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Arctic ungulates at the northern edge of terrestrial life

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Abstract: The 2 ungulate species that occur in the High Arctic, *Rangifer tarandus* and *Ovibos moschatus*, exhibit considerable adaptive plasticity in response to habitat variability throughout their circumpolar distribution. *R. tarandus*, however, has a much wider latitudinal distribution and occurs within a wider range of both forest and tundra habitat types than *O. moschatus*, reflecting greater morphological, physiological, and behavioral plasticity. As a consequence, muskoxen have been less successful than caribou and reindeer in maintaining populations at their southern limits. Muskoxen, however, existed throughout Pleistocene glaciations in the cold periglacial steppes of Eurasia and North America and find the closest analog to this vegetation type in the High Arctic, where they have been more successful than *R. tarandus* in maintaining their populations.

Key words: High Arctic, *Ovibos moschatus*, *Rangifer tarandus*, insularity, adaptability.

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Introduction

A broadly acknowledged ecological paradigm states that the diversity of plant and animal species declines from the equator to the poles along a latitudinal gradient (Fischer, 1960). Both Wallace (1878) and Darwin (1860) in the mid-1800's were impressed by the great diversity of species they observed in the tropics, in contrast to temperate latitudes. The paucity of plant and animal species at high latitudes has been interpreted largely on the basis of the climatic extremes that exist there, viewed from a human bias, rather than an ecological or biogeographical perspective. For terrestrial macrophytes, the small amount of the Earth's surface that is not covered by the seas or glacial ice in polar regions, in contrast to lower latitudes, has placed limits on the potential for habitat diversity which has been an important constraint on their presence there. In addition, since the end of the Pleistocene, virtually all plant and animal life in the High Arctic (characterized by a growing season of 2-2.5 months; only 8 mammal species, 10-20 nesting bird species and 50-115 vascular plants; Bliss, 1981) has arrived there from only the single direction of the lower latitudes. Although dispersal of some plant and animal species has occurred longitudinally within the Arctic, those species also had a southern origin.

Further complicating the occupation of land areas in the High Arctic by plants and animals has been the insular characteristic of the ice-free lands present there. Even Greenland, of continent size, is fractured into a multitude of "islands" of ice-free land separated from one another by broad expanses of the ice cap and glaciers extending from it to the surrounding sea.

Primary Productivity in the High Arctic

The major constraints on plant growth in the High Arctic, in addition to the limited available ice-free land area, include the brief summer season during which temperatures are warm enough and light is present for photosynthesis; the limited available moisture wherever the land is free of ice; and the limited availability of essential nutrients in the poorly developed soils. In spite of these severe constraints, plants do grow in the High Arctic and produce sufficient plant biomass to support a complex of vertebrate herbivores, a few of which, like muskoxen and caribou (reindeer), are resident there throughout the year.

Although vascular plant species ate relatively few in the High Arctic (less than 150 species in northern-most Greenland; Bay, 1992), in contrast to lower latitudes, those present are highly adapted to the extreme conditions that exist there (Savile, 1972). High arctic plants are frost tolerant during the growth period and they grow and mature rapidly, taking advantage of the 24 houts of daily solar insolation. Their prostrate or low growth form benefits from solar warming at the soil surface, and the graminoids and forbs translocate most of their accumulated photosynthates to overwintering live tissues below ground or in the moss layer at the end of the growth season.

Plants growing in the poorly developed soils of the High Arctic are often nutrient limited. Plants, such as the Leguminosae and alder (*Alnus* spp.) that support nitrogen-fixing bacteria in root nodules, although present throughout much of the Arctic, do not reach the High Arctic (Bay, 1992).

Ungulates in the High Arctic

Plant production in the High Arctic is low in contrast to lower latitudes, and it is reasonable that fewer herbivores occur there, both in number of species and total biomass (Kaufman, 1995; Klein & Bay, 1994). Those vertebrate herbivores that occur in the High Arctic have special adaptations to deal with the seasonal variability in weather and in quality and availability of plant material for food. Birds avoid the climatic extremes of winter and the associated decline in quality and availability of forage through migration. Because of the insular nature of the High Arctic, mammals do not have the option of migration to lower latitudes. MacArthur (1972) proposed that in North America, species are limited in their northern distribution by physical conditions, whereas their southern distribution is limited by biotic interactions. I think, however, that this generalization reflects an anthropocentric bias nurtured by the human preoccupation with the severity of the arctic climate.

Factors of the environment indirectly related to climate may play equally important roles. For example, the southern distributions of the boreal forest cervids, moose (*Alces alces*) and deer (*Odocoileus* spp.), in North America are limited in the arid West by availability of suitable habitat, which includes shrubs or trees as cover and winter forage. Thus, they are limited by the biotic characteristics of the habitat, which in turn are products of climatic constraints on growth of trees and shrubs, a physical constraint. Similarly, muskoxen and Peary caribou (*R.t. pearyi*) are limited in their high arctic distribution by the distribution and production of plants suitable as forage, and the availability of plant biomass throughout the year (Fig. 1). Thus, it is biotic constraints as mediated by the climate of the High Arctic, that determines where these species may exist rather than the direct effect of climate on the animals.

Both caribou and muskoxen are morphologically, physiologically, and behaviorally well adapted to the climatic extremes of the Arctic (White *et al.*, 1981). Nevertheless, it is climatic extremes, through their effect on forage production and availability, that have primary influence on limiting population numbers of ungulates in the High Arctic. The direct effects of these climatic extremes on the animals are the increased energy costs associated with traveling through, and foraging through, deep snows, loss of access to forage due to icing conditions, the added energy costs of thermoregulation, and lost foraging opportunity during extteme winter storms.

The two species of ungulates that have occupied the High Arctic have evolved different physiological, morphological, and behavioral attributes that enable them to exist there. The muskox, that during Pleistocene glaciations was ptesent throughout the semiarid periglacial steppe that extended from southern Europe across Asia into North America (Kurtén, 1968), is well adapted as a generalist grazer of graminoid vegetation (Guthrie, 1984). Its large body size and large rumen (White *et al.*, 1981) enable it to digest grasses and sedges

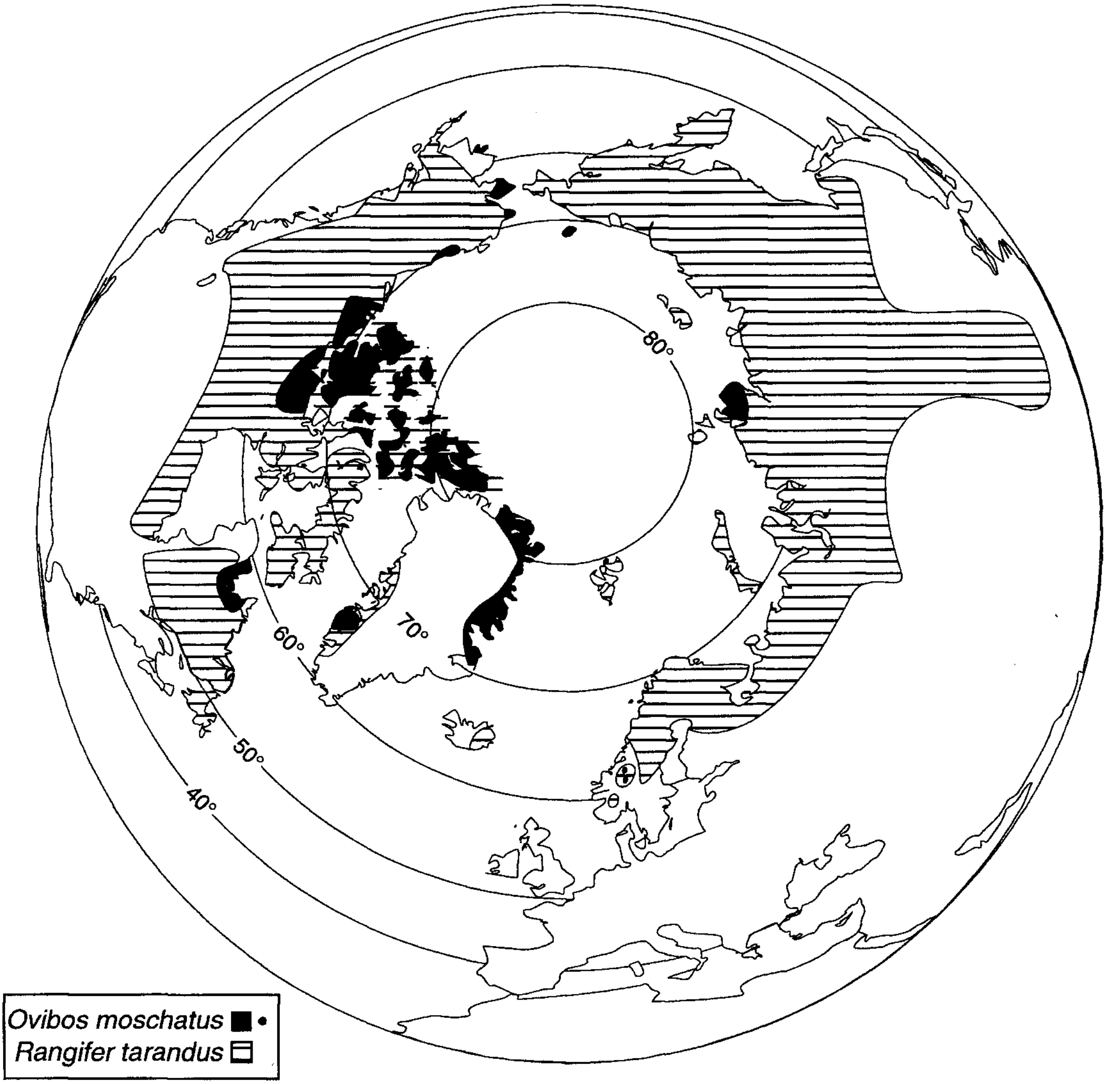

Fig. 1. Holarctic distribution of *Rangifer tarandus* (caribou and reindeer) and *Ovibos moschatus* (muskoxen), including reintroductions of muskoxen to historical range in northern Alaska, and introductions outside of historical range in western Alaska, Quebec-Labrador, western Greenland, Norway, Sweden, and the Taimyr Peninsula and Wrangel Island of Russia.

with a high fiber content, especially during winter. Muskoxen also are highly energy conservative in virtually all of their life processes, including daily activity, seasonal movements, predator avoidance, and social interaction (Jingfors, 1980; Klein, 1992). Morphologically, their low surface to body mass ratio and extremely efficient insulative pelage equip them well to conserve body heat during the extreme cold of high arctic winters.

Caribou and reindeer, in contrast to muskoxen, have morphological constraints that are the heritage of their Cervidae origin. These are their small body size and long legs, relative to muskoxen, which limit their rumen size and give them a relatively high surface to body mass ratio. Their life style and its adaptation to the High Arctic have, therefore, evolved in a different direction than muskoxen. Rather than being highly energy conservative as are muskoxen, caribou must expend much more energy per unit body mass for survival (Fancy, 1986; Thing *et al.*, 1987; Klein, 1992), and with smaller rumen capacity, must be much more selective for forage of high digestibility. Although caribou are better adapted than muskoxen for foraging through deep snow, in the High Arctic suitable forage for them is most frequently found in areas with least winter snow accumulation. White *et al.* (1981) have shown that long fiber graminoids are poorly digested by caribou and reindeer. Peary caribou, as a result of work by Thomas & Edmonds (1984) and Parker & Ross (1976), are known to be highly selective foragers, focusing heavily on *Luzula* spp., mosses, and lichens in winter and willow (*Salix arctica*), *Saxifraga oppositifolia*, and other forbs in summer. Low plant species diversity and low plant biomass in the High Arctic, especially for non graminoid species, necessitates high mobility for selective foragers. Parker & Ross (1976) found Peary caribou to be much more mobile in their daily foraging than muskoxen in the Canadian High Arctic. A selective foraging behavior requiring high mobility in high arctic *Rangifer*, in an environment of low and dispersed plant biomass, with long winters without plant growth has presumably selected for small body size. This seems counter intuitive relative to thermoregulation and Bergman's rule. Small body size, however, in the high atctic winter in an ungulate species with moderately high energy requirements per unit body mass (White *et al.*, 1981), can be mote easily maintained in an environment of extremely low usable plant biomass. Additionally, the relatively smaller body size in *Rangifer* than in muskoxen, necessitates selection for running speed in *Rangifer* for predator avoidance. This behavior selects for long leg length (Klein *et al.*, 1987) with associated higher energy costs expended for locomotion and thermoregulation. Exceptions do occur, however, as in the case of the Svalbard reindeer (*R t. platyrhyncus*), that live in a predator-free environment with limited options for movement because of the insular nature of their habitats (Reimers, 1977). Their long isolation from competition with muskoxen may also have been a factor in their unique adaptations of short legs, larger rumen capacity, and high capability for body fat storage (Klein & Staaland, 1984).

Limiting Factors for Ungulates in the High Arctic

The adaptations of *Rangifer* and *Ovibos* for life in the High Atctic have enabled these two ungulates to occupy available and accessible habitats there. Nevertheless, the extreme climatic conditions that exist in the High Arctic with periodic short and long term climatic fluctuations have accounted for wide fluctuations in population numbers of high arctic ungulates with localized extinctions, followed by repopulation of suitable habitats (Melgaard, 1986; Syroechkovskii, 1995).

The greater locomotive efficiency of *Rangifer* (Klein, 1992), and wide adaptability to substrates and habitats have enabled them to gain access, duting the Holocene, to large areas of the Holearctic that have not been reached by muskoxen. These include Newfoundland and the Quebec-Labrador peninsula, the southeast and west coasts of Greenland (Meldgaard, 1986), Svalbard, Franz Josef Land (Zale *et al.*, 1994), Novaya Zemlya, Severnaya Zemlya, and the New Siberian Islands (Fig. 1). In a few of these areas, populations have subsequently declined to extinction or have periodically been reestablished through movements from adjacent continental populations (Meldgaard, 1986; Syroechkovskii, 1995). Similarly, in northern and northeastern Greenland, caribou have periodically been present, with intervals of absence, over at least 7000 years, presumably the retutning populations derived from movements from Ellesmere Island in the Canadian High Arctic (Meldgaard, 1986). The most recent population in northeast Greenland was *R. t. eogroenlandicus*, an endemic subspecies, persisted there until around the turn of the last century (Meldgaard, 1986).

The less mobile muskox has been much slower to colonize areas of the Atctic that presumably would support it, however, human assistance in recent decades has established it in western Greenland and on the Quebec-Labrador peninsula and reestablished it in former habitats in Alaska, the Yukon Territory, and on the Taimyr Peninsula of Russia (Klein, 1988) (Fig. 1).

The muskox has also been less successful than caribou and reindeer in maintaining its populations when confronted by hunting by indigenous and western cultures. In the High Atctic of Greenland (Vibe, 1967) and Canada (Barr, 1991) where humans have been absent from vast areas until recent times, the muskox has been more successful in maintaining its populations in association with climatic extremes than have caribou. This difference appears to be a function of the muskox's capability of using low quality, high fiber forage, which constitutes the greatest portion of the total available plant biomass in winter in the High Arctic (Klein

& Bay, 1990). Forage biomass in the sedge meadows used by muskoxen is more stable than the forages eaten by caribou, with the exception of lichens, which are scarce in the High Arctic. In addition, the energy conservative life style of muskoxen and their capability ofi accumulating larger fat reserves than most high arctic *Rangifer* (Thing *et al.*, 1987; Reimers *et al.*, 1982), gives them an advantage when forage is limited in winter.

Predation by wolves is undoubtedly a factor in further reducing populations ofi both muskoxen and caribou in the High Arctic that may already be suppressed by climatic extremes affecting forage availability. Although extremely low populations of ungulate prey will not likely sustain wolfi populations in the insular-like disjunct habitats of the High Arctic, there are likely differences in how wolves affect low density populations of muskoxen versus caribou. As densities of prey populations decline so do those of wolves. Minimal pack size for efficient predation on muskoxen, especially adults, must be greater than for predation on the much smaller high arctic caribou. Thus, as both prey and predator densities decline, muskoxen may be less vulnerable to predation by wolves than caribou. Additionally, the disjunct nature of units ofi habitat for muskoxen in the High Arctic may result in less predation on that species when wolfi numbers are also low.

The periodic presence of wolves in northern and northeast Greenland in this century (Dawes *et al.*, 1985), during which muskoxen persisted as the only ungulate prey, also demonstrates that wolves were not capable of driving muskoxen to extinction in association with the climatic extremes ofi the High Arctic. Instead, wolves died out, allowing for recovery of suppressed muskox populations. It is noteworthy that although muskox numbers in northeast Greenland declined markedly around the turn of the last century the endemic caribou (*R. t. eogroenlandicus*) declined to extinction (Vibe, 1967). Vibe postulated climatic extremes as a primary factor in the decline of muskoxen and the extirpation of caribou, however, wolves may also have been a factot.

It is appatent that proximity to the North Pole has not limited arctic ungulates in their northward distribution. Both species have reached the northernmost land areas, although densities decline markedly with increasing latitude. Periodic extirpation of populations has occurred regionally in the past in association with climatic extremes that have limited forage production and access to it. The muskox, however, has been a somewhat better survivor under the environmental constraints of the High Arctic than has been the caribou.

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