation suitable as caribou summer forage (*e.g.*, Gramineae and Cyperaceae) and winter forage (*e.g.*, *Salix*) may have occurred somewhere on northern and/or eastern Baffin Island from at least 16,000 BP to the present. One or more sites were probably capable of supporting small caribou populations at any time throughout this period.

Severe snow and/or icing conditions may have made forage inaccessible during warm, wet periods (*e.g.*, 14,000 BP to 8000 BP (Short *et al.*, 1985)). However, in any given winter, snow cover conditions are highly variable on Baffin Island (Jacobs, 1989). If small caribou populations survived on Baffin Island throughout the late Wisconsin glaciation, they may have adapted through major

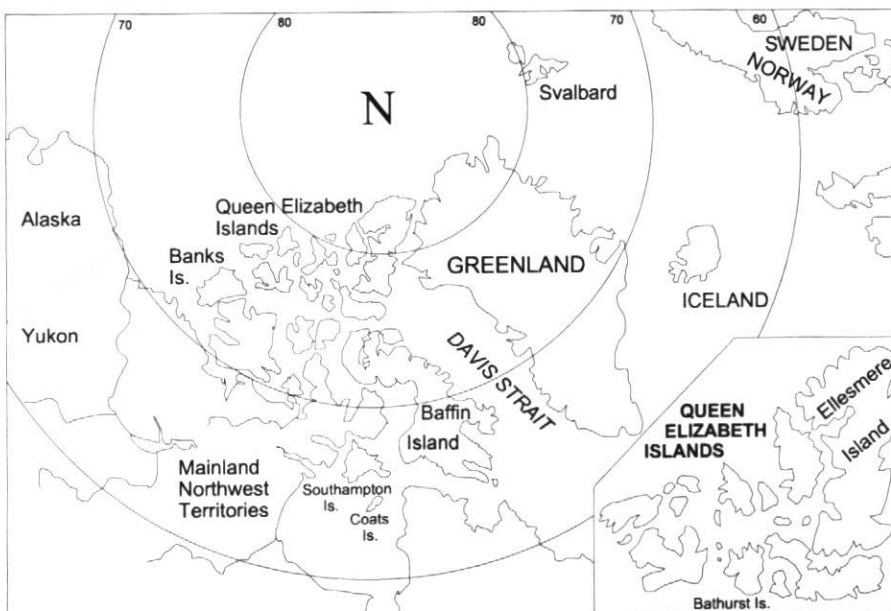


Figure 2 Some locations inhabited by Arctic tundra caribou in the Northern Hemisphere.

shifts in their winter ranges in response to depleted forage and/or severe snow conditions. Under such conditions, the population may have dropped to only tens of animals at various times. Such severe bottlenecks could have caused a rapid increase in the genetic distance between Baffin caribou and other sub-species (Chakraborty and Nei, 1977). Subsequent immigration of caribou onto Baffin Island after 8000 BP would explain the current heterozygosity of Baffin caribou at the transferrin locus (Røed *et al.*, 1991).

If caribou did not survive the late Wisconsin glaciation on Baffin Island, *Rangifer tarandus groenlandicus* would have colonized Baffin Island after 8000 BP, as suggested by Banfield (1961). A subsequent population bottleneck, followed by further immigration, could explain the present heterozygosity of transferrin alleles in Baffin Island caribou. Although Baffin caribou have historically gone through massive fluctuations in population distribution and density (Ferguson, unpubl. data), it is difficult to envision environmental conditions which would have reduced the population to a few tens of animals after the deglaciation of the western portion of the island.

Adaptive Capacity of Caribou

Unfortunately, the oldest caribou remains from Baffin Island date to only about 3000 BP (D. Stenton, pers. comm., 1989). Several fossils, dating 40,000-8000 BP and genetically consistent with current Baffin caribou, would be needed to demonstrate that caribou survived in a Baffin refugium. However, it is unlikely that such fossils could be found if only a few tens of animals survived during this period.

If caribou did survive the late Wisconsin on Baffin Island and other high arctic refugia, it would suggest that the species can adapt to large changes in global climate. Co-operative research into paleoclimatic changes, paleovegetation and the genetic distinctiveness of caribou on Baffin Island and other parts of Nunavut may help elucidate the adaptive capacity of caribou. However, future anthropogenic climate change could occur at a rate surpassing that capacity.

FORAGING ECOLOGY OF ARCTIC TUNDRA CARIBOU

I identify *Rangifer tarandus* that occupy arctic tundra habitats year-round as "arctic tundra caribou." In Canada, this eco-

type is found on arctic islands from Coats and Baffin islands in the southeast, north to Ellesmere Island, and west to Banks Island, and on the northeast mainland of the NWT (Fig. 2). These caribou include the sub-species, *R. t. pearyi*, *R. t. groenlandicus* and interbreeds in Canada and Greenland. Arctic tundra caribou also occur on Svalbard (Fig. 2) and on islands north of mainland Siberia (*R. t. tarandus*). Although arctic tundra caribou include several subspecific types, their foraging ecology is similar because they can not use relatively productive and extensive continental treed habitats during winter. During winter, these caribou feed on vegetation that is exposed by wind removing the snow, or must dig (or crater) through a hard snow cover to find senescent tundra vegetation that is, except for lichens, of low digestibility. In most winters, forage across a large portion of their winter range is inaccessible, reducing usable winter range to a fraction of summer range.

Population Dynamics

The population dynamics of caribou may also be influenced either directly or indirectly by wolf or human predation (Bergerud, 1988, 1996), summer weather and/or vegetation (Crête and Huot, 1993; Le Hénaff and Luttich, 1988; Skoog, 1968) and interspecific competition (Vincent and Gunn, 1981). These data are derived mainly from populations that live in forests year-round or at least during winter, however. I have found no evidence in the literature indicating that any of these factors have played major roles in population fluctuations of arctic tundra caribou. Although predation and interspecific competition may be important factors in some circumstances, the literature does not reveal clear evidence for populations of arctic tundra caribou. It seems unlikely that summer forage could be a major factor, because the effective range of arctic tundra caribou is many times greater after the snow melt (Skogland, 1986), and potential forage increases substantially in quantity, quality and diversity during summer (White, 1983). During a population crash of reindeer introduced to St. Matthew Island near Alaska, Klein (1968) reported that summer forage had suffered little from the previous high densities of reindeer, while lichens had been depleted and essentially eliminated from the reindeer's winter diet. Sedges and grasses, potential summer forage, were expanding into

areas previously occupied by lichens on St. Matthew Island.

Winter Foraging

The many spatial and temporal scales that influence the winter foraging ecology of arctic tundra caribou can be visualized by considering the foraging choices of individual animals. At the smallest spatial scale, each caribou can choose between specific parts of the plant species present at the bottom of each crater dug through the snow. When cratering, the individual makes choices within foraging sites (*i.e.*, tens of metres), and between foraging sites (*i.e.*, hundreds to thousands of metres) depending partly on snow-cover characteristics (Skogland, 1978). The largest spatial scale affecting foraging choices during any given winter begins during the animal's summer-autumn migration. This migration theoretically gives each caribou many choices across all potential wintering terrain within the animal's migratory range, or a radius of up to 600 km for some caribou on southern Baffin Island (Ferguson, 1989). Clearly, individual caribou can adapt to the habitats that they encounter at many spatial scales, ranging from 5-10 mm (dependent on bite size and plant architecture) to hundreds of kilometres (dependent on their migratory behavior, fidelity to seasonal habitats, and physical barriers).

Temporal scales affecting caribou ecology are similarly variable. Caribou are affected by weather events that change the snow pack over periods of hours, days and months, as well as between years. In turn, individual caribou can adapt to such changes with simple choices such as expanding a previously dug crater instead of digging a new one or moving to alternative foraging sites nearby (Thing, 1977). Over a longer time scale, each individual caribou is affected by the impacts that previous grazing may have had on the forage currently available below the snow (Klein, 1968). Such impacts last 20-40 years (I. Jåma in Vibe, 1967; Klein, 1987). In these situations, caribou could adapt to previous grazing through emigration to new or well-rested winter ranges, assuming only limited physical barriers to dispersal (Leader-Williams, 1988). When assessing the relative importance of climatic factors, caribou ecologists should account for the cumulative impacts of grazing that could be the overriding limiting factor for up to 40 years after the fact.

EVIDENCE OF IMPACTS OF CLIMATE ON ARCTIC TUNDRA CARIBOU

Although Miller (1982) recognized that forage is the ultimate limiting factor for caribou populations, he suggested that other mortality factors do not allow caribou to reach densities at which forage would control populations on most ranges. According to Miller (1982) and Caughley and Gunn (1993), caribou populations are limited more by access to forage through the snow cover than by a shortage in the absolute food supply or other ecological factors.

Greenland Caribou Populations

Vibe (1967) reviewed available weather records and indices of wildlife populations on Greenland (Fig. 2) back to the 1700s. His hypothesis was that periods of wet, warm winters are unfavorable for caribou because deep snow and/or icing makes forage unavailable. During such periods, most Greenland caribou populations supposedly declined and in some cases became extinct. However, examination of his data reveals an inconsistent picture. After being limited for about 45 years, the West Greenland (Sisimiut) population increased after 1815 during a period of stable conditions with reduced winter precipitation. However, "the most important factor" was that climatic conditions had "forwarded regeneration of the vegetation" during the decades of low reindeer density (Vibe, 1967). "After 30 years' increase, the reindeer curve culminated around 1845-50, and from then... fell rapidly" (Vibe, 1967). He also acknowledged that this decline "may to some extent have been caused by overgrazing." Furthermore, the climatic situation that brought unstable wet winters began around 1865 (Vibe, 1967), while the population crash was largely complete by 1860 (Meldgaard, 1986). Although the period of wet winters may not have initiated the decline, it probably maintained the population at low densities as Vibe (1967) suggested.

Thing (1983) concluded that low lichen biomass on winter ranges due to excessive grazing was the primary cause of the next major decline of West Greenland caribou during the late 1970s. On the other hand, Meldgaard (1986) concluded that climatic change was the major cause of fluctuations in Greenland caribou populations because grazing pressure would lead to stabilization with only insignificant oscillations around an

equilibrium. Meldgaard's (1986) conclusion is not supported by the climatic data, however, assuming that he was applying Vibe's (1967) wet, warm winter hypothesis. Vibe (1967) acknowledged that the West Greenland population's most recent increase ironically began during a period of wet winters during 1959-1964, when the caribou suddenly expanded their winter range into areas where vegetation had not been grazed for many years. Meldgaard (1986) provided data showing colder, dryer winters during the subsequent population decline in the late 1970s. The published data for the 1959-1984 fluctuations of West Greenland caribou shows that both the increase and decrease phases occurred *in spite of* winter climatic conditions that should have produced opposite population trajectories!

Arctic Islands Caribou Populations

Miller *et al.* (1977a) found at least short-term (*i.e.*, 1-2 years) evidence supporting Miller's climate hypothesis during a decline of Peary caribou on the Queen Elizabeth Islands (QEI) (Fig. 2) during the early 1970s. After a winter with restrictive snow conditions in 1973-74, Miller *et al.* (1977a) detected a decline of 45% and 69% on the western QEI and adjacent Bathurst Island (Fig. 2), respectively. During that winter, malnutrition resulted in high mortality among all age groups and subsequently reduced population productivity. Would climatic conditions continue to appear as the dominant factor if vegetation and snow-cover data had been available over one or more decades?

Between 1961 (Tener, 1963) and 1973 (Miller *et al.*, 1977a), caribou had declined from 15,300 to 4,200 on the western QEI and from 3,200 to 770 on Bathurst Island. Miller *et al.*'s (1977a) study could not address the causes of these declines which occurred before the severe winter of 1973-1974. On the other hand, Inuit reported that caribou were emigrating from Bathurst Island at least during the late 1960s and early 1970s (Freeman, 1975). They suggested that the decline of caribou on Bathurst Island was caused at least partly by human activity during oil exploration.

The Bathurst Island population increased from about 290 in 1981 (Ferguson, 1987) to 1030 in 1988 (Miller, 1991). Indirect evidence suggests that immigration may have contributed to this increase. Between 1974 (Miller *et al.*, 1977a) and

1986-1988 (Miller, 1987, 1988, 1991), caribou numbers on the western QEI declined by about 1000, while numbers on adjacent Bathurst Island increased by about 800. Miller (1991) suggested that such movements are sporadic and are caused entirely by widespread forage unavailability produced by unfavorable snow/ice conditions. Although he suggested that these movements allow Peary caribou maximal use of ranges with the best forage, Miller (1991) did not suggest that the movements are caused primarily by density-dependent forage depletion. Because Miller *et al.* (1977a) and Miller (1991) did not provide direct evidence on landscape-scale snow cover conditions, forage depletion and/or inter-island caribou movements during these population changes, it is not possible to evaluate predictions of Miller's hypothesis.

Caribou Population Emigration and Impacts

Mass emigrations of caribou are poorly understood, but may be density dependent (Miller, 1982). One recent example comes from northwestern Greenland. Roby *et al.* (1984) concluded that caribou were extirpated from northwestern Greenland by the late 1970s. During winter 1989-1990, a significant number of Peary caribou apparently emigrated from Ellesmere Island to northwestern Greenland (Fig. 2), resulting in a harvest of more than 100 caribou by Greenlanders during May-November 1990 (A. Rosing-Avid, pers. comm., 1990). To my knowledge, no cause for this range shift has been offered. Inuit have observed shifts in winter distributions of large numbers of caribou over the past 100 years on southern Baffin Island (Fig. 2) (Ferguson, unpubl. data). According to Baffin Inuit, caribou sub-populations periodically emigrate en masse once local winter forage becomes depleted. Some Inuit also suggested that ground icing will not cause major problems unless there have been too many caribou for too long. Klein (1968) found that on St. Matthew Island, where emigration was not possible and after previous high densities of reindeer had depleted their winter forage, almost the entire reindeer population starved to death during a winter of extreme snow accumulation.

Similarly, Skogland (1985) suggested that density-dependent winter forage is the primary factor in regulation of population size among wild *Rangifer tarandus* populations on arctic and alpine tundra

on Svalbard and in Norway (Fig. 2). Further, he suggested that density-independent factors play a role only at high population densities. Based on studies of several wild tundra populations, Skogland (1986, 1989) pointed out that the dynamics of a given population also depend on several other factors, including the ratio of winter-to-total range, terrain characteristics within the winter range, and the type of winter diet (*i.e.*, vascular plants or lichen).

Reindeer on Svalbard (Fig. 2) apparently are limited by snow cover conditions that restrict accessibility to forage in most winters (Reimers, 1982). During especially severe winters, Svalbard reindeer do suffer high rates of mortality (Reimers, 1982, 1983; Tyler, 1987). However, limitation of population growth by climatic factors occurred after Svalbard reindeer eliminated terricolous lichens in historic times and subsequently switched to low quality winter forage (Brattbakk and Rønning, 1978, and Ekern and Kildemo, 1978, in Reimers, 1983). In some severe winters, these sedentary reindeer (Tyler and Øritsland, 1989) will emigrate when faced with starvation (Tyler, 1987), but will they emigrate when faced with depleted forage resources before severe snow conditions causes high mortality?

In 1978, 15 reindeer were introduced to a peninsula on northwestern Svalbard that had been unoccupied for about 100 years (Staaland *et al.*, 1993). This population increased to about 200 by 1989. Between 1979-1980 and 1988-1989, preferred lichen species had almost disappeared and the reindeer had begun feeding on a wider variety of forage species, similar to reindeer elsewhere on Svalbard (Staaland *et al.*, 1993). By August 1995, Staaland (*pers. comm.*, 1995) reported that reindeer apparently had begun to emigrate from the peninsula, without evidence of mortality caused by severe snow cover conditions. Such emigration could be predicted by the Inuit hypothesis, but not by Miller's hypothesis.

Lindsay (1973), Kightley and Smith (1976) and Leader-Williams *et al.* (1981) have reported major impacts of reindeer on the subantarctic island of South Georgia. Lichens and a preferred dwarf shrub, *Acaena magellanica*, were depleted first, while tussock grass, *Poa flabellata*, has become the reindeer's major winter forage and has been affected only at high reindeer densities. However, subantarctic tussock grasslands and other com-

munities have higher productivity compared to similar plant communities in the Arctic (French and Smith, 1985). Leader-Williams (1988) suggested that the persistence of reindeer on tundra islands depends on such resilient vascular plants. For island tundra populations, Leader-Williams (1988) viewed climate and emigration as playing secondary roles to forage resources in limiting population growth, and contrasted these to continental populations for which predation may be a dominant or secondary factor to forage.

Caribou on Coats Island have had little opportunity to emigrate in recent years because of year-round open water between Coats and Southampton islands (Fig. 2) (Gates *et al.*, 1986). Adamczewski *et al.* (1988) attributed limitation of this population to an interaction between historically depleted forage resources and variable snow-cover conditions. Forty-eight caribou were introduced to adjacent Southampton Island in 1968, and increased to 13,700 by 1991 (Heard and Ouellet, 1994). Although some evidence of overgrazing has been detected (Ouellet *et al.*, 1993), Southampton caribou have not suffered high winter mortality during years when caribou on Coats Island did (Heard and Ouellet, 1994). This led Heard and Ouellet (1994) to suggest that the effect of adverse weather on Arctic tundra caribou is dependent on population density. As pointed out by Ouellet *et al.* (1996), it is important to distinguish between the roles of density-dependent factors (*e.g.*, forage depletion) that may dampen population fluctuations of Arctic tundra caribou (*i.e.*, regulatory factors) and the roles of density-independent factors (*e.g.*, climate) that may introduce variability into those fluctuations (*i.e.*, limiting factors).

CONCLUSIONS

Rangifer tarandus has adapted and evolved in situations promoting both high (Røed *et al.*, 1991) and limited genetic diversity (Røed, 1985). The diversity of habitats and environmental situations that are currently occupied by this species attest to its adaptive capacity. Additional genetic analysis of caribou on Baffin Island, mainland NWT, and western Greenland is needed to define the genetic distinctiveness of caribou in these areas. Continued paleoecological work in refugia potentially occupied by *R. tarandus* is needed to reveal the extreme climatic conditions that caribou may have

survived over the millenia. Arctic tundra caribou probably represent the ecotype that may be most susceptible to the negative effects of climatic changes. The possibility that small numbers of caribou survived in isolated refugia for thousands or even tens of thousands of years suggests that the species may be able to adapt to future climatic change. The question remains, however: can this adaptable species survive the accelerated climatic changes that man may cause?

Studies on Coats and Southampton islands, Greenland, Svalbard, Norway and South Georgia support the density-dependent role of winter forage depletion in the short- and long-term population dynamics of arctic tundra caribou, as suggested by Inuit on southern Baffin Island. Additionally, the different dynamics of these populations illustrate the importance of examining forage, snow conditions, and caribou movements at several spatial scales. Where caribou have opportunities for dispersal over large islands or across archipelagos, future population trends of a given sub-population will depend on the grazing history, snow cover, density and other features of sub-populations in adjacent areas. At temporal scales involving decades or centuries, ecologists may find it useful to view caribou populations as "metapopulations" (Hanski and Gilpin, 1991) in which sub-populations are interconnected through winter range shifts that may be predictable, a concept that is part of Baffin Inuit knowledge.

Jefferies *et al.* (1994) concluded that there is no scientific evidence demonstrating long-term impacts of vertebrate herbivores on undisturbed northern plant communities. However, lack of such evidence does not imply that such impacts do not occur.

Jefferies *et al.* (1994) recommended both short- and long-term studies into the interactions between plant communities and northern herbivores. Studies examining spatial scales from habitat microsites to continental expanses will need to be integrated. These spatial scales must be overlaid with temporal scales extending over the decades necessary for the re-growth of heavily grazed tundra forage. Across these scales, interdisciplinary studies are required to assess the numerical and functional responses of caribou and their forage to density-dependent and density-independent ecological factors. Paleoecological research could help determine the envi-

ronmental extremes that this ecotype has survived. However, the logistic and financial implications of such efforts will require close co-operation between a diverse range of environmental scientists, including botanists, climatologists, glaciologists, paleoecologists and others. If the generations of ecological observations by Inuit (Ferguson and Messier, 1997; Gunn *et al.*, 1988) can be integrated successfully into this effort, unique historical models of caribou metapopulations could be developed, in turn yielding pertinent predictions that could be tested at the sub-population and meta-population levels. Once this work is completed, the impacts of anthropogenic climate change on caribou may be predicted.

Distinguishing between density-independent (*e.g.*, climate) and density-dependent (*e.g.*, forage resources) factors that may initiate population declines of arctic tundra caribou is critical for future management, if these caribou are faced with rapid anthropogenic climate change. If population declines are initiated primarily by density-independent factors, then populations should be kept at maximum sizes over large areas so that they have a numerical chance of surviving. However, if declines are initiated primarily by density-dependent forage depletion, then populations should be kept at low densities so that forage quality and quantity are maintained at high levels. In fact, planned extirpation of some sub-populations on depleted winter ranges could be a management tool allowing recovery of forage resources and re-introduction of caribou sooner rather than later, especially if climate change makes extirpation inevitable in heavily grazed areas.

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REFERENCES

- Adamczewski, J.Z., Gates, C.C., Soutar, B.M., and Hudson, R.J., 1988, Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada: Canadian Journal of Zoology, v. 66, p. 1986-1996.
- Andrews, J.T., Mode, W.N., Webber, P.J., Miller, G.H., and Jacobs, J.D. 1980, Report on the distribution of dwarf birches and present pollen rain, Baffin Island, N.W.T., Canada: Arctic, v. 33, p. 50-58.
- Arditi, R. and Dacorogna, B., 1988, Optimal foraging on arbitrary food distributions and the definition of habitat patches: American Naturalist, v. 131, p. 837-846.
- Banfield, A.W.F., 1961, A revision of the reindeer and caribou, Genus Rangifer: National Museum of Canada, Bulletin, n. 177, Biological Series, n. 66, 137 p.
- Bergerud, A.T., 1988, Caribou, wolves and man: Trends in Ecology and Evolution, v. 3, p. 68-72.
- Bergerud, A.T., 1996, Evolving perspectives on caribou population dynamics, have we got it right yet?: Rangifer, Special Issue, n. 9, p. 95-115.
- Brattbakk, I., and Rønning, O.I., 1978, Rikt planteliv langt mot nord: Forskningsnytt, v. 23, p. 44-51.
- Caughley, G., and Gunn, A., 1993, Dynamics of large herbivores in deserts: kangaroos and caribou: Oikos, v. 67, p. 47-55.
- Chakraborty, R. and Nei, M., 1977, Bottleneck effects on average heterozygosity and genetic distance with the stepwise mutation model: Evolution, v. 31, p. 347-356.
- Crête, M., and Huot, J., 1993, Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams: Canadian Journal of Zoology, v. 71, p. 2291-2296.
- Degerbl, M., 1957, The extinct reindeer of East-Greenland *Rangifer tarandus eogroenlandicus*, subsp. nov. compared with reindeer from other Arctic regions: Acta Arctica, v. 10, p. 1-66.
- Dyke, A.S. and Prest, V.K., 1986, Paleogeography of northern North America, 18,000 - 1,000 years ago: Map 1703A, scale 1:125 000, Sheet 1-3: Geological Survey of Canada, Ottawa, ON.
- Dyke, A.S. and Prest, V.K., 1987, Late Wisconsinan and Holocene history of the Laurentide ice sheet: Geographie physique et Quaternaire, v. 41, p. 237-263.
- Ekem, K., and Kildemo, K., 1978, Svalbard-reinens ernæring (*Rangifer tarandus platyrhynchus*, Vrolik): Joint thesis, Agricultural University of Norway, 130 p.
- Elton, C.S., 1924, Periodic fluctuations in the numbers of animals: their causes and effects: British Journal of Experimental Biology, v. 2, p. 119-163.
- Ferguson, M.A.D., 1987, Status of Peary caribou and muskox populations on Bathurst Island, N.W.T., August 1981: Arctic, v. 40, p. 131-137.
- Ferguson, M.A.D., 1989, Baffin Island, in Hall, E., ed., People and caribou in the Northwest Territories: Department of Renewable Resources, Yellowknife, NWT, p. 141-149.
- Ferguson, M.A.D., and Messier, F., 1997, Collection and analysis of traditional ecological knowledge about a population of Arctic tundra caribou: Arctic, v. 50, p. ??-??.
- Freeman, M.M.R., 1975, Assessing movement in an arctic caribou population: Journal of Environmental Management, v. 3, p. 251-257.
- French, D.D., and Smith, V.R., 1985, A comparison between northern and southern hemisphere tundras and related ecosystems: Polar Biology, v. 5, p. 5-21.
- Gates, C.C., Adamczewski, J., and Mulders, R., 1986, Population dynamics, winter ecology and social organization of Coats Island caribou: Arctic, v. 39, p. 216-222.
- Gunn, A., Arlooktoo, G., and Kaomayok, D., 1988, The contribution of the ecological knowledge of Inuit to wildlife management in the Northwest Territories, in Freeman, M.M.R. and Carbyn, L., eds., Traditional Knowledge and Renewable Resource Management in Northern Regions: IUCN Committee on Ecology and the Boreal Institute for Northern Studies, Occasional Publication, n. 23, p. 22-30.
- Hanski, I. and Gilpin, M., 1991, Metapopulation dynamics: brief history and conceptual domain: Biological Journal of the Linnean Society, v. 42, p. 3-16.
- Heard, D.C. and Ouellet, J.-P., 1994, Dynamics of an introduced caribou population: Arctic, v. 47, p. 88-95.
- Jacobs, J.D., 1989, Spatial representativeness of climatic data from Baffin Island, N.W.T., with implications for muskoxen and caribou distribution: Arctic, v. 42, p. 50-56.
- Jefferies, R.L., Klein, D.R. and Shaver, G.R., 1994, Vertebrate herbivores and northern plant communities: reciprocal influences and responses: Oikos, v. 71, p. 193-206.
- Keith, L.B., 1974, Some features of population dynamics in mammals: International Congress of Game Biologists, Proceedings, v. 11, p. 17-58.
- Keith, L.B., Cary, J.R., Rongstad, O.J. and Brittingham, M.C., 1984, Demography and ecology of a declining snowshoe hare population: Wildlife Monographs, n. 90, 43 p.
- Kightley, S.P.J. and Smith, R.I.L., 1976, The influence of reindeer on the vegetation of South Georgia: I. Long-term effects of unrestricted grazing and the establishment of exclosure experiments in various plant communities: British Antarctic Survey, Bulletin, n. 44, p. 57-76.
- Klein, D.R., 1968, The introduction, increase and crash of reindeer on St. Matthew Island: Journal of Wildlife Management, v. 32, p. 350-367.

- Klein, D.R., 1987, Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island: *Journal of Range Management*, v. 40, p. 336-338.
- Kotliar, N.B. and Wiens, J.A., 1990, Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity: *Oikos*, v. 59, p. 253-260.
- Le Hénaff, D. and Luttich, S., 1988, Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion: *Arctic*, v. 41, p. 79-87.
- Leader-Williams, N., 1988, *Reindeer on South Georgia*: Cambridge University Press, Cambridge, UK, 319 p.
- Leader-Williams, N., Scott, T.A. and Pratt, R.M., 1981, Forage selection by introduced reindeer on South Georgia, and its consequences for the flora: *Journal of Applied Ecology*, v. 18, p. 83-106.
- Lindsay, D.C., 1973, Effects of reindeer on plant communities in the Royal Bay area of South Georgia: *British Antarctic Survey, Bulletin*, n. 35, p. 101-109.
- Meldgaard, M., 1986, The Greenland caribou - zoogeography, taxonomy, and population dynamics: *Meddelelser om Grønland, Bioscience*, v. 20, p. 1-88.
- Meldgaard, M. and Bennike, O., 1989, Interglacial remains of caribou (*Rangifer tarandus*) and lemming (*Dicrostonyx torquatus*) from north Greenland: *Boreas*, v. 18, p. 359-366.
- Miller, F.L., 1982, Caribou *Rangifer tarandus*, in Chapman, J.A. and Feldhamer, G.A., eds., *Wild Mammals of North America: Biology, Management and Economics*: John Hopkins University Press, Baltimore, MD, p. 923-939.
- Miller, F.L., 1987, Peary Caribou and Muskoxen on Prince Patrick Island, Eglinton Island, and Emerald Isle, Northwest Territories, July 1986: *Canadian Wildlife Service, Technical Report Series*, n. 29, 65 p.
- Miller, F.L., 1988, Peary Caribou and Muskoxen on Melville and Bynam Martin islands, Northwest Territories, July 1987: *Canadian Wildlife Service, Technical Report Series*, n. 37, 58 p.
- Miller, F.L., 1991, Estimating Bathurst Island Peary caribou and muskox populations: *Arctic*, v. 44, p. 57-62.
- Miller, F.L., Russell, R.H., and Gunn, A., 1977a, Distribution, Movements and Numbers of Peary Caribou and Muskoxen on Western Queen Elizabeth Islands, Northwest Territories, 1972-74: *Canadian Wildlife Service, Technical Report Series*, n. 40, 55 p.
- Miller, G.H., Short S.K. and Andrews, J.T., 1977b, The last interglacial-glacial cycle, Clyde foreland, Baffin Island, N.W.T.: *Stratigraphy, biostratigraphy, and chronology*: *Canadian Journal of Earth Sciences*, v. 14, p. 2824-2857.
- Mode, W.N., 1981, Quaternary stratigraphy and palynology of the Clyde foreland, Baffin Island, N.W.T., Canada: Ph.D. dissertation, University of Colorado, Boulder, CO, 219 p.
- Ouellet, J.-P., Heard, D.C. and Boutin, S., 1993, Range impacts following the introduction of caribou on Southampton Island, Northwest Territories, Canada: *Arctic and Alpine Research*, v. 25, p. 136-141.
- Ouellet, J.-P., Heard, D.C. and Mulders, R., 1996, Population ecology of caribou populations without predators: Southampton and Coats Island herds: *Rangifer, Special Issue* n. 9, p. 17-25.
- Reimers, E., 1982, Winter mortality and population trends of reindeer on Svalbard, Norway: *Arctic and Alpine Research*, v. 14, p. 295-300.
- Reimers, E., 1983, Mortality in Svalbard reindeer: *Holarctic Ecology*, v. 6, p. 141-149.
- Roby, D.B., Thing, H. and Brink, K.L., 1984, History, status and taxonomic identity of caribou (*Rangifer tarandus*) in northwest Greenland: *Arctic*, v. 37, p. 23-30.
- Red, K.H., 1985, Comparison of the genetic variation in Svalbard and Norwegian reindeer: *Canadian Journal of Zoology*, v. 63, p. 2038-2042.
- Røed, K.H., 1987, Transferrin variation and body size in reindeer, *Rangifer tarandus* L.: *Hereditas*, v. 106, p. 67-71.
- Røed, K.H., Staaland, H., Broughton, E. and Thomas, D.C., 1986, Transferrin variation in caribou (*Rangifer tarandus* L.) on the Canadian Arctic islands: *Canadian Journal of Zoology*, v. 64, p. 94-98.
- Røed, K.H., Ferguson, M.A.D., Crête, M. and Bergerud, T.A., 1991, Genetic variation in transferrin as a predictor for differentiation and evolution of caribou from eastern Canada: *Rangifer*, v. 11, p. 65-74.
- Schaefer, J.A., 1995, High arctic habitat structure and habitat selection by muskoxen (*Ovibos moschatus*): A multiscale approach: Ph.D. Thesis, University of Saskatchewan, Saskatoon, SK, 150 p.
- Short, S.K., Mode, W.N. and Davis, P.T., 1985, The Holocene record from Baffin Island: Modern and fossil pollen studies, in Andrews, J.T., ed., *Quaternary Environments: Eastern Canadian Arctic, Baffin Bay and Western Greenland*: Allen and Unwin, London, UK, p. 608-642.
- Short, S.K. and Andrews, J.T., 1988, A sixteen thousand year old organic deposit, northern Baffin Island, N.W.T., Canada: Palynology and significance: *Geographic physique et Quaternaire*, v. 42, p. 75-82.
- Sigafoos, R.S., 1952, Frost action as a primary physical factor in tundra plant communities: *Ecology*, v. 33, p. 480-487.
- Skogland, T., 1978, Characteristics of the snow cover and its relationship to wild mountain reindeer (*Rangifer tarandus tarandus* L.) feeding strategies: *Arctic and Alpine Research*, v. 10, p. 569-580.
- Skogland, T., 1985, The effects of density-dependent resources limitations on the demography of wild reindeer: *Journal of Animal Ecology*, v. 54, p. 359-374.
- Skogland, T., 1986, Density dependent food limitation and maximal production in wild reindeer herds: *Journal of Wildlife Management*, v. 50, p. 314-319.
- Skogland, T., 1989, Comparative social organization of wild reindeer in relation to food, mates and predator avoidance: *Advances in Ethology*, n. 29, 71 p.
- Skoog, R.O., 1968, Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska: Ph.D. thesis, University of California, Berkeley, CA, 699 p.
- Slater, P.J.B., 1974, The temporal pattern of feeding in the zebra finch: *Animal Behavior*, v. 22, p. 506-515.
- Staaland, H., Schie, J.O., Grøndahl, F.A., Resen, E., Leifseth, A.B., and Holand, Ø., 1993, The introduction of reindeer to Brøggerhalvøya, Svalbard: grazing preference and effect on vegetation: *Rangifer*, v. 13, p. 15-19.
- Tener, J.S., 1963, Queen Elizabeth Islands game survey, 1961: *Canadian Wildlife Service, Occasional Paper*, n. 4, 50 p.
- Thing, H., 1977, A study of the behavior, mechanics and energetics associated with winter cratering in the caribou (*Rangifer tarandus* L.) in northwest Alaska, October 1975 - April 1976: University of Alaska, Biological Papers, v. 18, p. 31-72.
- Thing, H., 1983, Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region: *Danish Review of Game Biology*, v. 12, p. 1-53.
- Tyler, N.J.C., 1987, Natural limitation of the abundance of the high arctic Svalbard reindeer: Ph.D. thesis, Cambridge University, Cambridge, UK.
- Tyler, N.J.C., and Øritsland, N.A., 1989, Why don't Svalbard reindeer migrate?: *Holarctic Ecology*, v. 12, p. 369-376.
- Vibe, C., 1967, Arctic animals in relation to climatic fluctuations: *Meddelelser om Grønland*, v. 170, p. 1-227.
- Vincent, D., and Gunn, A., 1981, Population increase of muskoxen on Banks Island and implications for competition with Peary caribou: *Arctic*, v. 34, p. 175-179.
- Walker, D.A., Halfpenny, J.C., Walker, M.D., and Wessman, C.A., 1993, Long-term studies of snow-vegetation interactions: *Bioscience*, v. 43, p. 288-301.
- White, R.G., 1983, Foraging patterns and their multiplier effects on productivity of northern ungulates: *Oikos*, v. 40, p. 377-384.
- Wiens, J.A., 1989, Spatial scaling in ecology: *Functional Ecology*, v. 3, p. 385-397.
- Windberg, L.A., and Keith, L.B., 1976, Experimental analyses of dispersal in snowshoe hare populations: *Canadian Journal of Zoology*, v. 54, p. 2061-2081.
- Zoltai, S.C. and Tarnocai, C., 1981, Some non-sorted patterned ground types in northern Canada: *Arctic and Alpine Research*, v. 13, p. 139-151.