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Comparative ecological and behavioral adaptations of *Ovibos moschatus* and *Rangifer tarandus*

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Abstract: Caribou/reindeer and muskoxen are the only two ungulate species that have successfully occupied arctic tundra habitats. Although confronted with similar environmental constraints, their morphological dissimilarities have enabled them to develop unique behavioral and ecological adaptations that under most circumstances result in minimal overlap in use of forage resources. The large body and gut capacity of muskoxen have enabled them to adopt a strategy maximizing rate of forage intake and energy conservation, whereas caribou/reindeer of substantially smaller body size must pursue selective feeding, requiring high mobility and high energy expenditure. Responses to predators and insects by the two species show similar contrasts in associated energy costs. When confronted with environmental extremes that limit forage availability, competition for food may occur and the resulting differential success is a reflection of their divergent evolutionary routes.

Keywords: caribou, reindeer, muskox, ecology, behaviour, morphology

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Introduction

Muskoxen and caribou/reindeer are the only two extant ungulate species that successfully adapted to life in the Arctic. Derived from the divergent evolutionary lines of the Bovidae and Cervidae, they each responded to unique aspects of their morphology to follow markedly different routes of adaptation for existence under the environmental constraints of high latitudes.

Morphological characteristics

A comparison of the morphology of the two species (Table 1) shows that the muskox has a much larger body and shorter legs than caribou/reindeer, although shortening of the legs has been a product of domestication of reindeer. Small hooves in relation to body size in muskoxen result in a much greater foot loading than in *Rangifer* that have broad hooves and prominent dew claws. Weight in muskoxen is concentrated over the large forehooves in contrast to a more nearly equal weight distribution in *Rangifer.* The differences between the two species presumably account for greater efficiency in digging through snow to obtain forage by *Rangifer* (Klein *et al.,* 1987). Leg length is directly correlated with locomotive efficiency and barren-ground caribou have the lowest net cost of locomotion of any terrestrial mammal species studied (Fancy and White, 1985). The longer legs, coupled with more equal distribution of weight on legs and hooves, account for greater running speed of *Rangifer* (Schmidt-Nielsen, 1984).

Table 1. Comparative morphological measurements of muskoxen and caribou/reindeer.

Measurements		Muskox	Source	Caribou/reindeer	Source
Total weight (kg)		218–266	1	87–99	2
Chest height (mm)		484	3	730	4
% body length		25		41	
Hoof size (mm^2)					
Fore	Male	125	5	185	6
	Female	97.5	5	146	6
Hind	Male	98.3	5	170	6
	Female	92.4	5	138	6
Ratio of fore/hindfoot					
	Male	1.60		1.09	
	Female	1.25		1.06	
Foot loading (g/cm^2)					
Hard surface		770	1	184	4
Soft snow		570	1	125	4
Rumen-reticulum wt. (kg)					
Summer		28.9 ± 5.1	1	14.8 ± 0.8	2
Winter		23.2 ± 2.1	1	8.2 ± 0.1	2
% body weight					
Summer		14.1 ± 2.5	1	16.5 ± 1.1	2
Winter		11.3 ± 1.0	1	20.1 ± 1.4	2

1. D. R. Klein and H. Thing, unpub. data
2. Staaland *et al.*, 1979
3. McDonald and Freeman, 1984
4. Telfer and Kelsall, 1984
5. D.R. Klein, unpub. data
6. Thing, 1977

Differences in mouth and gut morphology between muskoxen and *Rangifer* are pronounced. The muskox has a wider muzzle than caribou/reindeer and greater rumen-reticulum size, which is scaled to body size (Klein, 1985).

Horns in muskoxen serve the dual function of social display, conspecific challenging and fighting among adult males, and weapons for defense from predators. The upturned, sharp-tipped horns, of nearly equal length in males and females, of these relatively large-bodied animals are apparently the result of selection for defense against predators (Gray, 1987). *Rangifer* are unique among the Cervidae because both sexes grow antlers, but they use their antlers primarily in social interaction. The large antlers of adult males are hardened and potentially useful as weapons against predators only for a relatively brief period in autumn and early winter associated with the breeding season (Pruitt, 1960). With the possible exception of the immediate postpartum period when adult females may use their retained antlers to defend their newborn calves from small predators, antlers on females seem to have their greatest function in providing hierarchical superiority over conspecifics during winter foraging and calving (Henshaw, 1968; Espmark, 1971).

Pelage differences between muskoxen and caribou/reindeer are also distinct. The dense, fine underwool and extremely long guard hairs of the muskox are unparalleled in insulative value. When lying with the short legs folded beneath it and the long guard hairs of the back and sides forming a blanket to the ground or snow surface, insultative efficiency is extremely high. The extreme insultative efficiency of the pelage and short extremities of the muskox are effective in limiting heat loss under conditions of extreme cold, but may be a detriment during

warm weather and when body heat must be lost after running. Caribou/reindeer have short, hollow guard hairs as the primary insulation and only a low density of finer underwool in winter. Through piloerective control of the stiff, hollow guard hairs, they can vary the insulative effectiveness of their pelage, in contrast to muskoxen with their dense fleece of underwool. Thus, caribou/reindeer with relatively long and less thickly haired legs and the capability of altering the thickness of their pelage have more flexible thermoregulatory capacity than muskoxen.

Muskoxen and caribou/reindeer have made use of their distinct morphological characteristics in their adaptation to life at high latitudes (Table 2); thus as a consequence of their morphological differences, their ecology and patterns of behaviour are also uniquely distinct.

Foraging dynamics

The foraging dynamics and diets of *Ovibos* and *Rangifer* are products of the morphological differences between the two species discussed above. The larger rumen-reticulum capacity in muskoxen allows longer rumen retention time and therefore greater digestive efficiency (White *et al.,* 1981). Although large rumen size requires large amounts of forage, the slower rate of turnover of rumen contents limits forage intake accordingly. This and the broad muzzle allow muskoxen to maintain rumen fill with forage of relatively low digestibility by rapid bulk feeding in areas of high forage biomass. By contrast, caribou/reindeer must be more selective feeders to obtain plant material of high digestibility for a rapid rate of passage of the digesta to meet nutrient requirements. The consequences of these two divergent dietary strategies of

Table 2. Adaptive advantages of morphological features of muskox and caribou/reindeer.

Morphological Features	Adaptive Advantages	
	Muskox	Caribou/Reindeer
Body size	Large body/low surface area= conservation of body heat; large body = predator defense	Smaller body = lower daily maintenance cost; lower cost of locomotion
Leg length	Short legs = energy conservation, and foraging efficiency in absence of snow	Long legs= greater speed for predator avoidance; efficient locomotion; efficient foraging through snow
Hoof size & loading	Larger forehooves = stability in rutting bouts and stationary predator defense	Broad hooves = buoyancy in soft substrate; efficiency in cratering & swimming. Equal size of hooves = speed of locomotion
Pelage	Dense and thick underwool + long guard hairs = maximum insulation, especially when lying, and defense from insects	Straight hollow hair, minimal underwool = high thermal regulatory efficiency, increased buoyancy in water
Muzzle width	Broad mouth = efficient bulk feeder	Narrower muzzle = efficiency in selective feeding
Horn/antler characteristics	Permanent, upturned, sharp-tipped horns of equal length, in sexes effective for defense against predators. Englarged boss in males absorbs shock of rutting clashes	Antlers provide hierarchical feeding advantages through winter and during calving to productive females. Massive antlers of males provide social status in the rut, are shed prior to full winter
Rumen/reticulum size	Large rumen scaled to body size = slow rate of passage of digesta and efficient digestion of low-quality forage, favors bulk feeding	Smaller rumen = more rapid rate of passage, quick turnover of nutrients, and lower energy cost of movement

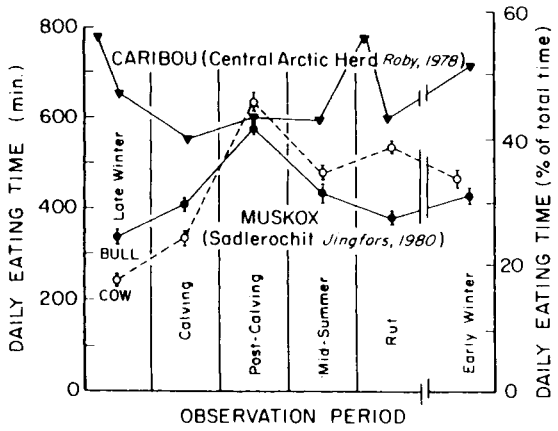

Fig. 1. Comparative feeding time of muskoxen and caribou in northern Alaska.

the two species is marked. The narrow muzzle of caribou/reindeer is better equipped for selective foraging but requires greater mobility on a daily and a seasonal basis. This can be compensated for through their longer legs, broader hooves, and more appropriate body conformation. Caribou spend more daily time feeding than muskoxen in comparable habitats, with the exception of the post-calving perion when daily feeding times are nearly equal and muskox feeding times are at a maximum (Fig. 1).

Comparison of time spent feeding during the post-calving period is complicated by insects, against which caribou/reindeer are less well defended than muskoxen. The greater daily movements rates of caribou/reindeer at this time are accounted for by movements associated with insect avoidance in addition to those required for feeding (Fig. 2). Migratory caribou travel over a linear distance of up to several thousand kilometers annually in their seasonal tracking of forage of high digestibility. Muskoxen, in contrast to caribou, are for the most part relatively sedentary, although seasonal movements may occur in some areas (Jingfors, 1980; Thing *et al.*, 1987; P. Reynolds, viva voce).

Lichens dominate the winter diet of migratory caribou whereas vascular plants, including forbs, leaves of willow *(Salix)*, and sedges, are the major constituents of the summer diet. Considerable variation in the winter diet of caribou/reindeer exists along a latitudinal gradient from south to north (Klein, 1985). Woodland-dwelling caribou and the large migratory caribou herds are characterized by winter diets dominated by lichens, but in the High Arctic where lichen biomass is low, Peary caribou *(R. t. pearyi)* and Svalbard reindeer *(R. t. platyrhynchus)* make heavy use of willows and select some mosses (Fig. 3).

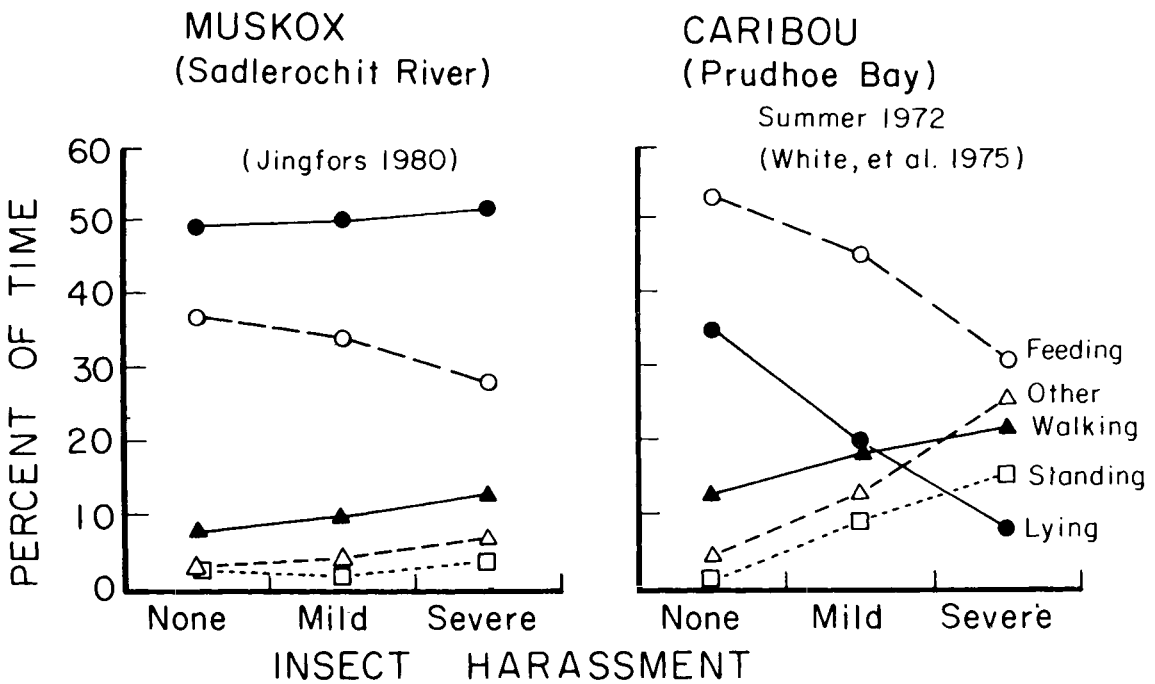

Fig. 2. Differential response of muskoxen and caribou to insects in northern Alaska.

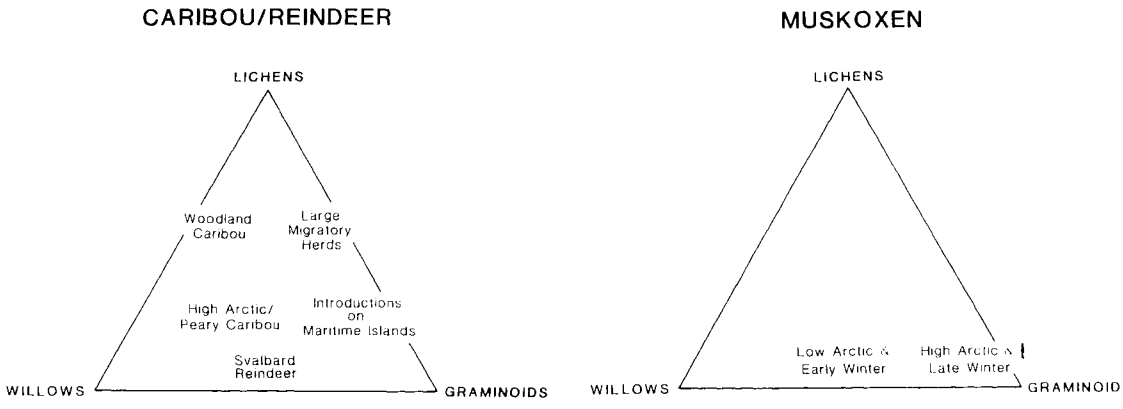

Fig. 3. Generalized winter diets of muskoxen and caribou/reindeer in relation to latitudinal and geographic location. Data from Tener (1965), Parker (1978), Boertje (1981), White *et al.* (1981), Thomas and Edmonds (1983), Thing *et al.* (1987), and Klein and Bay (1990).

Snow and their differential adaptability to it are important factors influencing foraging dynamics of the two species. Caribou are well equipped for locomotion in snow and for digging through it to obtain forage and are capable of migrating long dinstances over snow-covered terrain to optimize opportunities to secure diets of high digestibility in both summer and winter (Fig. 4). Muskoxen, by contrast, select areas with low snow accumulation and restrict their movements, especially in winter (Klein, 1985).

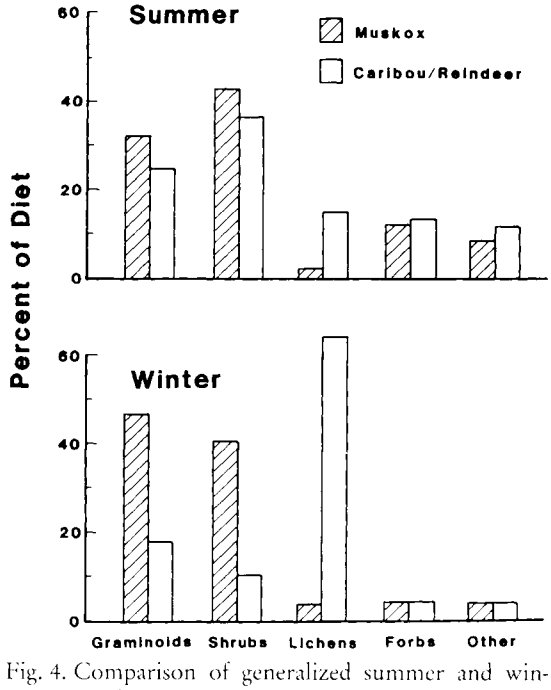

Fig. 4. Comparison of generalized summer and winter diets of muskoxen and caribou/reindeer in mid-arctic areas. Data sources as in Fig. 3.

In doing so they forego opportunities for selective foraging and their winter diets is generally dominated by graminoids of relatively low digestibility (Klein, 1985) (Fig. 4). Relative to caribou, availability of forage seems to be more important than forage type for muskoxen in winter. In some of the more southern areas of their distribution, willows that assume shrub form may be more readily available and therefore constitute a major portion of the muskox diet (O'Brien, 1988). Tener (1965) also found that willows were important for muskoxen in winter where they were available.

The consequences for the forage resource of a sedentary versus a wide-ranging foraging strategy of herbivores using it are potentially quite different. A wide-ranging foraging strategy would seem less likely to have detrimental consequences for the continued production of forage than one that is localized. Density of the herbivores is, however, a major determining factor as is the forage type involved. Lichens are much less resilient to the effects of grazing than most vascular plants and among the latter, graminoids are highly resilient (Klein, 1968). Therefore, muskoxen that have a relatively small home range and make heavy use of graminoids exist on a very resilient forage base. Henry *et al.* (1986) demonstrated that muskoxen may enhance productivity of sedge meadows in the High Arctic through grazing by accelerating the turnover of nutrients and through removal of the shading effect of accumulating leaf biomass. Willows, however, may not withstand continued heavy browsing by muskoxen, and in areas where muskoxen have been introduced to unoc-

cupied habitats, the extent of riparian willows declined (H. Thing, viva voce and D. Klein, per. obs.). By contrast, those caribou/reindeer with extremely large home ranges and that are seasonally migratory are usually dependent on lichens as a major winter dietary item. Overgrazing of the slow-growing lichens is limited by their restricted availability through the snow cover and the wide-ranging foraging habits of caribou/reindeer. Arboreal lichens are available as forage only where they can be reached by the animals, who are often aided by the support of accumulated hard-packed snow or wind that fells trees or blows lichens from their crowns. Ground lichens are often protected by snow cover through which caribou/reindeer must dig to obtain them, with the result that snow adjacent to feeding craters that is disturbed as a consequence of its displacement from the craters or by trampling is often so dense that the energetic cost of digging adjacent to old feeding craters becomes excessive (Pruitt, 1959).

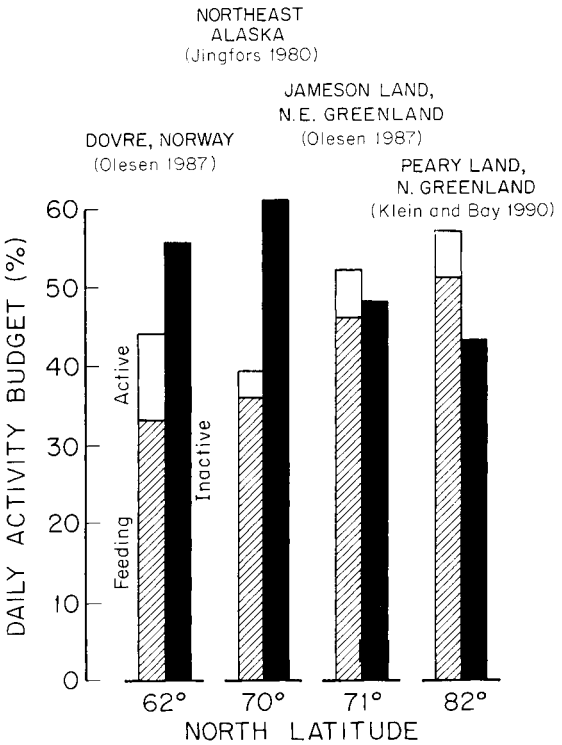

Fig. 5. Latitudinal gradient in daily feeding times in muskoxen.

Activity budgets

Daily and seasonal activity patterns of muskoxen and caribou/reindeer are a function of their unique morphological and associated physiological and dietary differences. Muskoxen pursue an energy-conservative life style that is compatible with large body size, high insulative value of their winter pelage with limited thermoregulatory plasticity, dependence on low-quality forage in winter, resistance to insect harassment, low locomotive efficiency, and ability to defend themselves from predators without running. Caribou/reindeer, by contrast, lead an active life style requiring a relatively high energy turnover. They are morphologically and physiologically adapted for efficient locomotion over varying substrates, including speed in running, which is their most effective predator avoidance strategy. They are vulnerable to insect harassment and respond by increasing activity. To maintain an energetically costly life style they must be selective feeders that track forage of high quality and digestibility seasonally and through annual migratory movements.

A comparison of activity budgets as reflected in feeding time (Fig. 1) and movement rates (Fig. 2) of muskoxen and caribou in northern Alaska showed that throughout the entire year daily activity of caribou exceeds that of muskoxen in the same general area. A possible exception is the post-calving period when feeding times may be similar. Activity patterns of both species, however, may vary with latitude. For example, time spent feeding increases with increasing latitude during summer in muskoxen (Fig. 5), apparently as a function of the lower density of available forage biomass and the need to maximize intake of high-quality forage during the brief summer growth period (Klein and Bay, 1990). Comparison of caribou activity budgets from Alaska and caribou/reindeer at higher latitudes also reflects the need for high arctic ungulates to maximize dietary intake during the brief arctic summer when both forage quality and available biomass are high and physiological activity is greatest (White *et al.*, 1981). The Central Arctic Herd at 70°N in Alaska spent about 40% of daily activity feeding during summer (Roby, 1978) whereas Svalbard wild reindeer at 78°N spent about 60% (Reimers, 1980). Reduced insect harassment at high latitudes and absence of predators on Svalbard likely contributed to these differences.

Differences in predator avoidance strategies between *Ovibos* and *Rangifer* (grouped stationary defense in the former versus alertness and swift running speed in the latter) presumably contribute to the divergence in energetic expenditures. An exeption is the Svalbard reindeer, which in the absence of predators and serious insect harassment, evolved toward the muskox ecological niche with shortened legs, capability to use low-quality forage and to accumulate large fat reserves, and an energy-conservative life style (Klein and Staaland, 1984).

Timing of parturition in the two species reflects differences in their seasonal energetic strategies and predator avoidance behaviour. Caribou/reindeer, with closely synchronized timing of birth within a population, minimize predation on neonates by the *swamping effect* (the concentration of newborn calves in time and space, thus reducing the risk of predation per animal). Their migratory behaviour also locates calving away from predators concentrated on wintering grounds. This strategy, however, requires extended precalving movements with associated energy costs (Fancy, 1986). Calving in muskox populations usually extends over several weeks. Apparently selective pressure for synchrony of calving has not been strong. Their predator defense and sedentary nature give equal protection to neonates independent of birth date. The increased energy expenditure of migration associated with timing of birth or separation from predators in caribou/reindeer is avoided by muskoxen.

Population limiting factors

Differences in behaviour and ecology of *Ovibos* and *Rangifer* predispose them to differences in the importance of population limiting factors. Predators can be more important in limiting *Rangifer* populations than appears to be the case for muskoxen. Muskoxen often live at much lower population densities that caribou or wild reindeer and are frequently remote from other large herbivores; under these conditions their populations may not be sufficient to support resident populations of wolves *(Canis lupus).* Migratory caribou/reindeer, however, may expose themselves to several discrete predator populations in their seasonally separate ecosystems. Wolves often depend primarily on caribou where they coexist, but wolves have not been able to sustain their populations for long periods in northern Greenland where muskoxen have been their only large herbivore prey species (Dawes *et al.,* 1986).

Insects have a much more dynamic effect on the energy balance of caribou/reindeer than on muskoxen (White *et al.,* 1975; Jingfors, 1980), although the more northern distribution of most muskoxen coincides with decreasing frequency and intensity of potential insect harassment. Insects, primarily mosquitoes (Culicidae) and biting flies (Simuliidae), may account for pronounced mortality of neonates in woodland caribou *(R. t. caribou)* (Kelsall, 1968), and increased winter mortality of calves of barren-ground caribou *(R. t. granti)* has been associated with heavy infestation by larvae of parasitic flies *(Oedemagena tarandi* and *Cephenomyia trompe)* following a warm summer favorable to insects (Davis *et al.,* 1980).

Overgrazing of forage resources as a density-dependent limiting factor would be expected more frequently among sedentary than migratory species. This generalization for muskoxen and caribou/reindeer must be adjusted to account for the relative resistance to grazing pressure of the forage types within their habitats. Graminoids, which dominate the diet of muskoxen, are much more resilient after grazing than lichens (Klein, 1968). Furthermore, lichens throughout much of their distribution in the boreal forests of North America and the taiga of Eurasia are subject to catastrophic destruction by forest fires, which temporarily remove vast areas as potential sources of winter forage for caribou and reindeer.

Availability and quality of forage and climatic extremes seem to be primary limiting factors for both muskoxen and caribou/reindeer living at similar latitudes. The extinction of *R. T. eogroenlandicus* in Northeast Greenland was apparently associated with extreme snow and icing conditions brought about by the reduction of sea ice off the coast (Vibe, 1967). Muskoxen survived, although populations were greatly reduced, apparently through their ability to subsist on extremely poor quality forage available in areas of low snow accumulation. In the Canadian High Arctic, muskox and Peary caribou populations have fluctuated widely in response to stochastic climatic extremes (Parker *et al.,* 1975).

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