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Address: c/o NVH, Institute of Arctic Veterinary Medicine
Stakkevollvn. 23 B
N-9005 Tromsø
Norway
e-mail: Nor.Rangifer@veths.no

Telephone: +47 77 68 43 10 *Telefax:* +47 77 68 44 11

Bank account: 4760 56 92776 *Postal account:* 0801 2116358
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A hypothesis to explain lichen-*Rangifer* dynamic relationships

Eldar Gaare

Norwegian Institute for Nature Research (NINA), Tungasletta 2, N-7005 Trondheim, Norway.
e-mail: eldar.gaare@nina.nina.no

Abstract: A small group of fruticous lichen species, *viz. Cetraria nivalis, Cladonia mitis, C. stellaris,* and *Stereocaulon paschale* forms extensive mats in the most winter habitats of *Rangifer tarandus* populations in Norway. The plant communities accessible for grazing are often found on easily drained, moraine ridges. These lichen species are perennial, lying on the ground while growing slowly at the top. As they decompose they add humus to the top of the soil profile. The lichen mats catch all water from small showers, thus preventing vascular plants from obtaining a more regular water supply. Grazing removs whole plants and gradually makes larger and larger holes in the lichen mats. Wind and water erode the humus, with only coarse gravel remaining. This diminishes the soil water storage capacity. Without grazing, lichens will gradually build a humus layer, which would improve the soil water storage capacity. In time vascular plants then would take the place of the lichens. I propose the hypothesis that by (over-)grazing *Rangifer* improve their winter pastures by making conditions more favourable for lichens than for vascular plants.The fact that lichens are more scarce on habitats with more and regular precipitation, 1) in more oceanic climates, 2) on soils with more silt, and 3) on bird perches with thick peat due to regular fertilising, support this hypothesis.

Key words: *Rangifer,* reindeer, caribou, lichen, grazing, secondary succession.

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Introduction

In today's management of *Rangifer* populations, semi-domestic and wild, the carrying capacity is often linked to the lichen resources (e.g. Gaare & Skogland, 1980) The objective is to balance the population's yearly intake of lichens and damage from trampling of the lichen mat to its annual regrowth. For the Russian reindeer industry, Andreev (1954) recommended a 3-4 year pasture rotation. One year of grazing should be followed by 2-3 years of lichen regrowth. This conservative management practice has not been the rule in the Fennoscandian semi-domestic reindeer ranges. There most of the winter pastures seem to day to be severely overgrazed. In Norway's wild populations this objective is reached by a rigorous control of the hunt in many of the more than 20 separate ranges.

With studies from Norway, I will first show why conservation of the lichen resources is good in the short term. Then I question this practice, and discuss why it may be unwise for long term resource management.

The relationship between lichens and *Rangifer* has been recognised for a long time. Linnaeus (1735) called the lichens they ate during the winter *Lichen rangiferinus,* a group now separated in several species belonging to many genera.

When the lichen pastures are good, *Rangifer* may have an intake of 80% lichens. The mats of fruticose lichens are composed mostly of species belonging to

Alectoria, Cetraria, Cladonia and *Stereocaulon.* In continental and subcontinental arctic, sub-arctic and alpine landscapes, such lichens often dominate on dry and exposed hills and ridges. In the boreal forest, lichens dominate on easily drained soils between the scattered trees in the taiga and on the forest floor in the open pine forest. In the forest, epiphytic lichens, *viz. Alectoria, Bryoria* and *Usnea,* add to the available winter food. The reindeer may survive without lichens, as on Svalbard (Ekern & Kildemo, 1978; Brattbakk, 1985), but commonly lichens dominate on winter range (Gaare, 1968; Gaare & Skogland, 1975; Eriksson *et al.,* 1981; Chernov, 1985). Therefore, throughout their distribution, *Rangifer* populations benefit from the species unique ability to digest lichens well.

The Snøhetta case

The Snøhetta range at 62°N in the mountain ranges of Southern Norway occupies 3300 km², all above the subalpine birch forest. Fig. 1 show that it is one of more than 20 largely isolated wild reindeer populations in southern Norway (Krafft, 1981). The Snøhetta population was estimated to be a few hundred reindeer in the 1930's (Per Holaker, pers. comm. 1964). By heavy hunting it had been kept low since a protection period in 1901–1905. The war of 1940–1945 provided a partial protection and allowed the population to grow. Table 1 shows the development from 1946. The rapid rise of the population to 8000–12000 in the 1950's, soon depleted the lichen pastures and this was a matter for much concern. A severe reduction hunt followed up to 1969. Apart for a rise to about 3000 heads in 1977-1983 managers have maintained the population at a low 2000 head in order to allow the lichen pastures to recover.

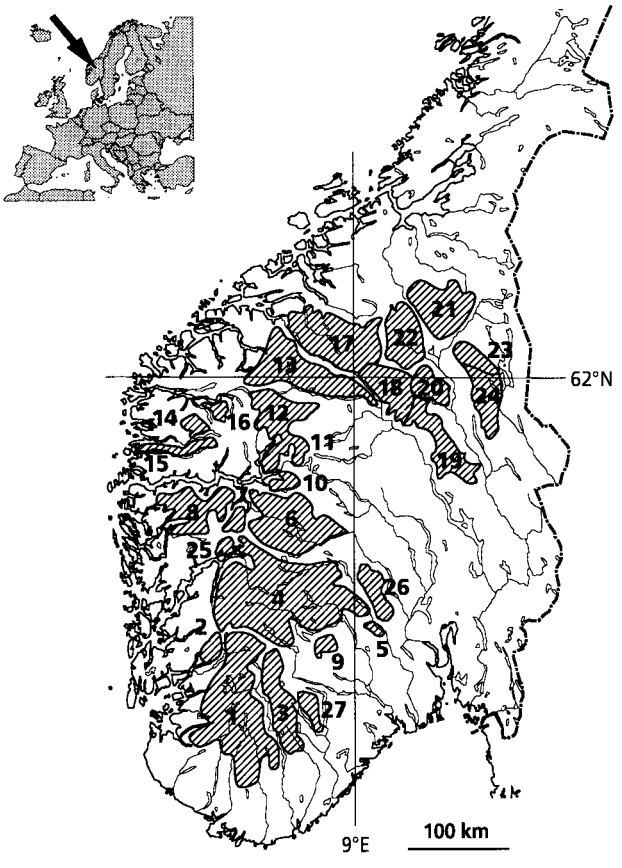

Fig. 1. Wild reindeer ranges in Norway. . Some ranges are small and isolated and marked (*). Ranges where irregular inter migrations are known are grouped: (A) 1 Setesdal Ryfylke, 2* Skaulen-Etnefjell, 3 Setesdal Austhei, 4 Hardangervidda, 5 Blefjell, 6 Nordfjella, 7* Raudafjell, 9 Brattefjell-Vindeggen; (B) 10 Lærdal-Årdal, 11 Vest-Jotunheimen, 12 Ottadalen Sør, 13 Ottadalen Nord; (C) 14* Førdefjella, 15* Sunnfjord, 16* Svartebotn; (D) 17 Snøhetta 18 Rondane Nord, 19 Rondane Sør, 20 Sølnkletten, 21 Forelhogna, 22 Knudshø; (E) 23 Tolga østfjell 24 Rendalen. Total area occupied by wild reindeer are 36000 km², total population 38000 (March 1995). The map is redrawn after Krafft (1981).

Railway construction, ending in 1921, divided the range. According to local residents, the small population at that time did not cross the railway along the natural east-west migration route used formerly. But as the population grew, the old migration routes were re-established (Skogland & Mølmen, 1980), despite the railway and a parallel highway. These routes were in regular use every autumn and spring during the period 1957-1983 involving a minimum of 10-50% of the herd. After that, the use of eastern winter ranges became more irregular, and not reported since 1985.

Norway has today few large predators, and hunting has been the dominant mortality factor in all reindeer populations since 1900 (Arild Landa, pers. comm.). In Snøhetta, the annual hunt has been about 367±53 animals over the last 12 years or about 18% of the winter population. The producti-

Table 1. Wild reindeer population in the Snøhetta range, and its density on the winter lichen pastures. Density is calculated on the basis of the lichen cover in heaths covering ridgetops, mainly *Loiseleurio-Arctostaphylion* (Kalliola, 1939). Such heaths was estimated to 517-634 km² (c.i.) in an aeroplane surway (Gaare, unpubl.). The calculation is based upon official censuses (Norwegian Directorate for Nature Management).

Year	Heads	Heads/km²	(95% conf.int.)
1946	4700	10,0	16,3
1955	12000	25,6	41,5
1960	15000	32,0	51,9
1962	12000	25,6	41,5
1966	6000	12,8	20,7
1969	1200	2,6	4,1
1972–1977	2000	4,3	6,9
1978–1983	3000	6,4	10,4
1984–1995	2000	4,3	6,9

The precipitation is about 300-400 mm/yr in this eastern part of the range. The vegetation on the ridges belongs to the alliance *Loiseleurio-Arctostaphylion* (Kalliola, 1939) with a typical lichen coverage of 65-85%.

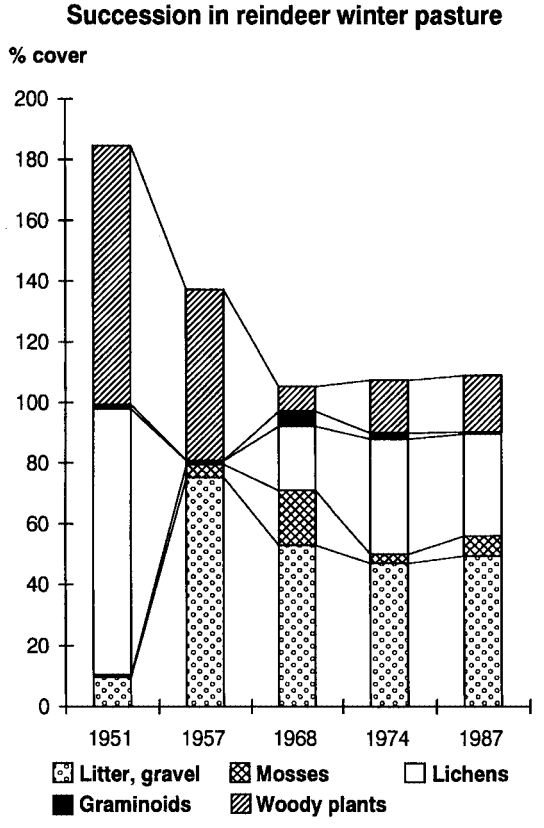

Fig. 2. Recovery of winter pastures in the Snøhetta range after the population high in the 1950's. Data from Nordhagen (1963) for 1951 and 1957 and Gaare (unpubl.) for 1963-1987. The more than 100% coverage in Nordhagens data is in part due to a transformation from Hult-Sernander scale to percent coverage.

vity of the herd thus seems to be rather low, confirmed by the annual calf counts in summer (Jordhøy *et al.*, 1996). This population produced an average of about 40 calves per 100 females 2 years and older between 1976-1995 compared with 25 and 70 in other wild reindeer populations in Norway.

Table 1 also shows reindeer density on the winter pasture. The accessible winter pasture is 17.4±5.2% (95% c.i.) of the total area with 13.2% of this belongs to the *Loiseleurio-Arctostaphylion* (Kalliola, 1939) alliance in the low, and 4.2% to *Juncion trifidi* (Kalliola, 1939) in the middle alpine region (Gaare, unpubl. data). For the whole range we have between 517–634 km² (c.i.) of lichen dominated heaths where most grazing occurs. Thus the animal density related to the area of the lichen mats is even greater than the table indicates.

About 14 animals to 1 km² of lichen mat will balance the annual growth of lichens (Gaare & Skogland, 1980). The table show that the densities were much higher in the 1950's, causing overgrazing.

This eastern range was monitored in terms of percent cover of major plant groups from 1951 to 1987 by Nordhagen (1963) and Gaare (unpubl. data).

Fig. 2 represents changes in cover from a representative stand near Nordhagen. When heavy grazing depleted the lichen cover from 75 to 2%, wind and water erosion removed much of the humus layer and only coarse gravel remained. During a period of 7–10 years, mosses and graminoid species increased from 2 to12% cover. This vegetation in turn became the necessary shelter for lichen fragments. Over the next 20 years thereafter the former lichen mat gradually was restored. This observation confirmed what was shown elsewhere in heavily grazed areas: mosses increase first, then graminoids, (Palmer & Rouse, 1945; Andreev 1954; Pegau, 1970).

In other studies commenced in 1963 I found that the grazing had depleted the lichen mats on ridge tops from 1200 to 25 g/m². In the arid environments of such ridges, with rapidly drained soils and low precipitation, a large proportion of the area is

left non vegetated. To keep an optimum annual production available for winter food, it is important not to graze excessively.

Research on lichen mats, (Andreev, 1954; Kärenlampi, 1971; Yarranton, 1975 and Gaare & Skogland, 1980) show a logistic type of growth after disturbance, with an intrinsic growth rate of about 0.20, and a potential maximum biomass of 1200–1500 g/m^2 dry matter at about 30 years, depending on climate and species. The logistic growth form implies that the annual growth at low biomass will be 20%, at middle 10%, and at maximum biomass 0%. Thus a mature lichen mat grows at the top and rots at the base at the same rate. Annual growth is a maximum of 50–70 g/ m^2 at medium biomass of 500–700 g/m^2 (Gaare & Skogland, 1980).

The management of the Snøhetta herd since the early 1960's was based on these findings and interpretations. As a result of the population reduction and subsequent shift in winter grazing to neighbouring ranges, the lichen mats are now restored to medium biomass over large areas.

Long term considerations

Lichens get water from water vapour in air, dew and small showers. A dry lichen mat of 3–5 cm height can catch the water in a shower of 1–3 mm before the soil is wetted. On rapidly drained mineral soils, under a dry climate, and at a certain precipitation regime, this ability make lichens successful competitors with higher plants, which get water only from the soil reservoir. If no grazing occurs, the lichen mat will continue to grow and form litter by rotting at the base. Over time the soil humus content grows and this improves the water storage capacity of the soil, (Andreev, 1954; 1968). At some point, vascular plants get a stable enough water supply to compete successfully with lichens for light. The relative abundance of lichens will then decline, the highly palatable reindeer food is replaced in winter by dry graminoids and dwarf shrubs, both of lower digestibility.

The long term monitoring necessary to document this has not been conducted anywhere. I will draw attention to three relations that support this hypothesis. A more steady supply of water for vascular plants may happen if 1) the amount of precipitation increases and becomes more regular, 2) the water storage in the mineral soil is improved by increased content of silt and clay, and 3) the water storage is improved by an increased amount of organic content in the soil.

1) The accessible vegetation covering the hills and ridges in areas with poor acid rock show a high, 75% or higher in arid climate, coverage of lichens in the non grazed state (Fig. 2, year 1951). If we move to more oceanic parts of the range, with annual precipitation of 300 mm, this changes. At 800 mm/year the lichen coverage is down to 50–60%, and at 1200 mm/year it is 20–40% (Gaare, unpubl. data). Instead mosses, graminoids and particularly crowberry (*Empetrum* sp.) increase. Less sunshine and higher air humidity at the coast, adds to this effect. In the coastal lowlands, the comparable vegetation is a *Calluna*-heath with scattered lichens only on the most exposed sites (Dahl, 1987).

2) If we compare ridgetop vegetation in rich and poor soils under the same precipitation regime, we find that lichen dominates more on acid soils. The proportion of silt and clay is larger where the rock is more easily weathered. This improves the soils water storage capacity to the benefit of rooted vascular plants.

3) Also on arid parts of the range, bird perches are found on ridges where the surrounding vegetation is a lichen dominated heath. The perch is occasionally a mire hummock with 30-50 cm deep peat with *Sphagnum* spp., *Eriophorum* sp. and *Rubus chamaemorus.* In its central bottom is a boulder of about 20 cm. This boulder was a resting place and the steady fertilisation by guano has, since the last glaciation (8000 yrs BP) developed the vegetation into mire hummock amidst a dry heath.

All three examples are mainly based on experience from the Norwegian region. They support the hypothesis that when the water storage capacity of the soil on such ridges is improved, the dominance of the fruticose lichens decreases. These pastures will then have smaller amounts of suitable winter food for reindeer maintenance.

A herd of *Rangifer* will increase if the sum of annual hunting and natural mortality are lower than recruitment. This will continue as long as the grazing allows (Klein, 1968) until overgrazing of the lichen mats occurs. If possible, the animals move to other winter areas, if not, natural mortality will reduce their numbers drastically. This allow the

lichen to re-establish as is shown in Snøhetta range. But if we keep the population low, I predict that lichens gradually will decrease in the available winter pastures as humus is added to the soil and water holding capacity increases. They will be replaced by plants with lower digestibility and the reindeer carrying capacity of the range will decrease. To avoid this, the reindeer population should be allowed to overgraze their lichen pastures once every 25 years or so. Consequently, the soil will dry, humus will blow away, some of the vascular plants will die and part of the surface will begin a new successional sequence.

It appears that the dynamic relation between the reindeer population growing at a faster rate than the lichen mats, keeps the secondary succession of the vegetation development after denudation at an early stage. In this stage, lichens dominate on grounds accessible for winter grazing reindeer, a successful coevolution. How general this conclusion is, depends on the climate and soil factors. The structure of the population and the animal grazing behaviour may be equally important. But it is everywhere true that reindeer management should be range oriented, and on a 100-year perspective rather than a 10 year one.

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Peary caribou, muskoxen and Banks Island forage: Assessing seasonal diet similarities

Nicholas C. Larter & John A. Nagy

Department of Resources, Wildlife, and Economic Development, Bag Service #1, Inuvik, NT, X0E 0T0 Canada.
e-mail: banks@inukshuk.gov.nt.ca

Abstract: Peary caribou (*Rangifer tarandus pearyi*) and muskoxen (*Ovibos moschatus*) on Banks Island had considerable similarity in their annual diets, with monthly similarities ranging from 17.8–73.3%. Diet similarity was more pronounced in areas of high muskox density (*ca.* 1.65/km^2) than in areas of low muskox density (*ca.* 0.4/km^2). Willow (*Salix arctica*) and sedge (*Carex aquatilis* and *Eriophorum* spp.) represented >80% of the monthly diet of muskoxen. The caribou diet was more diverse, and was dominated by sedge, willow, *Dryas integrifolia*, and *Oxytropis maydelliana*, Lichen use was rare, likely as a consequence of low availability on Banks Island. Lichen standing crop was estimated at 2.96 g/m^2. The differences in muskox diet between high and low density areas could not be explained by differences in forage distribution or standing crop. We discuss diet similarities of caribou and muskoxen and potential consequences for the current Peary caribou population in relation to winter weather conditions and increasing muskox density.

Key words: diet overlap, food competition, arctic, Northwest Territories, *Rangifer tarandus pearyi, Ovibos moschatus.*

Rangifer, 17 (1): 9–16

Introduction

Between 1972 and 1994 Peary caribou (*Rangifer tarandus pearyi*) numbers on Banks Island decreased from *ca.* 12,000 (Urquhart, 1973) to 709±128 (SE) animals, excluding calves (J. Nagy & N. Larter, unpubl. data). Contrastingly, during that same period, muskox (*Ovibos moschatus*) numbers, excluding calves, increased from *ca.* 4,000 (Urquhart, 1973) to 64,608±2,009 (J. Nagy & N. Larter, unpubl. data). The decrease in caribou numbers was attributed to a variety of factors including severe winter weather, predation, harvest, inter-island movements, and competition with muskoxen as reviewed by Nagy *et al.* (1996). The actual cause or causes of the decline remain unknown. However, in order to manage the recovery of the Peary caribou population on Banks Island, it is important to assess dietary overlap and the potential for food competition between the 2 species given the current animal numbers and forage abundance and distribution.

Caribou and muskoxen are the only ungulate species successfully occupying arctic tundra environments. Caribou and muskoxen have different morphological adaptations which have presumably enabled them to utilize forage resources with little overlap (Klein, 1992). Muskoxen represent the classic grazer (Hofmann, 1989). With a large body size and gut capacity, they are capable of processing large amounts of low quality forage. Caribou are representative of a mixed feeder type, and are inter-

mediate between roughage feeders and concentrate selectors (Hofmann, 1989). Their smaller body size and smaller gut capacity, combined with a higher fasting metabolic rate than muskoxen (Tyler & Blix, 1990), require them to pursue a more selective feeding strategy. In contrast to muskoxen, caribou meet their nutritional requirements by a relatively rapid rate of passage of highly digestible forage (Klein, 1992).

Lichen is an important winter food for barrenground caribou on the mainland, but in the high arctic islands which support low lichen biomass, caribou use other forages, usually willow and graminoids (Reimers *et al.*, 1980; Klein, 1992). In west Greenland, where lichen biomass was apparently depleted by overgrazing (Staaland & Olesen, 1992), both muskox and caribou diets were dominated by monocots. In areas inhabited by muskoxen only, willow became an important summer diet component (Thing *et al.*, 1987). Therefore, both animals demonstrate the ability to utilize a variety of forages when availability dictates. Muskoxen can clearly make good use of high protein, low-fibre foods (White *et al.*, 1984; Adamczewski *et al.*, 1994) and even though they show many attributes of classic grazers they can be quite selective in their feeding (Oakes *et al.*, 1992). Despite their relatively wide muzzles muskoxen are remarkably adept at finding the leafy portions of forage and rejecting larger stems (J. Adamczewski, pers. comm.).

Reconsideration of data on muskox and caribou ecology implies that competition for food may occur where muskox concentrations are high (McKendrick, 1981), and that overlapping winter diets may adversely affect caribou numbers (C. Olesen, unpubl. data).

In this paper we report preliminary findings on the Peary caribou and muskox diets, monitored on a monthly basis, the current forage distribution and standing crop of the 4 major terrestrial habitats in areas of high and low muskox density on Banks Island, and compare our findings with previous work.

Study Area

Banks Island is the most western island in the Canadian Arctic Archipelago and covers approximately 70,000 km^2. The climate is Arctic Maritime along coastal areas where weather stations are located, tending toward Arctic Desert inland. Winters are long and cold; summers are short and cool. Precipitation is low with an annual mean of 9 cm (Zoltai *et al.*, 1980). Sachs Harbour is the only permanent settlement on the Island. Zoltai *et al.* (1980) provided a general overview of the geology and glacial history.

Habitat types were adapted from Kevan (1974), Wilkinson *et al.* (1976), and Ferguson (1991). There are 4 major terrestrial habitats: i) wet sedge meadow, ii) upland barren, iii) hummock tundra, and iv) stony barren. Wet sedge meadows (WSM) are generally level hydric and hygric lowlands characterized by *Carex aquatilis*, *Eriophorum scheuchzeri*, and *Dupontia fisheri*. Upland barrens (UB) are well drained sites found on the upper and middle parts of slopes. Vegetation is dominated by *Dryas integrifolia* and *Salix arctica*. Hummock tundra (HT) is found on moderately steep slopes characterized by individual hummocks which are vegetated primarily by dwarf shrubs (*D. integrifolia*, *S. arctica*, and *Cassiope tetragona*). Stony barrens (SB) have a coarse gravelly substrate and are sparsely vegetated. This habitat is found on wind blown areas, ridges, and gravel and sand bars. A more detailed description of the flora can be found in Porsild (1980), Wilkinson *et al.* (1976), and Zoltai *et al.* (1980).

Methods

Two field camps were established in June 1993 on southcentral Banks Island: one camp located in a high density muskox area (1.64 muskox/km^2), 90 km ENE of Sachs Harbour, and the other in a low density muskox area (0.41 muskox/km^2), 130 km ENE of Sachs Harbour. Two or 3 permanent straight line transects were marked off in each of the 4 major terrestrial habitat types located in each of the high and low muskox density areas.

Fresh (< 4 hour old) Peary caribou faecal samples were collected opportunistically during all field trips. The location and habitat the samples were collected from was recorded. Additional samples were collected from hunter killed animals and from 12 animals taken during a collection in winter 1993-94. A total of 124 samples were collected from all months, range of 5–18 samples/month, except January. We present monthly diet composition pooled across sex and age classes with the individual caribou as the sample unit. June and November data are pooled across years.

Preliminary analysis of data collected during March and May, 1993 indicated that the mean sedge component of individual muskox faecal samples

(n=70) collected from 22 groups of muskoxen was similar to the mean sedge component determined by lumping the individual samples across groups, 62.9 *vs.* 64.2% respectively. Also, the SD associated with the mean of 70 individual samples (34.31) was higher than any SD associated with one of the 22 groups (average SD = 7.98, range SD 0.042 – 32.3 with 16 groups having SD < 7.98). Therefore, we assumed that composite samples of fresh (< 4 hour old) muskox faeces from a number of individuals were representative of a group of muskoxen, and that by sampling groups instead of individuals we would be able to get a better measure of the diet over a larger portion of the population. Consequently, we used the composite sample from a muskox group as the sample unit. Initially the sample unit consisted of samples pooled from 5 pellet groups. This was reduced to 3 pellet groups/muskox group. We collected muskox faecal samples from mixed sex and age groups during all months except January and September in the high density area. The number of groups sampled each month ranged from 1 - 10, representing between 5 and 152 animals. In the low density area, samples were collected during April, June, July, August, and October. The number of groups sampled each month ranged from 1 – 7 representing between 30 and 89 animals. The location, habitat the samples were collected from, and group size was recorded. We present mean monthly diet composition of muskoxen with groups as the sample unit, weighted by the number of individuals in a group. June to August data are pooled across years.

Faecal samples were thawed, air dried for 24 hours, oven dried at 60°C for 48 hours, and ground through a 1 mm screen with a centrifugal mill. Subsamples (1 g) were forwarded to the Composition Analysis Laboratory, Ft. Collins, Colorado for analysis. Diet composition was determined by analyzing plant fragments (Sparkes & Malechek, 1968) according to Hansen *et al.* (1976). The microhistological technique has inherent limits, such as an inability to separate some species, and a limited percent of identifiable fragments in the slides (Johnson *et al.*, 1983; Barker, 1986). We deemed this method suitable for this study, since differing proportions of forage classes, not changes in individual species composition were of importance, and this method had been used in previous work on Banks Island. We used the following forage classes: sedge (Cyperaceae), willow (*S. arctica*), grass (*Gramineae*), rose/saxifrage (Rosaceae and Saxifragaceae), legume (Leguminosae), lichen (*Cetraria* spp., *Cladonia* spp., *Cladina* spp., *Peltigera* spp., and *Thamnolia subuliformis*), and other (other forbs, moss, and *Equisetum* spp.). There were traces of unidentifiable forb material in 6 samples, (4 caribou and 2 muskoxen, ranging from 0.33 – 0.89%) which were included in the other category, and traces of unidentifiable grass material in 51 muskox samples, (ranging from 0.46 – 1.93%) which were included in the grass category. We present results from samples collected prior to September, 1994. We used the Renkonen index (Renkonen, 1938; Krebs, 1989) to compare monthly percent diet similarity (PS) between Peary caribou and muskoxen in both high and low density areas.

Forage availability was assessed by 2 measures, standing crop and the presence/absence of forages in plots. Twelve 0.125 m^2 plots (Wein & Rencz, 1976) were clipped along 2 or 3 permanent transects in each habitat at both camps at 3 times during the snow free period: mid-June, mid-July, and mid/late-August. Transect lengths ranged from 90 to 450 m depending upon habitat type. Plot locations were assigned systematically without replacement based upon total transect length in each habitat. We clipped the following forages at ground level: sedge, grass, legume (*Oxytropis* spp., *Hedysarum mackenzii.*, and *Astragalus alpinus*), ericad (*Cassiope tetragona*), rose/saxifrage (*Dryas integrifolia*, *Saxifraga* spp.), and other forbs. Lichen was plucked from the substrate. Only current annual growth of willows was clipped. In the laboratory, sedge, grass, and *Cassiope tetragona* samples were separated into their live and dead components; willow was separated into leaf/bud and stem components. All samples were oven dried at 60°C for 48 hours and weighed to 0.1 mg. We used ANOVA to determine whether there were habitat, sampling time (June, July, August), area (high *vs.* low muskox density), and year effects on the standing crop of each forage. Because there were no year effects, we pooled data across years. Since growth rate of lichen is low, we calculated the mean standing crop from all the plots clipped in upland habitats (UB, HT, and SB) pooled across sampling time and year.

Occurrence data were collected during each clipping episode and again in early August. We lumped forages into the same 8 classes as above. We compared the occurrence of forages in similar habitats between low and high density muskox areas using a X^2 contingency analysis.

Results

The annual diet of caribou was dominated by sedge, willow, legume, and rose/saxifrage (Fig. 1). Willow was the dominant component during June to August. Legume and rose/saxifrage were dominant components during December to April. The sedge component remained relatively constant at *ca.* 25% each month. Lichen and grass use was negligible.

The annual diet of muskoxen was dominated by sedge and willow in both high and low density areas (Fig. 2). There was a high percent similarity (PS>89) of muskox diets between high and low density areas with the exception of a larger proportion of willow in the June and legume in the July diet in the high density area which reduced PS to 52 and 76, respectively (Table 1). From October to March willow represented *ca.* 20–48% of the monthly diet. Willow use peaked in May at *ca.* 70%. Sedge use ranged from a low in May (*ca.* 28%) to a high in August (*ca.* 83–93% high and low density areas respectively).

Monthly PS of caribou and muskoxen (from both high and low density areas) ranged from 18 to 73. Monthly PS was generally >30.0 for most months and greatest in the high muskox density (Table 1). Sedge (*Carex* spp. and *Eriophorum* spp.) and willow made up substantial portions of the annual diet of both caribou and muskoxen (Figs. 1 and 2).

In areas of high muskox density, standing crop of legumes and *Dryas integrifolia* were significantly ($P<0.01$) greater than in areas of low muskox density. Mean standing crop of legumes, pooled across time and all 3 upland habitats ($n=228$), and *D. integrifolia* ($n=312$), pooled across time and all 4 habitats, were 2.15 g/m^2 and 4.64 g/m^2 *vs.* 0.41 g/m^2 and 3.53 g/m^2 in high and low muskox density areas respectively. No other forages showed an area effect on standing crop. The standing crop of lichen was 2.96 g/m^2 ($n=456$).

X^2 analysis of the occurrence data indicated significant differences ($P<0.01$) in occurrence of forages between the high and low density muskox areas in the 3 upland habitats. There were no differences in wet sedge meadows. In

Table 1. The Renkonen index of percent similarity (PS) of the monthly diets of caribou and muskoxen in high density areas (C/MH), caribou and muskoxen in low density areas (C/ML), and muskoxen in high and low density areas (MH/ML) determined from this study. The PS of the seasonal diets of caribou and muskoxen in 1972–73 (C/M of summer and winter found at the bottom of the table) is based upon analysis of the data in Shank *et al.* (1978) and Wilkinson *et al.* (1976).

Month/ Season	PS C/MH	PS C/ML	PS MH/ML	PS C/M
February	58			
March	37			
April	18	22	93	
May	38			
June	73	34	52	
July	25	28	76	
August	43	33	90	
October	45	45	99	
November	52			
December	44			
Summer				48
Winter				68

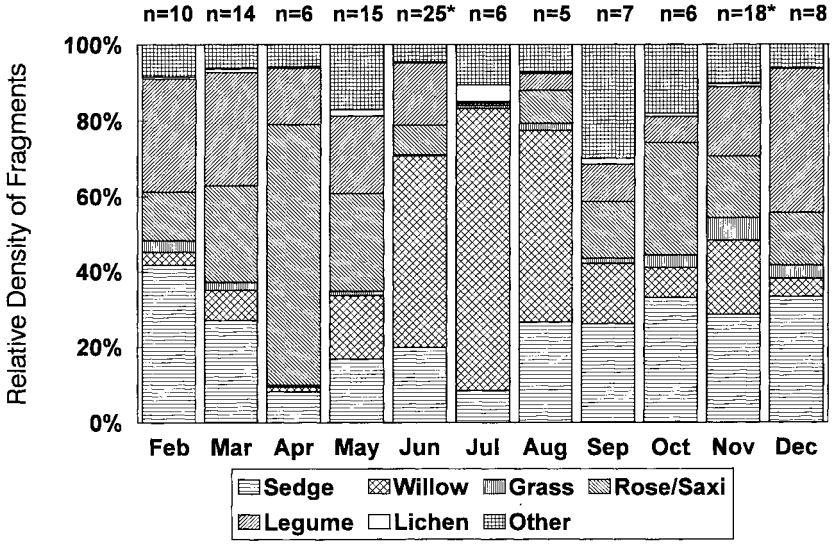

Fig. 1. Diet composition of Peary caribou, based upon the mean percent relative density of faecal plant fragments. n = number of samples (individuals). An asterix indicates data pooled over 2 years.

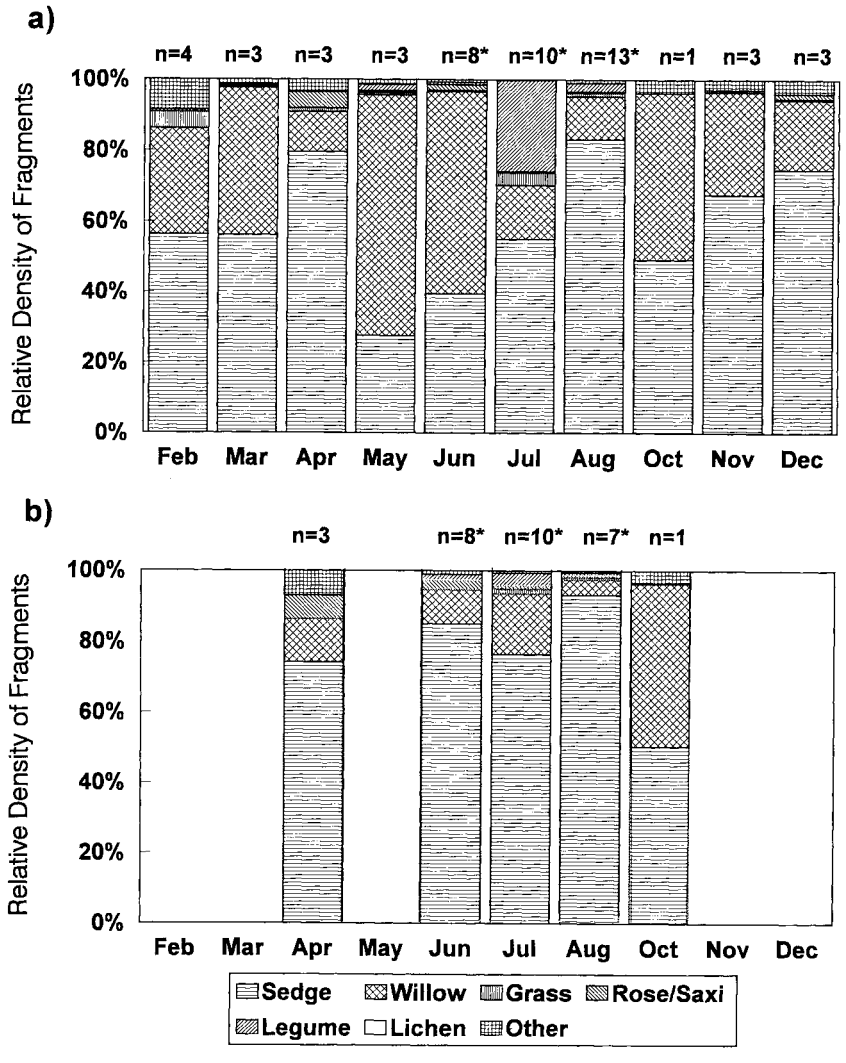

Fig. 2. Diet composition of muskoxen in high (a) and (b) low density muskox areas, based upon the mean percent relative density of faecal plant fragments. *n* = number of samples (groups). An asterix indicates data pooled over 2 years.

high density muskox areas, hummock tundra had more sedge and legume and less lichen, upland barren had more sedge, legume, grass, and willow, and stony barren had more sedge and less grass and other forbs than was found in corresponding habitats in low density muskox areas (Table 2).

Discussion

Studies on various Canadian arctic islands in the 1960's and 1970's suggested that caribou and muskoxen coexisted with little resource overlap (Tener, 1965; Kevan, 1974; Thomas & Edmonds, 1984). Studies were conducted in the early 1970's to compare diet composition of the 2 ungulates on Banks Island (Wilkinson *et al.*, 1976; Shank *et al.*, 1978) and the Parry Islands (Parker, 1978). Again, competition for food was generally ruled out because of little dietary overlap. Muskox summer and winter diets were both dominated by graminoids, generally sedges

Table 2. The percent frequency occurrence of various forages in the 3 upland habitats located in high and low density muskox areas: hummock tundra (HT, 84 plots), upland barren (UB, 96 plots), and stony barren (SB, 84 plots). See text for forage class descriptions.

Habitat	Muskox Density	Sedge	Willow	Grass	Ericad	Lichen	Legume	Rose/Saxifr.	Other
HT	High	86	45	35	4	29	31	92	36
n=84	Low	57	48	25	0	90	11	96	33
UB	High	90	27	44	0	78	32	93	24
n=96	Low	58	15	16	0	71	8	92	26
SB	High	66	5	7	0	85	1	88	8
n=84	Low	38	6	19	0	74	0	88	20

(*Carex* spp.) which were abundant in wet lowland habitats. Caribou summer and winter diets were both dominated by willow (*Salix* spp.), forbs, grasses and sedges which were abundant in drier upland habitats, but the proportion of willow in the winter diet was reduced.

Knowledge of forage availability is an integral requirement for documenting competition for food (Klein & Staaland, 1984; Gunn, 1990), yet data pertaining to forage availability was conspicuously absent from previous studies. Therefore, Wilkinson *et al.*'s (1976) conclusions about the lack of competition between muskoxen and caribou on Banks Island are not surprising. Their study was conducted in summer, when forage quality and availability are highest.

Currently, the caribou population on Banks Island is 16-fold smaller and the muskox population 16-fold larger than in 1972, therefore previous results and conclusions are likely to differ from ours. Although Wilkinson *et al.* (1976) and Shank *et al.* (1978) ruled out competition for food between muskoxen and caribou, their results demonstrated substantial similarity (PS) in diet between the two species during both winter (March) and summer (August) (Table 1.). PS in the diets found in the 1970's may be inflated somewhat in relation to our findings because the diet was only partitioned into 5 components versus our 7 components. Our findings indicated: i) considerable similarity in diet between the 2 ungulates regardless of muskox density, ii) a noticeable absence of lichen in the diet of caribou, iii) a noticeable absence of grasses in the diet of both caribou and muskoxen, and iv) sedges and willows were found throughout all habitats, but grasses were found mostly in upland habitats.

The diet of caribou was more diverse than that of muskoxen, being dominated by 4 major forage groups, sedge, willow, rose/saxifrage, and legume. There was a distinct seasonal shift in proportions of willow, rose/saxifrage, and legume. Willow use was greatest during June through August, presumably when new growth leaves and stems are high in crude protein and energy content. Rose/saxifrage and legume, as well as sedge, predominated from October to May. Sedge and rose/saxifrage occur in all three upland habitats and wet sedge meadows on Banks Island, whereas legumes occur only on the upland habitats. The grass component of the diet reported in the early 1970's (Wilkinson *et al.*, 1976; Shank *et al.*, 1978), was noticeably absent in the 1990's. Rose/saxifrage, legumes, and other forbs appear to have replaced this component of the diet. The lack of lichen in the diet was consistent with previous findings (Shank *et al.*, 1978), and is likely related to low availability. Larter & Nagy (1996) found similar percentages of lichen in the rumen contents and faecal material of mainland barren-ground caribou during winter indicating that the proportion of lichen in the diet, determined from the analyses of faecal plant fragments, was not significantly influenced by high lichen digestibility during winter. The 2.96 g/m^2 we report is almost 5-fold lower than the 14 g/m^2 reported on Coats Island (Ouellet *et al.*, 1996), an island considered to have a low standing crop of lichen.

The muskox diet was dominated by seasonally varying proportions of sedge and willow regardless of muskox density. Standing crop and occurrence of sedges in wet sedge meadows was similar between areas, and therefore could not explain the larger proportions of sedge in the diet of animals in the low density area. The increased occurrence of legumes in the diet of animals in the high density area during July may be related to availability. Legume standing crop and occurrence in upland barren and hummock tundra habitats was greater in those habitats present in the high density area. July is the peak in available crude protein of legumes (N. Larter & J. Nagy, unpubl. data).

The occurrence of willow in both the winter (March) and summer (August) diets of muskoxen in the high density area was 2–3 times greater than that found by Wilkinson *et al.* (1976) and Shank *et al.* (1978) in the 1970's. This difference cannot be attributed to the difference in technique used to determine diet. The macroscopic technique used by Wilkinson *et al.* (1976) and Shank *et al.* (1978) is more likely to overestimate willow than the microscopic technique we used, because willow particles are generally larger than those of other forages and are easily identifiable. Whether or not increased dietary willow is related to a decrease in sedge availability or an increase in willow availability is unknown. Sedge availability would appear to be high. Standing crop of sedges in wet sedge meadows in the peak of the growing season ranged from 53–65 g/m^2. This is greater than the 36 g/m^2 found in wet sedge meadows at Sverdrup Pass, Ellesmere Island, where the diet of muskoxen is almost exclusively sedge (Raillard, 1992). Increasing competition for sedges may have resulted in an increase in the use of other forages, like willow. Smith (1996) demonstrated that wet meadows subjected to grazing by a

high density of muskoxen had decreased net aboveground primary productivity, and that over-compensation of plant growth did not occur.

Increasing use of willows, especially during winter, by a rapidly increasing population of muskoxen is of immediate concern. During winter, willows are dormant and many years of growth can be removed, possibly more than could be replaced during one growing season. Willow twigs of ≥4 years growth have been found in the rumen of adult muskoxen during April (N. Larter & J. Nagy, unpubl. data). Continued cropping of most previous years twigs and buds may stress willow plants beyond recovery and increase plant mortality. Reductions in new growth of willows during June to August may have serious consequences for caribou who utilize them as a primary food source during this time of lactation and body growth.

The elevated winter use of willows may be somewhat higher than normal for our March and May data because the high density muskox area data were collected in 1993. During winter 1992-1993, Banks Island had more snowfall than in subsequent winters, resulting in a deeper and denser snow cover of wet sedge meadows and upland barrens during late winter. Muskox crater sites were rare in wet sedge meadows, with the majority in upland habitats (N. Larter & J. Nagy, unpubl. data). These snow conditions may have forced muskoxen to feed more in uplands, where there is a higher proportion of willow forage, and therefore may have biased our data. Regardless, data collected in November, December, February and April of the following winter showed much higher willow use than that found in the 1970's. Snow depth and density in wet sedge meadows and upland barrens was lower and nearer normal during the 1993–1994 winter (N. Larter & J. Nagy, unpubl. data).

Much of the traditional wintering area of caribou overlaps the high density muskox area. Any dietary overlap with muskoxen may be magnified should harsh snow conditions occur. Similar habitats provide relatively similar standing crops of eight major forage classes with the possible exception of legumes and *Dryas integrifolia* which are more prominent, both in occurrence and standing crop measures, in the high density muskox areas. However, because we have not completed habitat mapping in these areas, these data must be treated with caution regarding an absolute measure of forage availability. Higher frequency occurrence of forages does not necessarily indicate increased standing crop.

Although caribou and muskoxen have different morphological and physiological adaptations which enable them to utilize forage resources with little overlap, our interpretation of data reported by Wilkinson *et al.* (1976), and Shank *et al.* (1978) suggests dietary overlap of forage classes occurred in the early 1970's on Banks Island. Dietary overlap between caribou and muskoxen has since become evident during 11 months of the year, is greater in areas of high muskox density, and may increase during winters with elevated snow depth and density. Currently, data cannot disprove or prove that forage competition has occurred or is occurring. However, given: i) increased willow utilization by a rapidly increasing muskox population, which may increase during harsh winters, and ii) the four-fold increase in density of a relatively sedentary potential competitor for food in traditional caribou wintering areas between 1985 and 1994, the potential impact of muskoxen on the caribou winter range and availability of willows may well be a factor limiting the recovery of the Peary caribou population.

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Brief communication

A Comparison of digestive Tract Morphology in muskoxen and caribou from Victoria Island, Northwest Territories, Canada

Hans Staaland[1], Jan Z. Adamczewski[2] & Anne Gunn[3]

[1] Dept. Biol. Nature Conservation, Agric. Univ. Norway, 1432 Ås, Norway.
[2] Dept. Vet. Anatomy. 52 Campus Dr., Univ. Saskatchewan, Saskatoon, Sask. Canada S7N 5B4.
Present address: c/o Sathu Renewable Resources Board, Norman Wells, Northwest Territories, Canada, X0E 0V0.
[3] Wildl. Manage. Div. Dept. Renewable Resources, Wildlife & Economic Development, Govt of NT, Yellowknife, NT Canada X1A 3S8.

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In areas of Canada, Greenland and Alaska where muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus* subspp.) coexist, there is a potential for overlap in foraging, particularly at high population densities (Vincent & Gunn, 1981; Staaland & Riis Olesen, 1992). The potential for competition should be greatest in winter, when plant senescence and snow cover restrict foraging choices. To date, studies of food habits in sympatric caribou and muskoxen generally have provided little evidence of competition (Wilkinson *et al.*,1976; Thomas & Edmonds, 1984). The numbers of caribou and muskoxen on Victoria Island, Northwest Territories increased from 1970 to 1990 (Gunn, 1990) and the two species have been observed in relatively close proximity (1–2 km) near Cambridge Bay at the southern end of the island. Based on their digestive anatomy, ruminant species have been classified along a grazer-intermediate feeder-concentrate selector continuum (Hofmann, 1989). Grazers are identified by relatively large rumens and omasa and relatively small hindguts (caecum+large intestine), while concentrate selectors tend to have relatively small rumens and omasa and more pronounced hindguts (Hofmann, 1989). Hofmann (1989) has suggested a substantial correlation between digestive anatomy of ruminants and their ability to digest particular forages, although Gordon & Illius (1994) and Robbins *et al.* (1995) have challenged the strength of this correlation.

We examined the digestive tracts of 10 muskox cows ≥3 years old and 10 caribou cows ≥2 years old shot by Inuit hunters in November 1992 near Cambridge Bay, to provide a physiological background for comparisons of digestion and foraging strategies of the two species, under winter condition with restricted foraging choices. The digestive tracts of the study animals were removed at a field camp and measured within 2–5 hours of death, following the methods of Staaland & White (1991) and Staaland & Thing (1991). Mean species values (±S.D.) were compared by *t*-test with significance at $P<0.01$.

The mean body mass of the muskoxen (216±20 kg) was three times greater than that of the caribou (72±4 kg), and total (wet) alimentary fill was greater in both absolute and proportionate terms: 50.4±5.9 kg *vs.* 13.5±2.3 kg, and 234±29 g kg^{-1}

Table 1. Content and tissue weight of sections of the alimentary tract of 10 female muskoxen and 10 female caribou from Victoria Island. Values are expressed as % of total fill or as % total tissue weight.

	Rumen/retic.	Omasum	Abomasum	Small int.	Hindgut
		Content			
Muskoxen	72.9±2.3	6.6±1.6a	1.5±1.0	8.9±1.1	10.1±1.0a
Caribou	70.1±3.8	4.0±0.9b	1.6±0.6	9.5±2.2	14.8±2.7b
		Tissue			
Muskoxen	47.6±1.1a	15.0±1.0a	5.3±0.4a	17.6±1.2a	14.5±1.3
Caribou	60.2±2.4b	5.5±0.6b	4.4±0.6b	15.6±1.9b	14.3±1.4

Figures followed by different letters are significantly different ($P<0.01$).

BM *vs.* 188±33 g kg^{-1} ($P<0.01$) in the caribou. Distribution of alimentary content differed between the two species (Table 1), with a greater omasal fill in the muskoxen and a greater hindgut fill in the caribou, but similar proportions in the ruminoreticulum, abomasum and small intestine.

The total mass of alimentary tissue, stripped of fat, was greater in absolute terms in the muskoxen (9.4±0.8 kg *vs.* 4.4±0.4 kg) but smaller in proportionate terms (43.3±3.1 g *vs.* 60.7±4.8 g tissue kg^{-1} BM). The greatest difference in distribution of tissue weights was found in the omasum, which was nearly 3 times as large in the muskoxen as in the caribou (Table 1).

The relative mass of rumen tissue was greater in the caribou than in the muskoxen. This may, however, simply be a consequence of the relatively larger surface area of a spherical organ (like the rumen) with a smaller volume. The total length of the intestine was 40.7±5.1 m in the muskoxen and 26.6±1.2 in the caribou; of the total, the hindgut (caecum to anus) was a smaller proportion ($P<0.01$) in the muskoxen than in the caribou (34.6±2.9% *vs.* 40.8±2.4%).

The alimentary fill and tissue characteristics of muskoxen are consistent with their designation as "grazers" (*sensu* Hofmann, 1989) as shown in Greenland by Staaland & Thing (1991). In much of the Canadian arctic archipelago, northern Greenland and the Svalbard islands, lichens are scarce and the vegetation has a preponderance of graminoids, forbs and bryophytes. During winter, muskox diets are dominated by sedges and grasses on Victoria Island (Schaefer, 1995) as in Greenland (Thing, 1984), and graminoids are among the most widely available forages. Muskoxen have also been shown to have the slow rate of passage (Adamczewski *et al.*, 1994a) and exceptional ability to digest graminoid forages (White *et al.*, 1984; Adamczewski *et al.*, 1994b) predicted by Hofmann's (1989) model. Combining these traits with a low metabolic rate (Nilssen *et al.*, 1994) muskoxen can be relatively sedentary in winter (Jingfors, 1981; Wilkinson et al., 1976), remaining in areas with relatively high biomass.

Caribou, in contrast, are continuously nomadic in their feeding (Thomas & Edmonds, 1984), Russell *et al.* 1993). With a relatively high metabolic rate (Tyler & Blix, 1990) and a relatively rapid rate of passage (Valtonen *et al.*, 1983), they are less able to subsist on slowly fermenting, fibrous graminoids and tend to forage in areas with relatively low biomass, selecting the most nutritious parts of plants such as flowerheads, seed heads and winter-green leaves (Thomas & Edmonds, 1984). Despite the low biomass, the quality of the selected diet can be relatively good with high concentrations of minerals and good digestibility (Staaland *et al.*, 1983). Results of this study suggest, however, a substantial ability of Victoria Island caribou to adapt to lower quality forages in winter. As in Svalbard reindeer (*R. t. platyrhynchus*) (Staaland & White, 1991), the fill of the hindgut is relatively larger than in Norwegian reindeer (*R. t. tarandus*). Alimentary characteristics of Victoria Island caribou are consistent with those of intermediate feeders (sensu Hofmann, 1989), as the omasum is substantially larger than in concentrate selectors like roe deer (*Capreolus capreolus*) (Holand & Staaland 1992).

Because arctic island caribou and reindeer tend to have larger hindguts and omasa than Norwegian reindeer (Staaland & Riis Olesen, 1992), these subspecies may be better adapted to being "grazer-like" than more southerly subspecies. However, the studies of Gordon & Illius (1994) and Robbins et al. (1995) indicate that the correlation between digestive anatomy and function in ruminants is in many cases limited. Feeding trials with domestic reindeer fed unsupplemented hay suggest that their ability to digest fibrous graminoid forage is mediocre

(Syrjälä-Quist, 1985), supporting Hofmann's (1989) views. Further physiological studies may be needed to fully understand how ruminant alimentary tracts and their functions are adapted to different diets and foraging strategies.

Although caribou and muskoxen coexist in close proximity on southeastern Victoria Island, they appear primarily adapted to different diets and foraging strategies. Visual inspection and analysis of rumen contents for fiber and lignin from the study (unpubl.) also indicate a predominantly graminoid diet in the muskoxen and a more varied diet with a substantial browse component in the caribou.This should reduce the likelihood of competition for limited food resources in winter, as suggested for Peary caribou and muskoxen on Melville Island (Thomas & Edmonds, 1984).

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Brief communication

Pregnancy rate as an indicator of nutritional status in *Rangifer*: implications of lactational infertility

K.L. Gerhart[1,2], R.G. White[1], R.D. Cameron[1], D.E. Russell[3] & D. van de Wetering[3]

[1] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775 ([2]Current address: Department of Avian Sciences, University of California, Davis CA 95616, U.S.A. e-mail: klgerhart@ucdavis.edu)
[3] Canadian Wildlife Service, PO Box 6010, Whitehorse, YT, Canada Y1A 5L7

Key words: arctic, caribou, fecundity, parturition, reindeer.

Rangifer, 17 (1): 21–24

Introduction

Calf production in Rangifer spp. is often high, but predation (Bergerud, 1980; Skogland, 1991) or undernutrition (Skogland, 1985) may decrease calf survival and, therefore, recruitment. While food supply has long been recognized as a limiting factor for wild reindeer (*R. tarandus tarandus*) herds in Norway (Reimers, 1982; Reimers *et al.*, 1983; Skogland, 1985; Tyler, 1987), many North American biologists continue to emphasize the role of predators in the population dynamics of barren-ground caribou (*R.t. granti/groenlandicus*) (e.g., Bergerud, 1980; Davis & Valkenburg, 1991). However, studies in Alaska have demonstrated that body condition of female caribou is a determinant of pregnancy rate (Gerhart *et al.*, 1997) and parturition rate (Cameron *et al.*, 1993; Cameron & Ver Hoef, 1994), both of which increase directly with autumn body weight and fatness, as they do in reindeer (Reimers, 1982). A decline in fecundity is manifested as an increased frequency of breeding pauses (Dauphiné, 1976; Reimers, 1982; Cameron, 1994).

Probability of pregnancy may also be influenced by lactation status. At the same body weight and fatness, caribou that extend lactation through mid-November are nearly 50% less likely to be pregnant than those that are ceasing lactating (Fig. 1). This condition-unrelated decrease in fecundity appears to be an example of lactational infertility, in which

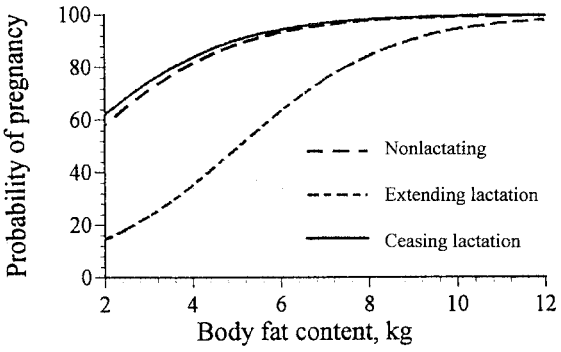

Fig. 1. Probability of pregnancy in relation to body fat content and lactation class for adult female caribou of the Porcupine herd. (Adapted from Fig. 2, Gerhart *et al.*, 1997).

suckling delays normal follicular development and ovulation by suppressing gonadotropin (principally luteinizing hormone) secretion (McNeilly, 1994). Here, we investigate the extent to which the proportion of females extending lactation influences the pregnancy rate of a caribou herd.

Methods

Simple population modeling was performed using a spreadsheet. Initial percentages of lactating and nonlactating females were similar to those observed previously in arctic caribou (e.g., Dauphiné, 1976; Cameron *et al.*, 1993). The percentage of females extending lactation was increased from 15 (Year 1) to 70 (Years 2–4), a range similar to that observed in the Porcupine Herd (Gerhart *et al.*, 1997). Pregnancy rates applied to each class of female, after Gerhart *et al.*, (1997), were assumed to be constant. Overall pregnancy rates for the herd were calculated as the weighted means of all classes.

Minimum sample sizes necessary to detect changes in pregnancy rate between years 1 and 4 were calculated according to Zar (1984) (at α=0.05, with 90% power, i.e., β=0.10), assuming equal samples sizes in years 1 and 4.

Results

Output of the model was as follows (Table 1):

In year 1, 85% of adult females in the herd were lactating, of which 15% extended lactation. Given pregnancy rates of 90 and 50%, respectively, for those ceasing and extending lactation, 84% of the lactating females were pregnant after the rut. Adding the nonlactating females

Table 1. Hypothetical changes in the pregnancy rate of a caribou herd as the percentage of lactating females that extend lactation increases from 15 (Year 1) to 70 (Years 2–4).

Year	Lactation class	% of females in herd (% of lactating females)	Pregnancy rate (%)
1	Nonlactating[1]	15	90
	Ceasing lactation[2]	72.5 (85)	84
	Extending lactation[3]	12.5 (15)	–
			Total 85
2	Nonlactating	15	90
	Ceasing lactation	25.5 (30)	62
	Extending lactation	59.5 (70)	–
			Total 66
3	Nonlactating	34	90
	Ceasing lactation	20 (30)	62
	Extending lactation	46 (70)	–
			Total 72
4	Nonlactating	28	90
	Ceasing lactation	22 (30)	62
	Extending lactation	50 (70)	–
			Total 70

[1] Females that are not lactating in autumn; pregnancy rate 90% (Gerhart *et al.*, 1997).
[2] Females that cease lactating by early November; pregnancy rate 90% (Gerhart *et al.*, 1997).
[3] Females that extend lactation through mid-November; pregnancy rate 50% (Gerhart *et al.*, 1997).

at a pregnancy rate of 90% yielded a value of 85% for the herd.

In year 2, with an increase to 70% extending lactation, the pregnancy rate of lactating females declined to 62%, resulting in an overall decrease to 66%.

In year 3, extended lactation remained at 70%, but high fecundity of the additional nonlactating females (i.e., those females which failed to become pregnant in Year 2) more than compensated for the lower pregnancy rate of lactating females. Consequently, the herd parturition rate recovered somewhat to 72%.

In year 4 and beyond, the pregnancy rate of lactating females remained at 62%, and that for the herd stabilized at 70%.

Discussion

We suggest that nutrient insufficiency during early lactation is the most important determinant of extended lacatation. In red deer, low plane of nutrition during lactation decreased milk yield and calf growth rate, but not maternal body weight (Loudon *et al.*, 1983; White, 1983); instead, suckling frequency was increased and ovulation delayed. In caribou, early growth strongly influenced autumn body weight: birth weight and growth to 3-4 weeks of age accounted for 78.6% of the variation in autumn body weight of wild Porcupine Herd calves (Gerhart, 1995). Caribou are almost entirely reliant upon milk nutrients for growth and maintenance prior to approximately 40 days of age (White & Luick, 1984; Parker *et al.*, 1990); therefore, early growth is directly related to maternal plane of nutrition (and maternal body reserves) during this period (White, 1983).

Lactating arctic caribou are apparently unable to produce enough milk to maximize growth of their calves in some years: both body fat content (Gerhart *et al.*, 1996) and growth rate (Gerhart, 1995) decreased during the insect harassment period. Thus variation in either nutrient availability during early lactation (e.g., timing of snow melt; Eastland, 1991) or intensity or duration of insect harassment (Russell *et al.*, 1993) might affect milk production, and therefore frequency of lactational infertility.

Pregnancy rate determined from females sampled randomly may lead to erroneously high estimates of nutrient availability and an overly optimistic potential for population increase relative to evaluations based on lactating females. For herds of caribou in which both parturition rate and oversummer calf survival are high (e.g., Table 1), most adult females will be lactating in autumn. If the percentage of females extending lactation increases, the pregnancy rate of lactating females will decline, thereby increasing the proportion of nonlactating females present the following summer. Because the latter are highly fecund, they will buffer the decrease in pregnancy rate of the herd, and herd productivity will remain stable.

In contrast, nonlactating females are numerous in herds characterized by low rates of neonatal survival. As a result, pregnancy rates are generally high (Skogland, 1991). If calf survival increases, however, high fecundity may not continue unless summer forage resources permit a lactating female to both provide adequate milk for a calf and gain sufficient weight or fat prior to the breeding season.

Monitoring pregnancy rates to detect changes in nutrition is best accomplished by sampling lactating females because they will be more responsive to changes in nutrient availability: nutrition influences pregnancy rate of lactating caribou both through autumn body condition and lactational infertility. Additionally, such monitoring may be less expensive: differences in pregnancy rate between years 1 and 4 (Table 1) are significant if 45 lactating females are sampled each year, versus 80 females sampled randomly from the herd.

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Relationship between Conception Date and Latitude in Muskoxen

Peter F. Flood & Susan C. Tedesco

Department of Veterinary Anatomy, W.C.V.M., University of Saskatchewan, 52 Campus Drive, Saskatoon, Saskatchewan, Canada S7N 5B4. e-mail: peter.flood@usask.ca

Abstract: It has been suggested that muskoxen calve earlier with increasing latitude but the available data do not seem to have been thoroughly analyzed. Therefore, estimated conception dates (n=657) from a wide range of latitudes were compared. The results indicate that conceptions occur about a month earlier in the arctic than at temperate latitudes. This conclusion is consistent with reported observations of mating behaviour and calving season.

Key words: *Ovibos,* season, calving, reproduction.

Rangifer, 17 (1): 25–30

Introduction

In many small mammals breeding begins later with increasing latitude and its timing is closely related to plant phenology and hence food supply (Sadlier, 1969; Bronson, 1985). In larger species with long reproductive cycles such as red deer (Fletcher, 1974), deer of the genus *Odocoileus* (Bronson, 1985; Lee, 1970) and North American wild sheep (Bunnell, 1982; Thompson *et al.,* 1982) there seems to be little or no change in breeding season with latitude provided the profound ecological changes associated with tropical or subtropical environments are excluded. However, none of the analyses of deer or sheep include data from north of the arctic circle. Reindeer, which do extend into the high arctic, breed later the further north they are found (Leader-Williams, 1988). The reindeer data however, include both wild and domestic animals as well as the genetically distinct Svalbard reindeer. Information on domestic sheep is often complicated by genetic differences between breeds but where the Merino was compared at four locations from near the equator to 41°S, there was no clear change in the time of peak incidence of oestrus; nonetheless, there was a very marked concentration of reproductive activity with increasing latitude. Thus the breeding season began sooner and ended later near to the equator (Hafez, 1952).

Seasonally breeding species differ in their characteristic time of birth and muskoxen, for example, calve about 4 - 8 weeks before sympatric caribou (Latour, 1987; Leader-Williams, 1988). Breeds of domestic sheep also differ markedly in the time of their breeding season even when they are kept at the same latitude, and crosses between breeds show intermediate characteristics (Lincoln *et al.,* 1990). Today, wild muskoxen are found from 58–83°N and during the Wisconsinan glaciation (about 20 000 BP) they were numerous as far south as 40°N (McDonald & Davis, 1989). Although there are now no natural muskox populations as far south as this, there are several confined herds that provide a basis for comparison. In a general review of the early literature on muskox reproduction it was suggested that conception occurred earlier at higher latitudes (Teal, 1959) and this was born out by more

recent studies (Rowell & Flood, 1988). Because, superficially, advancing reproduction when spring is delayed would seem to be counterintuitive, a more detailed survey of available data was conducted.

Methods

Muskox conception dates were estimated by one of two methods. In all cases other than Banks and Victoria Islands a gestation period of 235 days (Rowell *et al.,* 1993) was deducted from the known calving date. For Banks and Victoria Islands the stage of gestation was calculated from the dimensions of fetuses obtained from muskox cows shot on known dates. Regressions published previously (Pharr *et al.,* 1994) were used in the latter estimations. The dates of calving, apart from those from our own records of the Saskatoon herd, were obtained from Holst (1990), Karsten (1986) and Oeming (1965), or were kindly supplied by Gerald Binczik (Minnesota Zoo), Joel and Nancy Bender (Hamilton, Montana), and Peter Lent (Unalakleet, Fairbanks and Palmer). The sources of the fetal dimensions for Banks and Victoria Islands have been outlined previously (*Pharr et al.,* 1994).

Locations for study were selected because the number of known calvings exceeded six with the exception of San Francisco (6 records) and San Diego (5 records) which were included because of their extreme southerly location. Two kinds of record were excluded from the analysis to preclude bias caused by abnormally short pregnancies or differences in fertility between sites. First, isolated calvings (n=5) that occurred more than ten days in advance of the main group of calvings at a given location were removed. Second, all values (n=260) that lay more than 20 days after the first calving in the main group at each location were excluded in order to avoid animals that had not conceived at the first mating. Twenty days is the length of the oestrous cycle in muskoxen (Rowell & Flood, 1988). The total number of records was 657 and 392 of these were included in the final analysis.

The locations for which data are available fell into three groups by latitude; they were the two arctic islands, 5 sites in Alaska and Sweden between 60°N and 65°N, and 11 temperate locations south of 60°N. These are referred to as "Island", "Boreal" and "Temperate" respectively. The estimated times of conception in these broad groupings were compared using Kruskal-Wallis and Mann-Whitney tests ("Statview" for Macintosh, Abacus Concepts, Inc, Berkeley, California, USA).

Mating may have been artificially delayed in the confined herds at Unalakleet, Fairbanks and Palmer by keeping the males and females separate until a predetermined date early in the breeding season. Fortunately the date when mating was first permitted was known in many cases and varied somewhat from year to year. In order to determine the effect such controlled breeding on the time of conception, the day mating was first permitted was plotted against the estimated day of conception and the results evaluated by simple regression.

Results

Fig. 1 illustrates a strong inverse relationship between estimated conception date and latitude, and includes details of the locations studied. Conceptions occurred over a month earlier on the arctic islands (median date, 19 August) than they did at temperate locations (median date, 29 September). Locations in Alaska and Sweden were intermediate (median date, 20 September). The

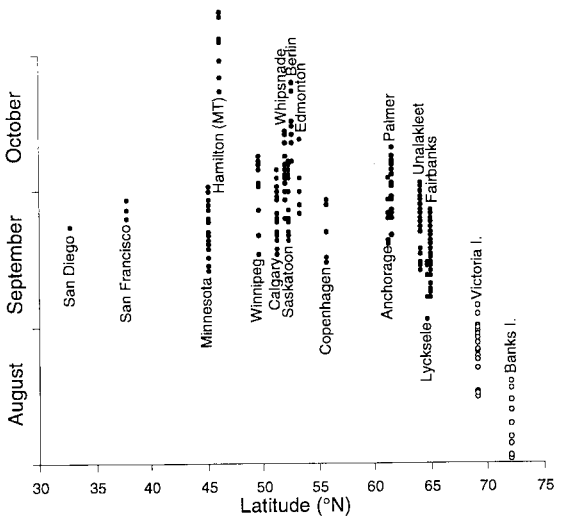

Fig. 1. Estimated muskox conception dates from calving date (solid circles) and fetal dimensions (open circles) plotted against latitude. The location is shown adjacent to each column of points. The total number of observations at each location and the number shown on the graph after truncation (in parentheses) are: Anchorage, 6 (6); Banks Island, 39 (19); Berlin, 18 (12); Calgary, 39 (22); Copenhagen, 22 (5); Edmonton, 7 (7); Fairbanks, 207 (152); Hamilton, Montana, 8 (7); Lycksele, 12 (6); Minnesota, 43 (27); Palmer, 32 (18); San Diego, 5 (1); San Francisco, 66 (3); Saskatoon, 30 (16); Unalakleet, 85 (44); Victoria Island, 31 (18); Whipsnade, 28 (18); Winnipeg, 21 (12).

differences between the Island, Boreal and Temperate groups were all significant ($P<0.0001$). The distribution of the points could either be seen as a smooth curve or a "broken stick" with the point of inflection close to 60°N.

As expected, in those confined herds in which the bulls were only allowed access to the females in the breeding season, the later the bulls and cows were put together the later conceptions occurred. In addition, the later in the year that mating was first permitted, the shorter was the interval to conception. It therefore appears that when the bull was introduced relatively early in the year, many cows had not begun to show oestrus. Thus the controlled mating system used in Palmer, Fairbanks and Unalakleet probably had little effect on the conception dates that were included in the analysis owing to the use of the truncation procedure. Further evidence for this view comes from the dates of unconstrained conceptions at Anchorage and Lycksele (Fig. 1) and the fact that none of the estimated dates of conception were less than eight days after the bulls were introduced when introduction occurred early in the season.

Discussion

Our results support Teal's (1959) contention that calving in muskoxen occurs earlier at higher latitudes. The data in Fig. 1 are significant but they depend in part on the assumption that the two methods used to estimate the time of conception yielded comparable dates. While it is most unlikely that the two methods gave identical results, we would argue that they are sufficiently close to allow the inferences made. The most obvious support for this view comes from inspection of the points in Fig. 1; they can be seen to form a continuous band with no obvious break where the method of analysis changed. Further, the data show the same trends in the parts of the curve based on fetal dimensions alone and on birth dates alone.

If the gestation period used in the analysis were too short, the advance in breeding season with latitude would be overestimated. The value we used (235 days) was based on detailed observation of ten pregnancies in young muskoxen kept in Saskatoon and may not be typical of older animals or animals in the arctic. The period of 8 months given by Groves (1992), which has presumably served as a useful rule of thumb, is seven days longer (adding the relevant months which always include February). If this gestation period had been used in our estimations, it would only marginally change the conclusions.

The artificial constraints placed on the beginning of the breeding season in Fairbanks, Palmer and Unalakleet are likely to have reduced the difference between the Alaskan and Temperate conception dates, while exaggerating the difference from the Island dates. Overall, without this effect the curve formed by the points in Fig. 1 would have been smoother. Even so we suspect that the induced error was small for the reasons given at the end of the results section. However, as in sheep and goats, the onset of oestrus may have been artificially delayed by the absence of males at the beginning of the breeding season (Lindsay, 1991).

There is substantial though incomplete agreement between the present analysis and behavioural reports in the literature (Fig. 2). The observed mating period on Bathurst Island (Gray, 1987) and the period of births at Kangerlussuaq (Olesen, 1993) match the present results particularly well. Limited observations on Ellesmere Island (Tener,

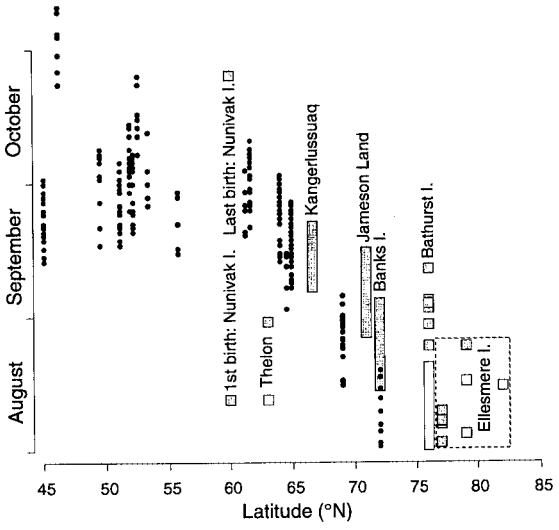

Fig. 2. Estimated muskox conception dates (solid circles) compared with observations of mating behaviour in the wild (open rectangles) and conception dates corresponding to individual calvings or calving periods reported in the wild (stippled rectangles). All are shown plotted against latitude (°N). The locations for the data shown by the rectangles are indicated. The dotted rectangle encloses observations on Ellesmere Island. The remaining locations are shown in Fig. 1. The behavioural information was obtained from Tener, 1965; Rowell, 1980; Thing, 1984; Gray, 1987; Latour, 1987; Lent, 1988 and Olesen, 1993.

1965; Rowell, 1980) also broadly conform to the expected trend. However, births on Bathurst Island (Gray, 1987) were later than would have been expected from mating behaviour, perhaps because conception was delayed by nutritional stress, and the estimated time of the earliest births on Banks Island (Latour, 1987) was two weeks later than predicted by measurement of fetuses. The reported calving season on Jameson Land on the East coast of Greenland (Thing, 1984) was also later than expected. The information for Nunivak Island (Lent, 1988) and the Thelon Game Sanctuary (Tener, 1965) has been included for completeness but it is so fragmentary that it adds little. To conclude, the information on calving season summarized in Fig. 2 supports the view that calving occurs earlier at higher latitudes even though the overall timing is somewhat later than would have been expected from fetal measurements.

The reason for the delay in reproduction seen at more southerly locations is not clear. The effects of captivity alone do not seem to provide an adequate explanation because the Boreal animals calved before the temporate ones though both were confined. Nonetheless, the brief superabundance of high quality forage available during the arctic summer is hard to duplicate in captivity and we are loath to reject the possibility that it advanced the breeding season.

Two hypotheses involving photoperiod receive little support from the present data. The first and simplest is that reproduction in muskoxen occurs at a fixed period of about 100 days after a critical daylength is reached around the vernal equinox. If the critical daylength were greater than 12 hours of light it would occur earlier at higher latitudes. The data as a whole do not fit this concept; the changes in breeding season north of 60°N are too great to be explained by any daylength that occurs further south. If only latitudes north of 60°N are considered, the time of conception can be neatly described by saying that it occurs about 108 days after the first day when the sun is in the sky for more than 19 h. Because the daylength and the lag period were chosen to fit the data, this observation implies little about causation but it does provide a simple means of estimating the time of the breeding season.

The second hypothesis depends on the assumption that the circadian day is shorter than the 24 h day. Thus in the high arctic, during the continuous light of summer, muskoxen might switch to the shorter circadian day in the absence of other cues and arrive at the breeding season sooner. This explanation fails to account for the change in breeding season with latitude seen south of the Arctic Circle and conflicts with the observation that the muskox circadian day differs little, if at all, from the 24 h day (Tedesco, 1996). A phenomenon which may or may not be related is seen in rams in which melatonin secretion has been abolished by pinealectomy or cranial cervical ganglionectomy. Such animals come into breeding condition several weeks earlier than their intact controls (Lincoln *et al.,* 1989). It is possible that the suspension of melatonin secretion caused by the continuous light of the arctic summer has a similar effect. Again, an explanation based on this phenomenon fails to explain the change in breeding season occurring south of the Arctic Circle.

Another factor that may influence the onset of the breeding season is the rate of change in daylength: for example in Saskatoon, daylength increases by seven minutes a day at its maximum in March, but at 71°N the increase can be over 27 minutes. In ewes, a change in daylength, rather than exposure to days of a specific length, is necessary to entrain the circannual reproductive cycle (Robinson & Karsch, 1987), and the amount of change in daylength affects the magnitude of the response (Robinson *et al.,* 1985). Therefore, the dramatic changes in photoperiod occurring in the arctic immediately after the period of continuous winter darkness may provide a more potent stimulus than the more moderate events further south.

Finally, in sheep, high temperatures delay the onset of reproduction (Dutt & Bush, 1955), increase embryonic loss (Bell, 1987) and adversely affect placental development (Bell *et al.,* 1989): high ambient temperatures may have similar effects on muskoxen kept at temperate latitudes. In muskoxen, delaying reproduction somewhat at times of nutritional stress has a possible medium-term advantage in that it would shorten the energetically demanding period of lactation that normally occurs prior to the availability of new growth. It is harder to see how reproductive delay would be an appropriate response to thermal stress but perhaps stress is a poorly differentiated event. It would be interesting to see if nutritional stress at arctic latitudes delays the calving season.

In conclusion, it seems that breeding season in muskoxen changes little through the temperate latitudes as in other ruminants, but is advanced from about 60°N northwards. The opposite is appa-

rently true of reindeer. Perhaps in muskoxen, the calf's maturity on entering the arctic winter is more critical than its mother's need for good quality nutrition during early lactation. This would be consistent with the substantial fat reserves often found in pregnant muskoxen in late winter (Adamczewski *et al.*, 1996). We see no single convincing explanation of the change in breeding season with latitude though there are a variety of mechanisms that may play a part. Perhaps the phenomenon has many causes.

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Brief communication

Nursing behaviour as a predictor of alternate-year reproduction in muskoxen

Andrea B. Schulman & Robert G. White

Large Animal Research Station, Institute of Arctic Biology, University of Alaska Fairbanks,
Fairbanks, AK 99775-7000, U.S.A. e-mail: ftabs@aurora.alaska.edu

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Introduction

Muskox (*Ovibos moschatus*) females generally produce one calf annually between late-April and early-June. Females nurse their calves until late-January or early-February (White *et al.*, 1989). At the Large Animal Research Station (LARS), 55 calves have been born and survived longer than one month since 1983. On six occasions, females at LARS have continued nursing calves through the following winter, spring, and summer (Table 1). Calves were weaned naturally at approximately 18 months-of-age rather than at the normal 9 months. During this prolonged nursing, the female did not produce another calf. She entered a breeding pause.

Parental investment theory suggests that the offspring's sex may influence the duration of the maternal investment period (Trivers & Willard, 1973). In polygynous species, such as muskoxen,

Table 1. Calves at the Large Animal Research Station, Fairbanks, AK that have exhibited prolonged nursing from 1983-1994. Calves in italics were used in the analysis. LP = Low plane, HP = High plane.

Cow (Age)	Number of previous calves	Calf	Calf sex	Birth date	Nutritional plane
Red (7)	5	Rufus	male	3 May 1988	LP
Red (9)	6	*Roxanne*	female	26 May 1990	LP
Brown (9)	6	*Anadyr*	female	21 May 1990	HP
Sine (7)	5	Xian	male	15 May 1989	LP
Sine (9)	6	*Sparbo*	male	1 Jun 1991	LP
Unni (11)	7	*Annie*	female	1 May 1994	HP

mothers would be expected to invest more in male offspring as male reproductive success may be increased most dramatically by slight advantages in body condition and body size. Of the six occasions at LARS, there have been the same number of males as females undergoing prolonged nursing (Table 1).

Parental investment theory also suggests that the mother's nutritional condition may influence the duration of maternal investment (Trivers & Willard, 1973). Mothers in poor nutritional condition may invest longer in a calf for that calf to be large enough to successfully compete with its cohort's members. The female muskoxen at LARS have been divided into high plane and low plane nutritional groups (see Methods) which receive different quality food. Females on the high nutritional plane that are lactating generally weigh more and have more body fat than low plane females (White *et al.*, 1989).

To determine a possible method of predicting when alternate-year reproduction might occur, we performed a retrospective, preliminary, analysis comparing the behavior of females that had and had not undergone breeding pauses. Our hypothesis was that the female's nutritional condition mediates adjustments in reproduction based upon factors other than, but not necessarily exclusive of, their nutritional condition. We suggest that a behavioral feedback between the cow and calf could allow the cow to physiologically monitor, or assess, the nutritional condition of her young through neonate appetite drive, expressed by the calf's nursing behavior. We predict that calves needing prolonged maternal care will nurse longer and more often than normal calves. Also, we predict that behavioral differences will be most evident during the rut or early post-rut period to balance the female's future reproductive effort with investment in the current offspring. During post-rut, the female may terminate a pregnancy (Rowell *et al.*, submitted) presumable in response to the physiological needs of her calf in an attempt to increase the future reproductive potential of that calf. We used behavior data collected by research volunteers in the LARS Earthwatch program to test our predictions.

Materials and methods

In 1987, White *et al.* (1989) divided the LARS captive population of muskoxen into high plane (HP) and low plane (LP) nutritional groups, which received different quality food (see White *et al.*, 1989 for description of diets). This variation represents a long or short duration of high-quality food that could occur in the wild. The LP group represents a short duration of high-quality food similar to years with early snow in autumn. Both groups receive *ad libitum* hay and grazing. The HP group was given a supplemental ration of commercial high-quality pellets (Quality Texture, Fisher Mills, Seattle, WA; White *et al.*, 1989). Beginning in 1988, calves on the HP of nutrition received *ad libitum* pellets and hay at all times via a creep feeder. A creep feeder is a feeder to which only the calves have access. Calves on the LP of nutrition were provided *ad libitum* brome hay.

From 1988, research volunteers from Earthwatch were trained to conduct behavioral observations. Volunteers observed focal animals over a 25-h period using continuous, all-occurrence sampling (Altmann, 1974) on up to three cow-calf pairs within a treatment group from late-May to early-November. Within an observation period, observers recorded all behaviors and behavior changes on a field computer. The computer's internal clock recorded the time of each behavior change, which allowed us to calculate the duration of each behavior and between-behavior intervals (Parker *et al.*, 1990; Tiplady, 1990).

Behaviors of cow-calf pairs, as well as individual cows that had previously been observed as a member of a cow-calf pair, were classified into 12 behavior categories: lying, standing, walking, grazing, feeding (from a hay-pellet feeder), drinking, playing, running, creep feeding (from a creep feeder), nursing (and termination of a nursing event), attempting to nurse, and out of sight. Nursing bouts of <5s are classified as unsuccessful nursing attempts (Tiplady, 1990).

We compared nursing behavior for calves that engaged in prolonged nursing with the same behaviors for calves that were weaned at the normal 9 months-of-age. Each calf exhibiting prolonged nursing was paired with a calf weaned at the normal time from the same cow to compare the behavior of a female before she does and does not undergo a breeding pause; these are termed prolonged-normal pairs. All prolonged-normal calf pairs were on the same nutritional plane. To partially standardize for age, development, variations in food supply, and the presence or absence of a bull, we divided the season into four categories. In the milk-dependent or pre-rumen function period, calves were <6 weeks of age. Pre-rut calves were 6 - 14 weeks of age, and in the rutting period (from late-Aug. to mid-Oct.) calves

were 12 - 23 weeks of age. During the post-rut period in late-Oct. until early-Nov. calves were 21 - 31 weeks of age. We used the average duration of nursing bouts per day, inter-bout interval, and the total time per day spent nursing as measures of nursing behavior. We then performed a distribution-free randomization test (Potvin & Roff, 1993; p. 1622-1623) on each of the three measures of nursing behavior during each age category for each calf pair and for the groups of normal calves and calves exhibiting prolonged nursing.

Results

We used behavioral data from three prolonged-normal pairs of calves from the same cow, and from a fourth pair of calves born to closely related cows, in the analysis (Table 1). There is a trend for calves in the LP of nutrition group (n = 4) to undergo prolonged nursing more often than calves (n = 2) in the HP of nutrition group (Table 1). Most comparisons between pairs of calves showed no significant differences in any nursing behavior during any seasonal category (Table 2). For pairs in which significant behavior differences were observed, both calves in the pair were the same sex. One pair of calves showed significant differences in one or more behaviors during each of the four categories, however, this pair of calves were born to different cows. Additionally, this pair showed significant differences in all behaviors during the post-rut period. A second pair (Table 2: Scooter-Anadyr) were significantly different in inter-bout interval during the post-rut period as well. Two pairs of calves were significantly different in total time spent nursing per day during rut (Table 2: Scooter-Anadyr and Horton-Sparbo). Two pairs of calves also were significantly different in inter-bout interval during the pre-rumen function period (Table 2: Andree-Roxanne and Horton-Sparbo).

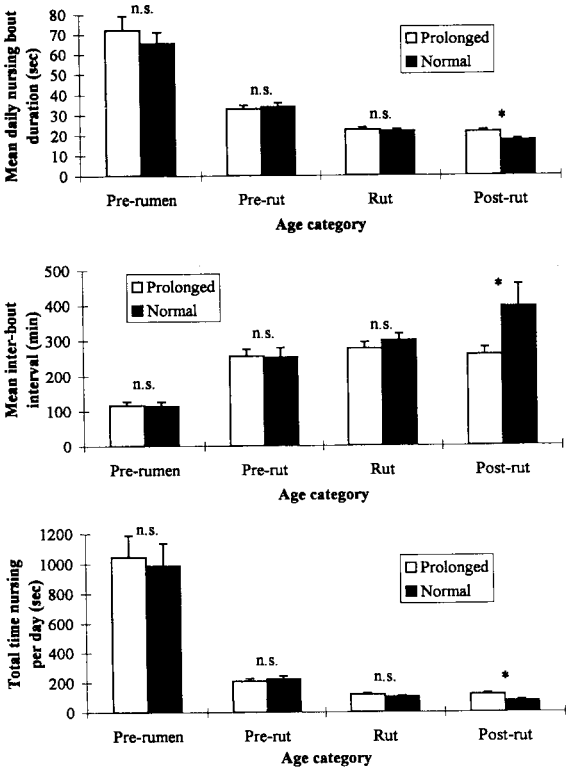

Fig. 1. Comparisons of mean nursing bout duration per day, mean inter-bout interval, and total time spent nursing per day between populations of normal calves and calves with prolonged nursing (n = 4). * = significance $p<0.05$ using distribution-free randomization test. Error bars represent one standard error above the mean. For a definition of the independent variable, see text.

Table 2. Summary of statistical tests using distribution-free randomization (number of randomizations = 10000). Behaviors listed are those for which there were significant ($P<0.05$) differences between calves undergoing normal weaning and those with prolonged nursing. Calves in italics were from different cows.

Normal calf	Calf with prolonged nursing	Pre-rumen function	Pre-rut	Rut	Post-rut
Scooter	Anadyr	n.s.	n.s.	Total time per day	Inter-bout interval
Ole	Annie	n.s.	n.s.	n.s.	n.s.
Andree	Roxanne	Inter-bout interval	n.s.	not available	
Horton	*Sparbo*	Inter-bout interval	Bout duration	Total time per day	All 3 behaviors
Group	Group	n.s.	n.s.	n.s.	All 3 behaviors

Comparisons between the population of normal calves and the population of calves exhibiting prolonged nursing showed similar trends as the pairwise comparisons. There were no significant differences in any behavior during the pre-rumen function, pre-rut, or rut periods (Table 2). However, during the post-rut period, significant differences were found for average duration of nursing bouts, inter-bout interval, and total time spent nursing per day (Figure 1).

Discussion

Our finding significant differences in nursing behavior during the post-rut period supports the hypothesis that female muskoxen use factors other than their nutritional condition to determine their reproductive strategy. After the rut, late-weaning calves nursed longer each day than the normal calves. This is consistent with our prediction that calves needing increased nutrition from the cows may behaviorally signal the cow during the latest time that she may be physiologically responsive to behavioral feedback. We argue that delaying the physiological decision until early in the post-breeding season could be one strategy for minimizing the reduction in a female's lifetime reproductive success associated with producing another calf while still investing in her current calf. The reproductive cost incurred by an error, i.e., weaning of a calf still in need of maternal nutrition, would be a delay in age to first reproduction of the current offspring, and/or poor development of the fetus.

We are unsure of the mechanism by which the female detects that the calf is undernourished. Presumably, calves that are physiologically in need of more nutritional support from the cow return to the cow more frequently in an attempt to nurse. This physiological need could be detected as shorter intervals between nursing bouts (see Loudon & Kay, 1984). Our results support this prediction because the population of calves with prolonged nursing, as well as two individual calves with prolonged nursing, had shorter inter-bout intervals than the normal calves. The calves are successful at getting milk because lactation continued past January. This suggests that the cow has the physiological capability to continue investing in such calves. However, the question as to why all calves cannot make use of this capacity still requires further investigation. This is highly relevant as calves of cows on the HP of nutrition also may be nursed through a second summer (Table 1). Since there have been HP calves undergoing prolonged nursing, the phenomenon appears to be based on individual attributes of the cow and calf. We cannot eliminate the hypothesis that factors other than the mother's nutritional condition influence the occurrence prolonged nursing. Thus, neither calf sex nor the plane of nutrition of the mother appears to be an unequivocal predictor of alternate-year reproduction.

We cannot reject the hypothesis that the calf provides a feedback to the dam that may influence her future reproductive effort. Further examination of the body condition of females that enter breeding pauses, as well as comparisons of the nutritional condition of calves that do and do not receive prolonged milk intake (i.e., maternal care), may clarify physiological benefits and costs of prolonged lactation. A combination of these physical and behavioral measures may serve as a better predictor of when a female will calve in alternate years.

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Direction of escape in reindeer

L. M. Baskin[1] & T. Skogland[2†]

[1]Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky Pr., Moscow, 117071 Russia.
[2]Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway. (Deceased)

Abstract: We tested the hypothesis that reindeer prefer to run uphill and upwind when escaping from man. Groups of wild and feral reindeer in Norway, Svalbard and on Wrangel Island were approached and their behaviour and direction of escape were recorded. Two stages of interaction with man were studied: first flight and final withdrawal. First flights proved to be away from man, upwind and uphill. Most final withdrawals were in the direction reindeer were moving when first observed.

Key words: behaviour, *Rangifer tarandus.*

Rangifer, 17 (1): 37–40

Introduction

To our knowledge, no authors have undertaken analysis of patterns of flight direction by reindeer. However, experienced herdsmen and native hunters often predict in fine degree the direction they expect reindeer to move when they are approached (Washburn & Lancaster, 1968; Baskin, 1970; Spiess, 1979). Understanding reindeer escape behaviour is potentially important for management and for understanding anti-predator behaviour. A herder usually approaches reindeer in a way that will elicit a predictable escape response, and the essential part of herding is being able to predict the direction of movement. Direction and rate of travel of reindeer are influenced by environmental factors (e.g. wind, terrain, relief), the quality of pasture, migratory motivation, position of neighbours, and if disturbed, where they were prior to disturbance. If reindeer consistently use escape routes with certain characteristics we could consider that behaviour as adaptive.

Naumov (1933) described a hunting method used by Nenets people which takes advantage of the tendency for reindeer in small bands, to move downwind of man. If a hunter moves around a herd, the herd in turn tries to move around the man. During whirling, the hunter and the reindeer, gradually come closer until the hunter is within shooting range. Herdsmen report that frightened reindeer usually run upwind and uphill (Baskin, 1974; 1991).

Study areas

Disturbance trials were conducted on two wild (Dovrefjell and Svalbard) and two feral (Forelhogna and Wrangel Island) reindeer populations in

1990–1994. The Dovrefjell wild reindeer population in Norway comprises several interacting subpopulations including those we observed in the Snøhetta and Rondane areas. Both subpopulations consist of about 2000 individuals, and are hunted annually at a sustainable rate of about 25% of the winter population size.

On the high arctic island of West-Spitsbergen, Svalbard, we studied a subpopulation of about 1000 animals in the Reindalen area. There are no large terrestial predators on Svalbard and no indigenous people have ever occupied the area.

The Forelhogna population, east of Dovrefjell in Norway, consists of about 1700 animals. They became feral in the mid-1950s and since 1968 have been hunted annually at a sustainable cropping of 40% of the winter population size (Skogland, 1989).

The reindeer population on Wrangel Island in the Bering Sea has been feral since 1974 when domestic herding was abandoned. In spring 1991, when our experiments were conducted, there were about 3000 animals. To control population size in recent years, reindeer have been herded annually by snowmobiles into a corral and slaughtered. However, more than two-thirds of the these individuals usually escape before reaching the corral. These survivors have become fearful of humans.

Methods

All populations except the Wrangel population were examined in March–early May, a month or more before calving. Wrangel reindeer were studied in June, a month after calving.

After locating a herd in an open area, we approached it upwind in order to present only a visual stimulus. For our trials it was important to consider whether reindeer first detected man by scent or by sight. The response to human scent evokes a stronger reaction because all the animals in herd often become frightened simultaneously. However, whether all the animals are aware of the smell depends on herd size, dispersal of animals in the herd, and wind direction. In contrast, after visual detection, reindeer often try to identify the intruder through other means. The intensity of the stimulus and the activity of reindeer prior to disturbance may also affect the response and the direction of movement. Here, only strong stimuli were used, specifically, walking purposefully toward the reindeer.

In general, we had no knowledge of factors influencing predisturbance behaviour. We sketched each scene, depicting the direction of approach, wind direction, terrain aspect and relief and tracks in the snow. We analyzed two main stages of response: first flight (the acute initial response), and final withdrawal, when reindeer became calmer.

We classified movement direction into six 60° sectors. A herd was considered to have moved upwind if the direction traveled was within 30° of the wind direction (i.e., within a sector of 60°). Runs towards the observer were excluded and treated separately, so only five sectors (totaling 300°) were considered. Therefore, in each trial, reindeer had a 20% probability of running away from man by chance alone. Significance levels were determined using G-tests (Sokal & Rohlf, 1981).

Results

Only in the Svalbard population was the principal flight of reindeer away from man (Table 1). However, away from man directions predominated with combined data for all of populations (Table 1). Sometimes just after the observer had been detected reindeer rushed towards man (Table 2). This was observed most often in the Forelhogna area. In other populations, such approaches were more common after first flight when animals had become more calm.

Moving upwind was typical for first flights of wild reindeer, but not of feral populations (Table 1). Wind direction did not influence the direction of final withdrawal in any of the populations.

In most cases reindeer moved uphill during both first flight and final withdrawal. The direction of reindeer movement prior to disturbance influenced direction of first flight and final withdrawal (Table 1).

Discussion

The hypothesis that reindeer generally fly by running away from man direction was not confirmed. However, experiments differed from situations usually encountered by herdsmen or during predator attacks because the investigator remained in place after reindeer had been alarmed.

The unexpected movements toward man were observed in both wild and feral populations. Reindeer usually moved around a man to a downwind position probably trying to recognize him better. Lent (1966) referred to such behaviour as "investigative behaviour". Juveniles and two-years-

Table 1. Routes of first flight and final withdrawal of reindeer after human disturbance.

Direction[a]	Dovrefjell		Svalbard		Wrangel	Forelhogna		All populations	
	Wild				Feral				
	%	*n*	%	*n*	*n*	%	*n*	%	*n*
				First flight					
Away from man	27.7	36	38.7*	31	33.3 18	21.4	14	31.3**	99
Upwind	50.0*	34	50.0*	30	23.5 17	38.5	13	43.6**	94
Uphill	62.1**	29	27.6	29	37.5 8	55.5**	9	45.3**	75
Along prior course	23.8	21	50.0*	8	40.0 10	66.7**	6	37.8**	45
				Final withdrawal					
Upwind	20.8	24	24.0	25	23.5 17	33.3	12	24.3	78
Uphill	58.8**	17	–	–	75.0** 8	60.0**	10	62.8**	35
Along prior course	37.5*	16	83.3**	12	40.0 10	62.5**	8	54.3**	46

[a] Expected frequency of flight away from man was 20%. The upwind, uphill and along prior courses were 16.7%.

* $P<0.05$. ** $P<0.01$.

old showed the greatest tendency to approach man. Adult females were more wary, preferring to stay in the most distant part of the herd and frequently led the herd away after approaching to within some critical distance. Approaches to man are probably evoked by predominance of curiosity over wariness. Young reindeer are inquisitive while adult females are cautious. Bull groups sometimes approached man but they usually moved downwind and then moved away.

Scenting and observing from an elevated position might be useful for detecting and escaping from predators. However, it is unclear whether it is most advantageous to move upwind or downwind. By running upwind, reindeer may avoid ambush, but by running downwind they can stay in contact with the alarming stimulus. By scenting a man, reindeer could more accurately monitor his movements. As we observed in five experiments, they became frightened if man moved >30° from an upwind position. The previously mentioned hunting "on circle" is based on this behaviour.

Why do reindeer try to continue moving in the same direction after encountering a man? Probably, it reflects an overall movement tendency that is only temporarily suppressed by alarm. Migratory motivation for a specific direction, such as movement toward the sea or to the north in early summer, is often strong. In Norway, where winter pastures are on mountain plateaux, reindeer follow very old routes (Skogland, 1986). In the Rondane and Forelhogna areas, they make regular circles within pastures every 5–6 days. We propose that disturbed reindeer tended to move in these directions.

Table 2. Initial reaction of reindeer to human disturbance.

% approaching man			
Feral reindeer		Wild reindeer	
Forelhogna	Wrangel	Svalbard	Dovrefjell
56.2	33.3	27.2	8.8

We confirmed the tendency of reindeer to flee from man upwind and uphill immediately after disturbance and the tendency to resume travel in the original direction during final withdrawal. Ultimately, taking into account all four factors discussed in this paper, it may be possible to predict the flight direction of reindeer when disturbed by man.

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In defence of "anecdotal data". A case study from a caribou area in West Greenland

Otto Blehr

Department of Archaeology, Stockholm University, S - 106 91 Stockholm, Sweden.

Abstract: The author pleads for a modification of ethological science that allows for the presentation of even tentative hypotheses, based on what is at present disparagingly referred to as "anecdotal data". It is argued that such data are crucial for the neglected study of the habituation of free-ranging large mammals. In such studies of learning, relevant behavioural observations lie outside the ethologist's control, and can only be replicated by further chance encounters. Observations in their anecdotal form should therefore be made available to other ethologists despite their lack of quantifiable data. This would allow for the creation of a pool of more or less unique observations helping to better understand behaviour.

Key words: *Rangifer,* muskox, ethology, habituation, methodology.

Rangifer, 17 (1): 41–49

Throughout June of the five consecutive years from 1985 to 1989 I carried out ethnoarchaeological surveys in the inland area north and northeast of Kangerlussuaq airport, Greenland. This is an important caribou (*Rangifer tarandus groenlandicus*) high density area.

On my return in May/June 1991 I found the situation changed. Descendants of the muskox (*Ovibos moschatus*) which had been introduced in the neighbouring area to the south in the 1960's, was fast approaching the carrying capacity of the area (Riis Olesen, 1993). This had led to some animals spilling over into caribou range at Kangerlussuaq.

My first observation of muskox-caribou interaction was from a mountain ridge facing the small hill where I had my base camp. From a down-wind position two female caribou approached a brink below which a muskox bull was grazing. Making visual contact with the muskox below, the caribou stopped and after some hesitant steps apparently panicked and dashed off, only stopping once to look back. During the following week I had the opportunity on two occasions to confirm similar flight behaviour by other caribou in their encounters with the muskoxen. During the same period I also regularly observed bands of caribou that were fleeing apparently for no obvious reason. However, on the occasions when I backtracked along their path, I inevitably met with the to the area new ungulate. In other words, caribou were observed to behave in precisely the same energy–expending manner towards muskox as they do in their confrontations with wolves (Crisler, 1956) and humans (Blehr, 1997). This should come as no surprise. After Lent (1966) there

seems to be no indication that the escape reactions of caribou differ according to the species causing the alarm (cf. Kelsall, 1957).

The initial contact between caribou and muskox thus seem to have disruptive consequences for the well–being of the former. The duration of this period before the whole population of caribou will be habituated to the presence of muskoxen, and stop wasting energy by fleeing when confronted with the new ungulate is therefore clearly important when evaluating the desirability of introducing muskoxen into an area where caribou are indigenous.

Three weeks of fieldwork in 1991 did not yield any observations of interaction between the two species which could sustain any hypothesis as to the initial phase of the caribou's habituation to muskox. However, I consider an observation in June 1986 relevant to a tentative hypothesis. Then I surprised two male yearlings up-wind of me. Upon discovering my presence they ran off in different directions. I stopped dead as soon as I saw them, and after a short run one of them halted and came back toward me, only to be scared away by the noise of my camera shutter. It returned almost at once, only to be scared away again by the same sound. The fact that yearlings approach in this way is not unusual at this time of the year, recently left by their mothers, they will often approach as long as one does not move and they do not get one's scent.

Unusual about this occasion was that the yearling started to graze about 15-20 meters away from me. It grazed back and forth, maintaining approximately this distance all the time. When after about 40 motionless minutes I again started to walk, it ran away and disappeared over a ridge ahead of me. When I reached the ridge, I observed the same animal grazing upwind of me at a distance of 20-25 meters. Without showing any signs of alarm it continued to graze as I walked by, occasionally looking up at me until I disappeared over the next ridge. The yearling had evidently developed what I consider to be an extraordinary, though undoubtedly temporary, tolerance towards me.

How can this observation, from a period before the muskox had started their expansion into the caribou area, be relevant for for an understanding of the caribou's eventual habituation to muskoxen? Assuming that the escape reactions of caribou do not differ depending on the species causing the alarm (Lent, 1966), I suggest that eventually yearling caribou might start to behave towards the presence of muskoxen in the same manner in which they behaved toward me. In this manner, it is possible that yearling caribou act as "brokers" during the initial stages of contact with another species, and that their tolerance will eventually spread throughout the entire population of caribou. But obviously, many more observations of the interactions between these two ungulates will be necessary before this tentative hypothesis can be strengthened or refuted. This does not, however, diminish the value of initial anecdotal observations. On the contrary, such data can, as illustrated in the above case, serve as a source of inspiration in generating hypotheses about habituation.

My main reason for presenting this example is merely to illustrate the use of so called "anecdotal data". The narrative above is necessarily anecdotal as it recounts a particular observation. Due to its anecdotal character, it is considered to be without scientific value by some biologists. Undoubtedly, rejection of data labelled as anecdotal is a reflection of methods used by biologists within experimental research. There data is not data until it has been presented in tabular form, and provides the basis for statistical analysis of a given hypothesis. I do not question the fruitfulness of this type of scientific approach in experimental research as such. However, as I argue below, I do feel that this fetishism of tabulation has consequences for ethological research.

Ethologists who have this attitude to data will when studying free–ranging animal populations have to confine themselves to counting anything which can be counted, however trivial, simply because such observations can be enumerated and put into tabular form. The number of observations considered necessary for hypothesis testing in these studies are by definition fairly easily obtainable. In other studies however, especially when, as in the above case, it is a matter of studying habituation in free–ranging large mammals, the situation is quite different. Here only persistence and good fortune will enable the observer to obtain the relevant data. This is simply because the observations required remain outside of our control, and therefore can be replicated only by further chance encounters. There is therefore a low probability that sufficient data for hypothesis-testing will ever be obtained, even after years of fieldwork. This might explain why ethologists avoid such studies.

As I pointed out above, such an "either/or" outlook, uncritically adopted from experimental research, naturally constrains the nature of biological

questions asked. What I therefore plead for is a less formalistic and rigid approach. I want to see an ethological science that allows for the presentation of tentative hypotheses on habituation, derived from the "anecdotal data" that is unacceptable at present. Hypotheses that next could serve as an inspiration to the international community of ethologists. And just as important, I would like to see the pool of more or less unique anecdotal observations these tentative hypotheses rest on become, so to speak, common property. In this manner, one might hope that sufficient data for hypothesis–testing within the ethological subfield of habituation could be acquired over time. Or at the very least, that a greater understanding of the processes whereby the behavioural forms under scrutiny are generated would be achieved.

The paramount importance of such a return to "descriptive ethology" can hardly be overestimated. Imagine, for instance, what would happen if the often–cited work by Crisler (1956) was submitted to a zoological journal today. It would be labelled anecdotal by the referees, and subsequently be rejected. Her unique observations on the interaction between wolves (*Canis lupus*) and caribou in the Brooks Range, Alaska, would have been lost to scientists. Another example might be Bubenik's (1975) pioneering study of the significance of antlers in the social life of barren ground caribou. But would any zoological journal today have accepted the article, rich as it is in "anecdotal data" and tentative hypotheses? Would it not also have been labelled anecdotal by the referees, with all the consequences which follow from such damning judgement?

I find this attitude to observations questionable. It appears as if dismissal by biologists of works as anecdotal on the grounds that they are based on non-tabulated data is simply an attempt to avoid scientific debate, rather than a serious criticism of methodology. As an anthropologist, I am baffled by this contempt for observations (cf. Tinbergen, 1963) that cannot be presented neatly in a tabular form which supposedly lends itself to statistical analysis of a hypothesis. In my experience, working with aspects of former lifeways in the Arctic, data has more often than not been of a fragmentary character, and I have therefore to be grateful when I am able to present even meager evidence to sustain the validity of a hypothesis.

I do not believe the outlook is as bleak for ethologists as it is for me. Nevertheless, they should accept that science provides no guarantees that a particular use of method will ensure final tests of truth about anything. So, instead of hankering for the respectability of what is seen as "hard" or experimental science, I would like to see students of animal behaviour free themselves from what I have labelled the "fetishism of tabulation", and instead to stand up to the challenge presented by the use of the so–called "anecdotal data". Not the least since data of this kind, as noted above, will be of paramount importance in the neglected study of habituation of free-ranging large mammals.

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Energy-expending behaviour in frightened caribou when dispersed singly or in small bands

Otto Blehr

Department of Archaeology, Stockholm University, S-106 91 Stockholm, Sweden.

Abstract: The behaviour of single, and small bands of caribou (*Rangifer tarandus groenlandicus*) when confronted by humans was compared with the energy–saving behaviour zoologists have ascribed to caribou in encounters with non-hunting wolves (*Canis lupus*). When confronted by me, or upon getting my scent, caribou ran away on all occasions. Their flight was occasionally interrupted by short stops to look back in my direction, but would continue on all occasions until they were out of sight. This behaviour is inconsistent with the one ascribed to caribou by zoologists when the intruder is a wolf instead of a human. In their view, the caribou stop their flight soon after the wolf gives up the chase, and accordingly save energy owing to their ability to distinguish between hunting and non–hunting wolves. However, small bands of caribou, as well as single animals, have never been observed to behave in this manner. On the contrary, the behaviour of caribou in such encounters is known to follow the same pattern as in their encounters with humans. Energy–saving behaviour is, however, sometimes observed when caribou become inquisitive about something in their surroundings. They will then readily approach as well as try to get down–wind of the object. When the object does not induce fear, it may simply be ignored, or charged before the caribou calm down. The effect of this "confirming behaviour" is that energy which would otherwise have been spent in needless flights from non-predators is saved.

Key words: *Rangifer,* wolves, anti–predator behaviour, energy expenditure, Greenland.

Introduction

Blehr (1990) discussed different techniques traditionally used by hunters of caribou and wild reindeer (*Rangifer tarandus*). The efficiency of hunting techniques was evaluated in terms of the evolutionary adaption of caribou/wild reindeer to predation by wolves (Mech, 1970; Bergerud, 1974). This includes the way in which caribou frequently stop to look back during flight from their traditional enemy. This behaviour was explained by the fact that a wolf cannot catch a healthy animal (Pruitt, 1965; Mech, 1970), and so caribou/wild reindeer stop at intervals to check whether they are still being pursued, because they apparently want to save energy (Blehr, 1990).

Since my ethological studies have been in areas where wolf is not part of the fauna, I have not personally had the opportunity to observe how caribou behave toward this predator. Nevertheless, I wish in the following seriously to question the existence of the energy–saving behaviour in caribou that Pruitt and Mech claim to exist. A claim that I took at face value when I wrote the above article. I have repeatedly observed single animals and small bands of caribou which have been frightened and have started to run away, only to make frequent stops to look back in my direction. But, crucial for our discussion here, the flight would continue after each stop until the animals were out of sight, even on the occasions when I stood quite motionless. The caribou's behaviour toward me thus differs radically from the apparently energy-saving strategy that Pruitt and Mech believe it to adopt when confronted with a non-hunting wolf.

Study area

The study was carried out in the high density caribou area located in the inland region north and northeast of Kangerlussuaq air port (ca. 67°N; 50°W), Sisimiut municipality, in the low Arctic area of West Greenland, roughly 700 km² (Fig. 1). Geomorphically it is rather uniform, with gentle east-west trending mountain ridges, valleys and lakes. In the north and east the mountain formations reach 550-650 m above sea level.

Dwarf scrub heaths, meadows, steppe and grassland characterize the vegetation. A notable feature are the innumerable caribou trails between the coast and the Inland Ice. The climate is continental, average January -18°C for January, and July +10,5°C. The annual precipation is less than 200 mm, whereof half falls between July and October (Bøcher, 1980).

Methods

Data on energy–saving behaviour of frightened caribou was looked for during ethnoarchaeological surveys throughout June in five consecutive years, 1985 to 1989, and a three week period in May/June 1991, by one obser-

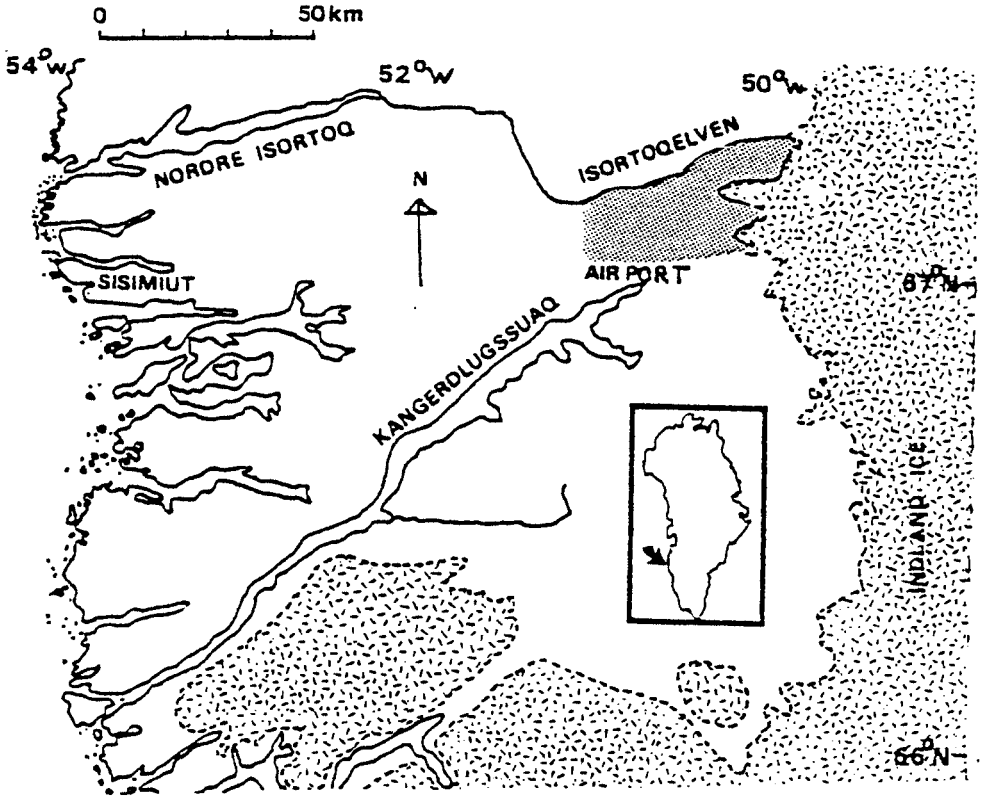

Fig. 1. The area of study (shaded) north of Kangerlussuaq airport, West Greenland.

ver travelling on foot looking for exceptions to the stereotypical flight behaviour. On the one occasion when an animal did not follow this pattern, the deviant behaviour was documented in detail (see Blehr, 1997). All encounters during the period June 15 to June 30, 1989 were recorded in order to provide an idea of the size and composition of the caribou bands during this period of the year.

Results and discussion

The fieldwork was carried out at a time of the year when most of the caribou were scattered throughout the area singly, or in bands with less than ten members (Table 1). My encounters with animals were therefore numerous. During a two week period in June 1989, I encountered totally 420 animals, not counting neonates (cf. Blehr, 1991). Average encounters a day were 8,3, with an average band size of 3,4 caribou.

Such small bands are typical of the ones found each spring before the forming of the large post-calving aggregates at the end of June or beginning of July. Bands of up to 30-40 animals where also occasionally encountered not deviating in flight behaviour from the one I detected in smaller bands. This number is the upper limit for what I will label "small bands" although de Vos (1960) found that the activity pattern in bands with less than 50 individuals appeared to be more closely coordinated than in larger bands.

Table 1. Age and sex composition of the groups of caribou encountered between June 15 and June 30, 1989. N: number of groups, M: all males, FFX: females/yearlings and females with neonates, MX: mixed groups (i.e., some mature males as well as mature females), Y: all yearlings.

	Number of animals		
Group Type	median	range	*n*
M	1	1– 3	12
FFX	3	1–26	66
MX	8	5–11	2
Y	1	1– 4	44
			124

The behaviour of caribou towards man in terms of flight or flushing distance are considered to vary considerably both within and between populations (Kelsall, 1957; de Vos, 1960; Lent, 1966; Bergerud, 1974; Bubenik, 1975). I have estimated this distance to be roughly 200-400 m. during my walkabouts. However, like Kelsall (1957), I found that the distance could vary

considerably. Obviously, the conspicuous lack of contextual data of relevance for the flushing distances given by the different authors means that their findings should be used with the utmost caution for comparative purposes. Be this as it may, what is of crucial importance here is what the caribou do after the initial flight. Do they stop "to save energy" when no longer pursued, or do they keep on fleeing until they are out of sight?

Leaving aside for the moment variations in the caribou's behaviour due to their age or sex, I found that their reactions to my presence, on the occasions when they were unable to scent me, usually followed the same general pattern. If I kept on walking after having been spotted, the caribou would immediately take fright and make a short run before stopping to look back. While facing me some would urinate, while others would move slowly back and forth on the same spot, or towards me, with a characteristic high-stepping gait. Then, sooner or later, one or more of the caribou would panic and dash off, followed, usually in tight formation, by the others. Though they would stop one or more times to look back, and their speed would eventually slow down to an easy trot, their flight would always continue until they were out of sight. This even proved to be the case when I was moving away from them.

On those occasions when I stood motionless, the initiative to flee would be taken by the animal that had become aware of me. The lag between alert and flushing time was also somewhat longer when I stopped walking once I had been spotted. Apparently less alarmed, they would run off in a looser formation (cf. de Vos, 1960). It also happened that when only a single animal discovered my presence both it and the rest of the band simply drifted away while grazing, looking back in my direction now and then until they disappeared out of sight. Let me add that this reaction to my presence was very rare. In most cases, the uneasiness indicated by the alarm pose of the caribou that had first sighted me would communicate itself to other animals which would then become aware of me. Despite the fact that I stood motionless, they would bunch together, and take flight followed by the rest of the band.

Except for cows with neonates, the caribou often tried to get down-wind of me after their initial scare. As a rule, one or more of them would succeed in this, but usually only after several fruitless attempts, as they tended to turn back too early. The first animal to reach a down-wind position would normally make one or two excitation jumps before it took flight in the customary manner.

While I have stressed the paramount role played by scent as a flight releaser in caribou that are both visually and olfactory aware of an intruder (cf. Murie, 1935; Bergerud, 1974), Kelsall (1968) has questioned their ability to perceive by smell alone. He regards each attempt the caribou make to go down-wind of whatever has alarmed them as successful. For him, their behaviour illustrates that caribou doubts the evidence presented by their sense of smell.

Bergerud (1974) argues however that scent seemed to be the most discerning sense which could release immediate flight behaviour prior to visual contact (cf. Murie, 1935). This might be true on most occasions, but I have observed animals, which, having scented me hesitated uneasily for a few minutes before finally fleeing. When camping in topographical bottlenecks, I have also observed that the animals' urge to keep to their initial route of travel was apparently strong enough to overcome the fright induced by my scent. Once downwind of me, they would immediately stop in their path and stretch their heads forward into the wind to take in my scent better. After the usual high-stepping gait on the same spot, urinating, and more head stretching, the animals would inevitably back track for a distance of anywhere between five and a couple of hundred meters, only to return in order to take in my scent again. In this manner, the animals could trot back and forth undecidedly for up to 15-20 minutes, before finally galloping away at full speed through the area downwind of me. Once beyond my scent, they stopped occasionally to look back in my direction in the usual manner, but would keep on fleeing until they passed out of sight. Other situations have also been recorded when scent has not triggered flight behaviour (Kelsall, 1957; de Vos, 1960; Bubenik, 1975).

Occasionally, caribou would insist on keeping to their route of travel even when I encountered them outside bottlenecks. This occurred when they were visually aware of me, but did not have my scent. After the initial bunching together, and a rush, usually back along their route, they would return at full gallop, making only a small detour around me (cf. Kelsall, 1957). On the occasions when my appearance had split a band, and I was blocking their line of travel, only small detours were made around me when the stimulus to rejoin other members of the band became dominant.

Whereas small homogenous bands rarely split when confronted with humans, the opposite seemed to be the rule on the two occasions I encountered post–calving aggregates of 300-400 animals that had formed. In such a band, animals in some of the scattered groups at the outer fringe of the aggregate would be the first to become aware of my approach. Their alarm pose, followed by the usual bunching together and subsequent rush, served to trigger off flight behaviour among animals in the neighbouring groups (cf. Lent, 1966). Neonates and cows which had become separated from each other in the tumult, rushed back and forth searching for each other. In this manner, panic spread from group to group through the whole band, resulting in smaller or bigger aggregates of caribou running hither and thither, depending upon where they had received the flight stimuli, or, if they were calves or cows, where they had last had been together. Sometimes single animals or groups stopped to watch the behaviour of others, before they again panicked and rushed off.

The lack of organized action was conspicuous (cf. de Vos, 1960). Only when most of the animals had become aware of my whereabouts did their movements become coordinated and directed away from me. However, before this stage was reached the large group of yearlings, which are such characteristic feature of a post–calving aggregation, had focused all their attention on me. Seemingly unafraid, the 20-30 yearlings in such groups would repeatedly make runs towards me, first stopping when the distance separating us was down to 15-20 meters. If I then stopped walking, they would stand bunched together and watch me intensely for half a minute or more. Some of them would then take fright and make short hesitant rush away from me followed by the rest. On the occasions I kept on walking, their stops were shorter, but regardless of my behaviour they soon returned. In fact, it appeared as if they never got tired of following me in this manner. First when the other members of the band had coordinated their flight away from me did their urge to follow them take precedence, and I would be left alone. It is tempting to suggest that it was such large groups of yearlings that Kelsall (1968) had in mind when he assumed that caribou seem to doubt the evidence offered by their sense of smell.

Considering the gregarious nature of the caribou, the flight pattern described above for post–calving bands appears mainly to be the result of the numerous contradictory stimuli the animals receive from their fellow–members when they are together in such large aggregates. No wonder, then, that this pattern differs from the one found in small bands where the situation is more easily surveyed, and thus makes the stimuli the animals act upon more congruent.

Since my field work was carried out for the most part in the period prior to post-calving aggregates, one could argue that the characteristic behavioural pattern I observed largely reflected the flight pattern of cows with neonates, which are known for their wariness at this time of the year. But apart from the fact that they never dared to approach me or go downwind of me before fleeing, and that they were the first animals in mixed bands actually to take flight (cf. Kelsall, 1957; de Vos, 1960; Lent, 1966; Bergerud, 1974), their behaviour when it comes to energy expenditure did not otherwise deviate from the general pattern I have described above. Another possible objection to the general conclusions I draw from my observations could be that they are based solely on the flight behaviour the caribou exhibit in June. Yet, observations by others confirm the general validity of my findings (Kelsall, 1957; Lent, 1966). In fact, caribou in summer and autumn may even be more easily frightened by humans than I have maintained (Kelsall, 1957).

That cows with neonates in mixed bands were the first to flee was not the only behavioural difference related to sex and age. Yearlings, who had just been left by their mothers upon the births of the new calves, would occasionally come trotting all the way up to me. But for this to happen I had to be downwind of them and take care to stay motionless after having been spotted. As for cows, they are on most occasions significantly more wary than bucks (Murie, 1935; Bergereud, 1974). Nonetheless, I have experienced situations when the caution of lone adult bucks has surpassed that of cows (cf. Kelsall, 1957).

It should be emphasized strongly that though differences were found in the caribou's behaviour pattern in the initial phase of their encounter with me, depending on their age and sex, these differences are of no relevance for my argument here. Of paramount importance, however, is what the caribou actually did after their initial rush away from me: And on this point, as we have seen, I found a clear pattern: Regardless of their age and sex I found that the single animals and small bands would eventually save themselves by flight. A flight only occasionally interrupted by short stops to look back in my direction. Even yearlings, who I found to display the most erratic behaviour of all age groups in the initial phase of their encounters with me, ended up by adopting the same stereotypical flight pattern as their elders.

How does this flight pattern accord with, or differ from the way caribou behave towards wolves which are not stalking or pursuing them? Amazingly, few first hand observations of such confrontations are documented in the literature. Yet, thanks mainly to the observations of Crisler (1956), I believe we are able to answer this question. Among her observations of wolf–caribou interactions in the Brooks Range of Alaska in 1953–54 was one where the wolf immediately stopped and sat down as soon as the cow checked her flight to take a look back at her pursuer. The caribou's behaviour may appear suicidal, but as a wolf apparently "prefers not to be eyed when approaching its prey" (Crisler, 1956:340), it stops its stalking once the caribou has sensed it. And also, since the wolf depends on the stimulus of a running animal before making a rush for it (Mech, 1970), the initiative is left with the caribou. This is obviously to the latter's advantage, since it means that the distance between wolf and caribou is frozen up to the moment when the caribou decides to flee. Thus, when the cow took off again, with the upward launch so characteristic of frightened caribou, the wolf followed it. Crisler repeatedly observed the caribou behave in this hesitating manner in encounters with wolves, a behaviour which is identical with the one the caribou generally display when scared by a human they cannot scent. Furthermore, the episode referred to above is also of special interest since the upward launch with which the cow took off tells us that it was really scared. Having taken real fright, its behaviour was no longer hesitant: It kept on running, even after it was no longer pursued. This was not an unique occurrence. On the same day, Crisler had twice observed other single cows which kept on running steadily in the same manner, even after their pursuers had given up the chase (Crisler, 1956).

From Crisler's documentation, it appears that single caribou are quite unable to distinguish between wolves

that are exhibiting appetitive searching behaviour and those that are not. The general validity of Crisler's findings is supported by Murie's observations of the flight behaviour of caribou in small bands on Mount McKinley in June 1939 and 1940 (Murie, 1944). In terms of energy expenditure the flight pattern of caribou in such bands, when confronted with non-hunting wolves, is identical to that displayed when they confront humans (Kelsall, 1957; Lent, 1966).

As Lent (1966) has pointed out, there seems to be no indication that the escape reactions of caribou differed according to the species causing the alarm (cf. Kelsall, 1957). This view is also confirmed by my observation of caribou-muskox interaction in 1991. In that year, the caribou north of Kangerlussuaq for the first time had regular contact with animals from the muskox population which had been introduced in the neighbouring area to the south in the 1960's. On three occasions I had the opportunity to witness these encounters and observe how the caribou behaved in precisely the same energy–expending manner towards muskox as they did in their encounters with me. I also had my first opportunity regularly to meet with bands of caribou that were fleeing apparently for no obvious reason. However, on the occasions when I backtracked along their path, I inevitably met with the new ungulate, which indicate that the caribou kept on fleeing long after they had lost sight of the muskox.

Taking into consideration the evolutionary adoption of the caribou to predation by wolves it should come as no surprise that the flight behaviour of the former is found to be the same towards humans and other species that cause alarm as it is towards the wolf. Accordingly, the energy-saving behaviour Pruitt (1965) and Mech (1970) ascribe to caribou in encounters with non–hunting wolves seems not to rest on empirical foundations.

But how are we to interpret statements that seem to support energy–saving behaviour? For example by Murie (1944), who maintain that caribou generally seem not to be worried much by wolves unless chased? Since we do not know all the stimuli influencing the escape behaviour of caribou, we cannot adequately explain all their reactions when face-to-face with a predator (cf. Lent, 1966). But if we wish to explain as many of these reactions as possible, we might start by differentiating between the content and magnitude of the stimuli they receive in different contexts. From my own experience an obvious distinction is between animals in large and small bands. Surprisingly, although band size is regarded as relevant in other contexts (Kelsall, 1957; de Vos, 1960; Bergerud, 1974; Whitten & Cameron, 1986), it has been ignored when it comes to the study of the caribou's flight behaviour. This is also true in Murie's work, but thanks to his documentations we are able to ascertain whether differences in behaviour were the result of membership of large or small bands (Murie, 1944). The statement above from Murie (1944) was synthesized from observations of caribou that are members of large bands where the flight stimuli they receive from other caribou are either lacking or inconsistent. If this is correct, then the hesitant behaviour observed among caribou in large bands in the presence of wolves cannot be interpreted as support for the energy-saving hypothesis. Instead, it must be seen as generated from the numerous contradictory stimuli the animals receive from their fellow–members when they are together in such large aggregates.

Finally, although Kelsall and I disagree as to the relative importance of the sense of smell as a flight releaser, we do agree as to why a caribou readily approaches, as well as tries to get down-wind of an object that arouses its curiosity. Such behaviour obviously indicates that it wants to investigate. Should the object turn out to be harmless, then it can be chased away, or simply be ignored. The effect of this "confirming behaviour" is that energy which would otherwise have been wasted in headless flights away from non-predators is saved. In July 1978, during an earlier visit to the area, I witnessed how a small band of seven caribou grazing on a mountainside stampeded when a hare (*Lepus arcticus*) suddenly appeared at very close range. When they stopped after a short run, one of them came back and charged the intruder, which ran away. The caribou then resumed grazing (cf. Thomson, 1975). Thus, the frightened caribou does indeed exhibit energy-saving behaviour. But, as this example illustrates, the situations when such behaviour result in energy actually being saved are quite different from the ones found when they are facing wolves.

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Editorial to Blehr's conference article with appendix

As an anthropologist, Blehr has been studying for years the relationship between caribou as a prey animal and man as a predator. A relationship that, besides the weapon technology of the hunter, has been determined by the possibilities and limitations inherited in the flight behaviour of the caribou. While carrying out an ethnoarcheological survey in a caribou high density area in West Greenland, Blehr used the opportunity to study flight behaviour of caribou as well.

On the basis of his findings, Blehr wrote the article «Energy-expending behaviour in frightened caribou when dispersed singly or in small bands», which to his amazement he found impossible to get published in a zoological journal. The referees were almost unanimous in their denouncement of the article as anecdotal, and thus, it in their view the article was without scientific value. Provoked by this he wrote «In defence of «anecdotal data». A case study from a caribou area in West Greenland» presented as a lecture in Fairbanks.

When Rangifer now chose to publish not only the latter paper that Blehr presented at the 2nd IAU conference in Fairbanks in 1995, but also in an appendix the article that gave the background for his conference lecture, it is in the belief that Rangifer as a journal should be more open for scientists other than biologists (cf. text on the journal's last cover page). This attitude is in accordance with what the Nordic Council for Reindeer Research wants the journal to be. Therefore, Rangifer is in certain cases open for papers not following the accepted or common natural scientific style. The Blehr case (shortened lecture article and appendix) gives an additional opportunity to illustrate the research method he pleads. His contribution will probably incite the discussions on both scientific method and editorial style.

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