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Introduction

At the Fourth International Reindeer/Caribou Symposium, held in Whiterhorse, Canada, 1985, Sweden declared it's intention to host the next International Reindeer/Caribou Symposium. A meeting with delegates from the participating countries was held and the Swedish offer was unanimously accepted. At the same meeting the experiences from earlier symposia were critically evaluated in order to achieve the best prerequisits possible for symposia to come. Some of the principal views declared were not to split the sessions in different meetings and in addition to concentrate more of the scientific presentations on poster exhibitions and poster sessions. The Fifth International Reindeer/Caribou Symposium, held August 18-22 1988 in Arvidsjaur, Sweden, was thus in principal arranged according to the views expressed in Whitehorse.

Arvidsjaur was chosen as site for the Symposium as it has long been a centre for reindeer herding and research activities. The excellent localities of the Norrland Dragon Regiment (K 4) put at our disposal and the hearty support of the township of Arvidsjaur and the Sami villages made the arrangements possible. In Arvidsjaur the USSR declared it's intension to arrange the next International Reindeer/Caribou Symposium to be held in 1991. The proceedings you now hold definitely close the Fifth International Reindeer/Caribou Symposium.

Claes Rehbinder
Secretary General

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The consequenses in Sweden of the Chernobyl accident.

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The accident in unit 4 of the Chernobyl nuclear power plant occurred at 1.23 a.m. on 26 April 1986. Substantial amounts of the radioactive material were released into the atmosphere, for example about 10 to 12% of the core content of radiocesium. Due to the high temperature the plume rose to high altitudes - several hundreds of meters to more than 1,000 meters.

The plume direction in the early phase was towards Scandinavia over the Baltic states at a height of about 1,500 m. The plume reached Scandinavia on 27 April but was not detected before the morning of 28 April when the personnel contamination control at the Forsmark nuclear power plant in the central part of Sweden gave the alarm. During the night between 28 and 29 of April a heavy rainfall occurred in some regions of the central and northern parts of Sweden. Much of the radioactive material in the air was washed out and thus deposited on the ground or vegetation. In the northern part of the most contaminated region in Sweden there was still snow on the ground and ice on the lakes. In the southern part the grass had just started to grow. The interception on vegetation at farmland was therefore rather small and most of the radioactive material was deposited on ground. In the woodland and mountain regions more of the radioactive material was intercepted by the coniferous trees and by the dwarf shrubs, mosses and lichens.

The ground deposition of the radiocesium in Sweden was measured by aircraft equipped with 4 NaI(Tl) crystals. The measurements were performed by the Swedish Geological Company (SGAB) and they also produced a map of the ^{137}Cs deposition expressed as Bq m^{-2}(Figure 1). The deposition in Sweden is very heterogeneous. In most of Sweden the deposition is below 3,000 Bq m^{-2}. Along the Baltic coast from Gävle up to Umeå there is a rather high ^{137}Cs deposition. In some areas there are more than 60,000 Bq m^{-2}. In a rather large part of Sweden from south of Umeå to the mountain region in the western part of Sweden there are ^{137}Cs depositions of more than 30,000 Bq m^{-2}. The main problems with radiocesium for reindeer husbandry in Sweden is within this region. The total ^{137}Cs fallout in Sweden during the 1960s was about 3,500 Bq m^{-2}.

The Swedish Radiation Protection Institute decided in May 1986 on the intervention level for radiocesium. The primary aim was to restrict the intake of radiocesium by food to people in Sweden so that the additional dose equivalent did not become higher then 1 mSv per year. For single years 5 mSv could be accepted. This is in accordance with the recommendation of ICRP. The Swedish intervention level was placed at 300 Bq of ^{137}Cs for all food including reindeer meat. In spring 1987 the level was changed to 1,500 Bq of ^{137}Cs per kg for reindeer meat as well as for game animal meat, fish, berries and mushrooms. A radiation dose of 1 mSv per year corresponded in 1987 to an yearly intake of about 50,000 Bq of ^{137}Cs calculated with the^{137}Cs/^{134}Cs ratio of 1987. During 1986 the ^{137}Cs activity concentration in samples from nearly all reindeer slaughtered in Sweden were determined to guarantee that no reindeer meat found in shops had ^{137}Cs activity concentration above the intervention level.

The ^{137}Cs activity concentrations in various kinds of animal material show very large variations. In reindeer, ^{137}Cs activity concentrations range form 100 to 40,000 Bq kg^{-1}, in moose from 20 to 3,000 Bq kg^{-1}, in roe-deer form 20 to 12,000 Bq kg $^{-1}$ and in cows' milk form nearly zero to 200 Bq kg^{-1}. These are mean values which have been found in a relatively large area. Higher values can be found in individual animals.

The main problems still existing in Sweden as a result of the Chernobyl fallout are associated with the reindeer and game animals, especially roe deer, moose and fish. From the radiation protection point of view, the remaining problem in Sweden due to the Chenobyl accident is that many people within the most contaminated regions eat large quantities of meat form reindeer, game animals and fish. Some of them will receive a dose equivalent of around 5 mSv per year due to intake of radiocaesium by foodstuffs. The problem will be very long-lasting, in fact no decrease in the ^{137}Cs activity concentrations have been found in, for example, roe deer and moose during the first 3 years after Chernobyl.

Key words: radioactivity, fallout, radiocesium

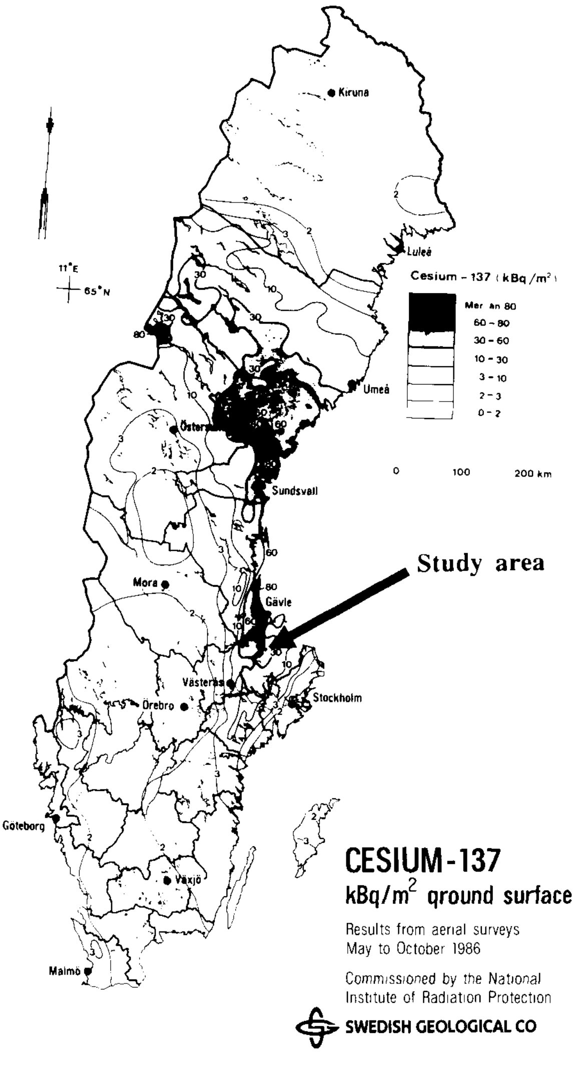

Fig. 1. The deposition of ^{137}Cs (kBq per m^2) in Sweden. Measurement performed by the Swedish Geological Company.

Key note address:

^{137}Cs in reindeer forage plants 1986—1988

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The entire Swedish reindeer area was to some extent contaminated by radionuclides after the accident at Chernobyl, USSR, in 1986. As much as 10% of the total emission of ^{137}Cs + ^{134}Cs may have hit Sweden, mainly as wet deposition. This took place over eastern and northern Sweden in connection with precipitation on April 28—30. Rain fell on the major part of the area and only in northernmost Sweden was the precipitation snow. No significant differences in estimated ^{137}Cs activity concentrations in the precipitation, whether rain or snow, were, however, found (Persson, Rode and De Geer, 1987).

The fallout hit the reindeer area when most of the ground, except knolls, southfacing slopes, river banks, etc ., was still covered with a more or less impenetrable layer of hard snow. Thus, arboreal lichens might have been the first forage plants with high activity concentrations of radionuclides that reindeer encountered. For example, in northern Jämtland, *Bryoria fuscescens* with 120,000 Bq ^{137}Cs $\cdot$kg^{-1} d.m. was found at Brattliden and at Torsfjärden the activity amounted to 34 000 on June 4 (Eriksson et al. 1987).

Most soils within the reindeer area have low pH, often high organic content and minor amounts of clays and minerals, which are important for binding radiocesium (Svenska Sällskapet för Antropologi och Geografi, 1953—1971). Thus, significant amounts of radiocesium are also found in vascular plants. At Tällvattenmon, county of Västernorrland, heather *(Calluna vulgaris)* with an activity concentration of ^{137}Cs amounting to 32 000 Bq$\cdot$ kg^{-1} d.m. was sampled on July 1986. At Mossavattnet, conty of Västerbotten, rhizomes of sedges *(Carex spp.)* were found with 12 000 Bq of ^{137}Cs $\cdot$ kg^{-1} d.m. on October 10 (Eriksson et al. 1987).

The task of the Reindeer Section is to concentrate on applied research directed towards the reindeer trade. Hence, the botanical work was from the beginning focused on monitoring ^{137}Cs in plants and parts of plants of direct importance to reindeer as forage.

A basic material consisting of *(Cladina arbuscula)*, heather and crowberry *(Empetrum hermaphroditum)* was sampled from almost all over the reindeer area with emphasis on the winter range. The plants were dried, ground and measured with a Ge (Li) detector by the Swedish Defence Research Establishment, Dept. of NBC Defence, Umeå (Eriksson et al. 1987).

During the fall, the Sami communities were offered a sampling scheme of their own by the National Board of Agriculture. About twenty lichen samples, mainly *Cladina arbuscula*, were sampled in most communities. Totally more than seven hundred samples were treated and measured by the Dept. of Radioecology, Swedish Univ. of Agr. Sciences.

Only the top third of the lichens was collected, as grazing is usually concentrated to this part of the plant. Also, the tops of the lichen thalli usually store the highest concentration of cations, for example ^{137}Cs (Lidén and Gustafsson, 1966, Tuominen and Jaakola, 1973).

From vascular plants, mainly annual shoots were sampled much for the same reason as for the lichen sampling.

Since ^{137}Cs activity concentrations in reindeer lichens *(Cladina spp.)* growing close together do not differ very much (Tuominen and Jaakola, 1973), all data on ^{137}Cs activity concentrations in reindeer lichens were processed and a map was produced, by means of floating mean values and block—kriging, showing the distributing of ^{137} Cs activity concentrations in reindeer lichens throughout the reindeer winter range (fig. 1).

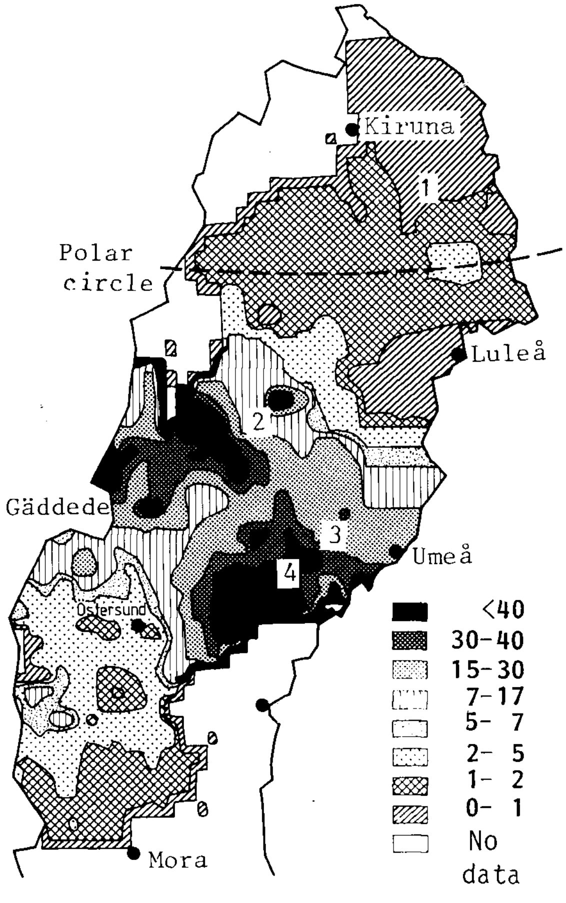

Figure 1. Cs—137 in reindeer lichens (*Cladina* spp.) kBq/kg DM. Permanent study plots: 1. Ullatti. 2. Rackosjön. 3. Bjurholm. 4. Kubbe.

The general pattern is much the same as the one found on the standard maps based on aerial surveys showing the ^{137}Cs activity deposition (SGAB, 1986, these proceedings, page 10). The peak areas, with ^{137}Cs activities in reindeer lichens well above 40 kBq · kg^{-1} DM. were found around Lake Vojmsjön, county of Västerbotten, in the NW corner of the county of Jämtland and in the interior part of the county of Västernorrland. It should also be noted that the whole of the county of Norrbotten is affected to some extent but, except for the SW part along the Skellefte river, not enough to bring reindeer meat above the action level.

Comparison between radiocesium activity concentration in the basic set of sampled forage plants of 1986, i.e. *Cladina arbuscula*, heather and crowberry from 130 sites revealed that the load in heather was about 40% ± 5 and that of crowberry was 20% ± 3 of that in *Cl. arbuscola*.

Activity concentrations of ^{137}Cs in forage plants growing on permanent plots (fig. 1) were measured in 1986—1988.

Among lichens, *Cladina arbuscula* is paid special attention. As compared to the 1986 level, status quo prevailed at three sites — Bjurholm, Rackosjön and Ullatti. A 40% decrease was noticed at one site — Kubbe. This decrease was even more pronounced in *Cl. rangiferina* (60%). The main difference between the status quo sites and Kubbe, is that Kubbe started out in 1986 with much higher ^{137}Cs activity concentrations in the ground vegetaion.

At one site — Rackosjön —, several samplings of *Cl. arbuscula* were carried out during the summer of 1987. (fig 3.) They revealed considerable fluctuations in the Cs—load. The low value (9304 ± 1160 Bq ^{137}Cs/kg), about 65% of the peak value, was registered at the height of the summer, when the wather had been rather dry for a period of time, whereas high concentrations were measured during periods of rainy weather. Uneven distribution of radiocesium within the sites, and fluctuations of radiocesium within the thalli due to precipitation may jointly be responsible for the fluctuating values. (Tuominen and Jaakola, 1973.)

Activity concentrations in bilberry *(Vaccinium myrtillus)* and crowberry were studied at the Bjurholm and Ullatti sites. On both sites there was a slight tendency towards raised levels from 1986 to 1988, bilberry having a slightly higher activity concentration of ^{137}Cs (fig. 2.)

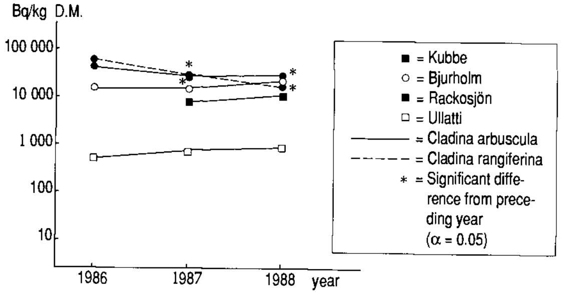

Figure 2. Cs—137 in reindeer lichens (*Cladina arbuscula* and *Cl rangiferina)*, 1986—1988

In 1986 and 1988 wavy hairgrass, *(Deschampsia flexuosa)* fire weed *(Epilobium angustifolium)* and buck—bean *(Menyanthes trifoliata)* were sampled at Rackosjön and measured for their activity concentration of ^{137}Cs. A statistically significant decrease of 57% (wavy hairgrass), 34%r (fire weed) and 14% (buck—bean) was registered.

Garmo *et al.* have monitored the activity concentration of ^{134}Cs + ^{137}Cs in some forage plants in Griningsdalen, Norway in 1986—1988.

A comparison shows:

	Garmo et al.	Eriksson
Wavy hairgrass	—56%	—57%
Buck-bean	—14%	—14%
Bilberry	—79%	± 0

Notwithstanding that the Norwegian figures show ^{137}Cs plus ^{134}Cs, the figures concerning wavy hairgrass and buck—bean are fairly similar. It is quite surprising then that the reduction of the activity concentration in bilberry differs so much.

During the summer of 1987 wavy hairgrass, fire weed and buck—bean were sampled repeatedly at Rackosjön. From a peak value of 1670 ± Bq · kg^{-1} DM. hairgrass decreased 88% in two months. Fire weed started out at 475 Bq · kg^{-1} DM. and dropped to a minimum of 119 ± 31 Bq in one month. A trend towards a secondary maximum was seen in wavy hairgrass, that starts its next year's growth in late summer. This second rise in activity concentration might have been supported by heavy rains in late July—August (fig. 3).

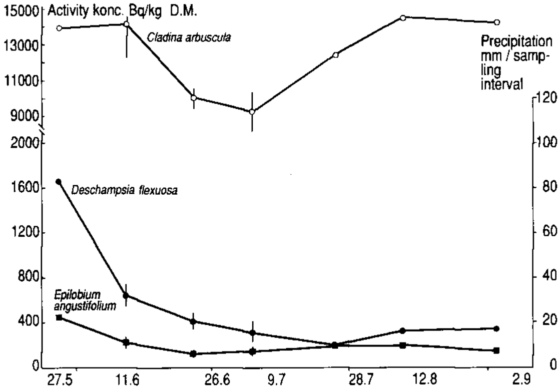

Figure 3. Temporal variations in Cs—137 activity concentration in *Cladina arbuscula, Deschampsia flexuosa* and *Epilobium angustifolium.*

Buck—bean was sampled on June 25 and on July 14. The rhizomes were, following Sjörs (1987), divided into annual shoots of 1985, 1986 and 1987 and measured. The shoots of 1985 and 1986 remained stable at around 1800 ± 130 Bq · kg^{-1} DM., whereas there was a decrease in the 1987 shoots from 3880 ± 490 Bq · kg^{-1} DM. to 1700 ± 160 Bq · kg^{-1} DM., i.e. 55% (fig. 4).

According to the plan, the permanent plots will be harvested at regular intervals during

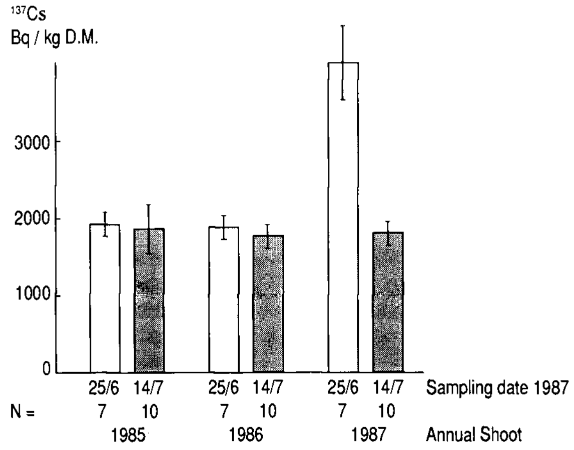

Figure 4. Cs—137 in annual shoots of buck—bean (*Menyantyhes trifoliata*).

years to come, providing data on the effective halflife of ^{137}Cs in important forage plants. However, it is now imperative to find out the transfer factor of ^{137}Cs from plant to reindeer meat during different seasons. It will then be possible to plan actions aimed at minimizing radiocesium in reindeer meat.

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Radiation effects in reindeer

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A considerable part of the Swedish and Norwegian areas used for reindeer herding was contaminated by radioactivity from the accident on April 26, 1986 at the Chernobyl nuclear power plant. Both winter and summer grazing areas were affected, mainly by radiocesium. Limited areas in the Swedich mountain region were found to be contaminated by more than 80 kBq/m^{2}of ^{137}Cs, but generally 40 to 60 kBq/m^2 were found. The levels of ^{137}Cs in lichens growing in such areas were up to 120 kBq/kg dry matter (Eriksson et al., 1987) but generally the levels were lower, around 30 kBq/kg d.m. Regular sampling of reindeer meat in the first year after the accident (NFA 1987) confirmed the seasonal variation observed earlier in radiocesium content of the muscular tissue (Lindén & Gustafsson 1967).

Earlier studies of radiocesium in reindeer have concerned the metabolism of the reindeer and transfer of this nuclide to reindeer meat consumers, especially Eskimos and Lapps who can have an extremely high reindeer meat intake (e.g. Lindén & Gustafsson 1967, Nestrueva *et al.* 1967, and Westerlund *et al.* 1987).

With the present level of radiocesium contamination, direct radiation effects have been hypothesised. The annual radiation dose to a reindeer containing a maximum amout of radiocesium, i.e. 60 to 70 kBq/kg muscular tissue in February or March according to NFA measurements, could be up to 0,5 Sv. Studies performed in domestic ruminants, like sheep and goats, show that the dose rate form such an internal contamination would be too low to give acute effects (see reviews by Still & Page, 1971and Bell 1985) in a reindeer. Experimental results show that internal contamination with large amounts of radiocesium will lead to bone marrow depression due to the rather homogeneous distribution of this element in the body of an animal. It has been shown that chronic intake of several MBq radiocesium per day will cause bone morrow depression of this kind and death in cattle and dogs (Shannon *et al.* 1965 and Boecker 1972). The direct cause of death is hemorrhage and infection due to thrombocytopenia and leukopenia, respectively. Although reindeer differ from these experimental animals, the effects of high levels of radiocesium would be expected to be the same. The use of more sensitive recent methods to detect irradiation of an animal, i.e. detection of micronuclei and chromosome aberations in cultured lymphocytes, has been used in reindeer with high body burdens of radiocesium (Röed *et al.*

1989)but the results have not indicated any increase in this type of damage to the chromosomes. Other more sensitive tests to detect decreased immunological response after irradiation could be tried but most probably it will be difficult to detect such an effect in normally free-ranging reindeer.

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Seasonal concentrations of cesium-137 in rumen content, skeletal muscles and feces of caribou from the Porcupine herd: lichen ingestion rates and implications for human consumption

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Abstract. The Porcupine caribou herd was monitored for cesium-137 during 1987 to address human health concerns over potential meat contamination by radioactive fallout from the Chernobyl accident, and to determine lichen intake rates based on body burdens of radiocesium. A total of 36 caribou were collected from northwestern Alaska and the Yukon Territories in March, June, September, and November. Mean radiocesium concentrations in skeletal muscle peaked in March at 133 Bq/kg fresh weight. This value should not prove hazardous to human health. Radiocesium concentrations in skeletal muscle (wet weight) ranged from approximately 22 to 50% of radiocesium concentrations in rumen contents (dry weight), and from approximately 15 to 37% of radiocesium concentrations in feces (dry weight).

Radioactivity in feces was significantly correlated with radioactivity in rumen contents. Computer simulations relating lichen intake rates to radiocesium body burdens are presented for 3 scenarios: (1) when seasonal intakes were adjusted to provide the optimum fit between simulated and observed radiocesium body burdens (2) when seasonal intakes were based on empirical data, and (3) when seasonal intakes were adjusted to yield a "conventional" radiocesium curve of a slow fall build-up prior to a late winter plateau.

Key words: Caribou, intake, cesium, lichens, Alaska

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Introduction

Barren-ground caribou *(Rangifer tarandus granti)* from the Porcupine herd were monitored for Cesium-137 during 1987 to address human health concerns over potential meat contamination by radioactive fallout from the Chernobyl accident. Radioassay of forage plants from the Fairbanks vicinity in August 1986 revealed only modestly elevated levels of radiocesium activity (White *et al.* 1986). However, similar data were not available for vegetation from the range of the Porcupine caribou herd in arctic Alaska and arctic Yukon Territories. Moreover, data were lacking for radiocesium levels in caribou muscle.

Radiocesium burdens measured for caribou in this study were also used to estimate seasonal lichen ingestion rates. Lichen intake rates have previously been estimated with the fallout radiocesium method (Holleman *et el.* 1971, Hanson *et al.* 1975, Holleman *et al.* 1979,). However, application of this method was restricted to the winter period when animals were assumed to have an equilibrium body burden of radiocesium.

This paper presents seasonal radiocesium levels in skeletal muscles, rumen content, and feces of caribou collected from northwestern Alaska and the Yukon Territories. Comparisons are made of radioactivity levels among muscles from the neck, shoulder, backstrap, and hindquarter. A two-compartment Kinetic model (Holleman et al. 1989) programmed with a simulation, analysis, and modeling routine (SAAM27) (Berman and Weiss 1978) was used to estimate seasonal lichen intake rates needed to produce observed body burdens.

Methods

Adult female caribou were collected from the Porcupine herd in March, June, September, and November 1987. Collection sites followed migration routes from Alaska in March and June to the Yukon Territories in September and November (Figure 1). One kilogram of muscle was removed from the shoulder, backstrap, and hindquarter of each carcass. The muscle samples were then radioassayed for cesium-137 using a Nuclear Data 1100 pulse height analyzer coupled with a shielded detection system (two opposing 5" NaI(TL) crystals). Rumen contents were oven-dried and counted using the same technique. Neck samples were radioassayed in triplicate in 13.5 ml sample tubes using the Searle Analytic 1195 automatic gamma counter with a 3" NaI (TL) well detector. Fecal samples were prepared by freeze-drying and pulverization, then assayed using the Searle Analytic 1195 gamma counter. Paired t-tests were used to test for differences among muscle samples. Analysis of variance

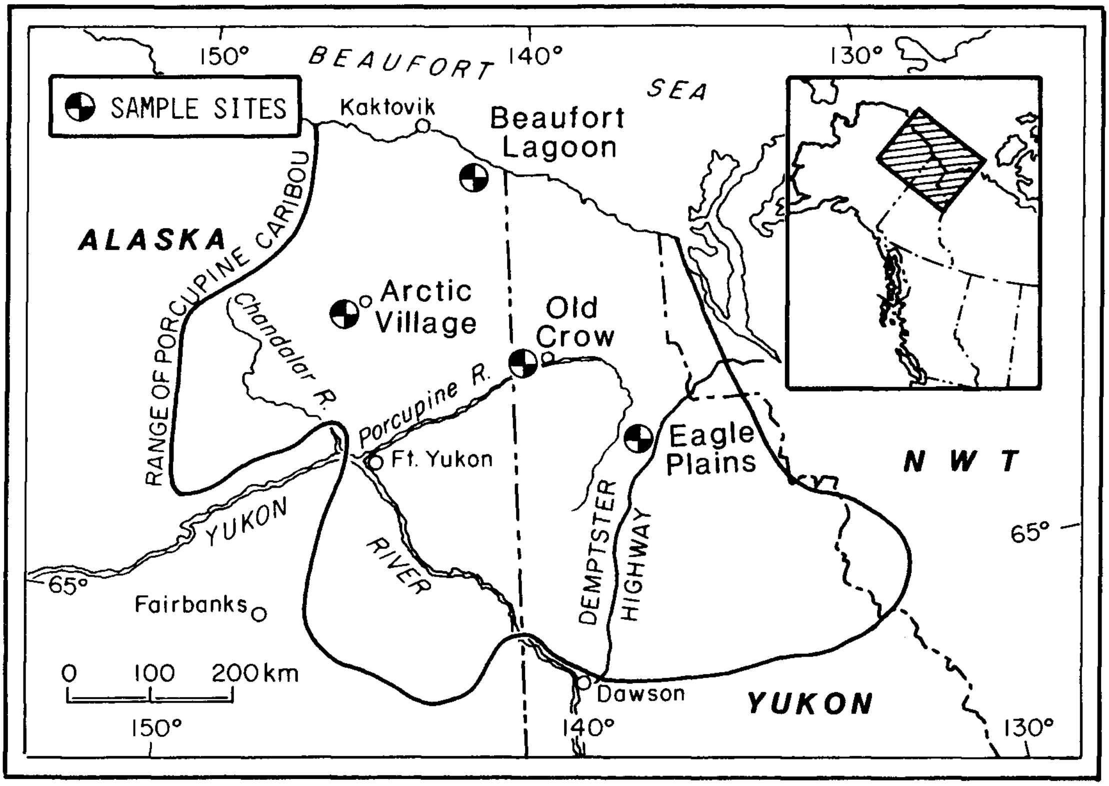
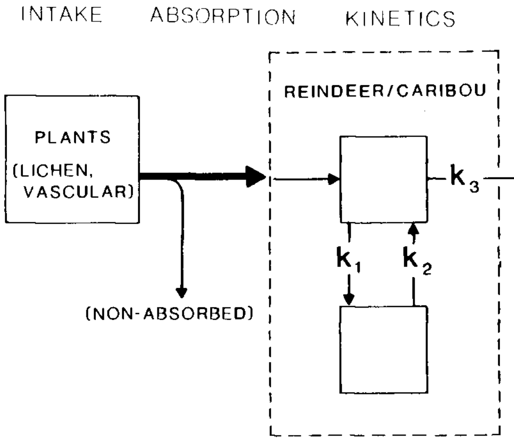


Fig. 1. Seasonal collection sites of caribou radioassayed for cesium-137. Collection dates were March 24 (Arctic Village), June 5 (Beaufort Lagoon), September 5 (Old Crow), and November 30 (Eagle Plains).

was used to test for differences among collection dates.

Lichen ingestion rates were simulated using the Kinetic model described by Holleman et al. (1989). In the model, the total body burden of an animal is represented by the sum of the two compartments (Figure 2), with the size of each compartment depending on the rates of cesium inflow and outflow. Radiocesium concentrations in food is multiplied by food intake rate to generate radiocesium intake. The radiocesium intake is then multiplied by a radiocesium absorption factor of 0.7 (Åhman 1988) to give the cesium inflow into compartment 1. The flow of cesium from each compartment (the K frational rate parameters, Figure 2) is computed as a function of potassium intake (Figure 3) and then corrected for animal body weight (Holleman *et al.* 1971). Seasonal body weights used in all simulations are based on data for the Porcupine caribou herd (White *et al.* 1988).



.2. A model showing the movements of radiocesium from plants through the two-compartmentalized reindeer/caribou.

Skeletal muscle, wnich accounts for 40% of animal body weight, was assumed to contain 80% of the radiocesium body burden (Holleman *et al.* 1971). The effective biological halftime of radiocesium was established at 8.2 years for lichens (Holleman 1974) and 2.0 years for vascular plants.

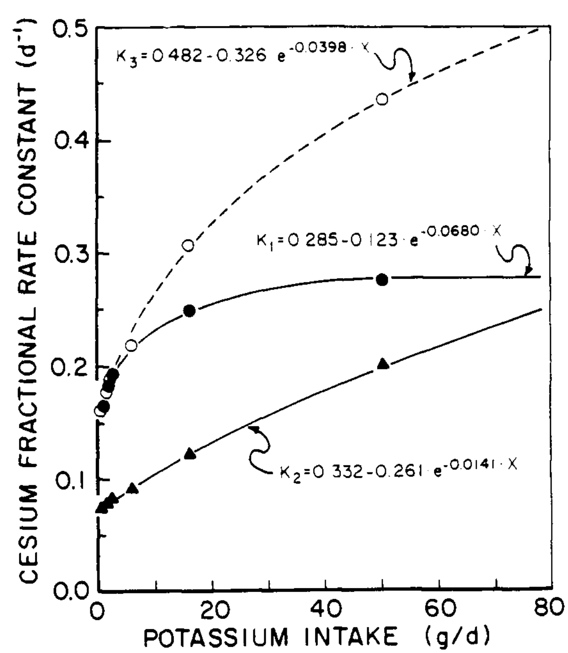


Fig.3. Modeled effects of potassium intake on the cesium fractional rate constants.

Results

Seasonal cesium-137 concentrations.

Cesium-137 concentrations in skeletal muscle ranged from a low of 26 Bq/kg in a neck sample collected in June, to a high of 232 Bq/kg in another neck sample collected in September (Table 1). When data were pooled from the four collection periods, radiocesium concentrations in shoulder and hindquarter samples were statistically comparable, and averaged 1 to 12 Bq/kg higher than radiocesium concentrations in neck and back muscles. When the data were analyzed by collection period, however, intermuscular differences in radiocesium concentration were not consistent between months. Cesium-137 concentrations were therefore averaged for the 4 muscle groups from each animal to yield estimates of mean cesium concentration in skeletal muscle for each collection period (Table 2). These mean values were used in the simulation of lichen ingestion rates.

Mean cesium-137 concentrations in skeletal muscle were significantly higher in March and September than in June and November (Table

Table 1. Seasonal radiocesium concentrations in 4 muscle groups.

	Cecium-137 (Bq/kg)				
	n	mean	SD	min	max
March					
Neck	11	122.6	24.1	80.0	158.0
Shoulder	11	139.8	18.4	121.7	176.2
Back	11	131.0	19.0	102.5	166.5
Hindquarter	11	138.0	19.6	110.6	169.1
June					
Neck	5	58.2	20.8	26.0	84.0
Shoulder	5	72.4	26.7	46.2	114.4
Back	5	85.7	28.7	55.8	129.6
Hindquarter	5	87.5	30.7	57.4	137.9
September					
Neck	8	114.4	54.3	72.0	232.0
Shoulder	8	137.2	39.1	87.2	201.1
Back	8	101.6	34.5	61.6	160.1
Hindquarter	6	118.3	27.7	77.2	161.7
November					
Neck	12	81.2	29.5	33.0	140.0
Shoulder	12	81.4	29.1	28.4	132.7
Back	10	70.5	22.8	30.2	106.9
Hindquarter	12	75.0	24.3	29.6	107.4

Table 2. Seasonal radiocesium concentratios in skeletal muscle (average of neck, shoulder, backstrap, hindquarter), rumen contents, and feces. Sample size in parentheses.

	Cesium-137 (Bq/kg)			
	March	June	Sept.	Nov.
Skeletal muscle* (wet weight)	133^{a**}	76^{b}	118^{a}	77^{b}
Rumen contents (dry weight)	287^{b} (11)	149^{c} (5)	538^{a} (8)	242^{b} (9)
Feces (dry weight)	455^{b} (11)	203^{c} (5)	802^{a} (1)	516^{b} (8)

* Average of neck, shoulder, backstrap, and hindquarter.

** Means with the same letter are not significandy different ($p < 0.05$) in comparisons across time.

2). Rumen contents and feces exhibited similar seasonal trends; however, September activity was significantly higher than March activity in both instances (Table 2).

Radiocesium concentrations in skeletal muscle (wet weight) ranged from approximately 22 to 50% of radiocesium concentrations in rumen contents (dry weight), and from approximately 15 to 37% of radiocesium concentrations in feces (dry weight). Radiocesium concentrations in feces correlated significantly with radiocesium concentrations in rumen contents (Figure 4) since both reflect the effect of immediate-term lichen consumption.

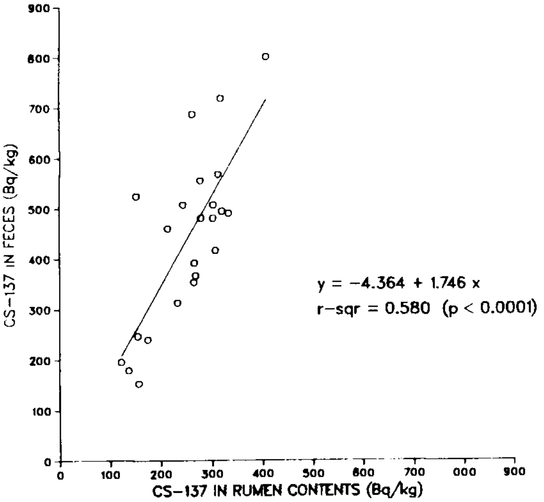


Fig.4. The regression between radiocesium concentrations in feces and radiocesium concentrations in rumem contents.

Simulation of lichen ingestion rates

Data on seasonal radiocesium concentrations in forage were not available for computation of cesium intake. Consequently, seasonal radiocesium concentrations in vascular plants were assumed to be 1/20 of lichen values. Seasonal radiocesium concentrations in lichens were estimated by solving the relationship between lichen radioactivity, proportion of lichens in the diet (Martell *et al.* 1986, Martell and Russell in prep.), and radioactivity in rumen contents. Radiocesium concentrations in lichens thus derived equalled 401 Bq/kg for March, 389 Bq/kg for June, 664 Bq/kg for September, and 353 Bq/kg for November. The agreement between March, September, and November estimates is even closer when the effective half-time of 8.2 years has been accounted for: lichens measuring 400 Bq/kg in January should measure 393 Bq/kg in March, 385 Bq/kg in June, and 370 Bq/kg in November. However, significantly higher radiocesium concentrations in September suggest either the occurrence of a radioactive hotspot, or the ingestion of a food source with a radiocesium concentration higher than that of lichen. The occurrence of a local hotspot is tenable because the caribou typically spend 2 to 4 weeks in the Old Crow-Porcupine River drainage in September-October during the course of fall migration. Alternatively, the ingestion of a highly contaminated food source is also plausible because of altered food habits during fall migration. For example, mushrooms are only present in the diet during the fall migration (Martell and Russell *in prep.*) and represent a likely source of high radiocesium contamination. Because we have no data to support or refute this hypothesis, however, this scenario has not been included in the present simulations. For simulation purposes, therefore, radiocesium concentrations in lichens (befor correction for effective half-time) were set at 400 Bq/kg throughout the year, with the exception of the first week in September when concentrations were elevated to 650 Bq/kg to simulate the occurence of a local hotspot. A transitional week before and after this period was also allowed so that radiocesium concentrations could slide to and from hotspot values.

When seasonal intakes were adjusted to provide the best fit between observed and simulated radiocesium concentrations (Figure 5), lichen intake declined only modestly between winter and summer. Following a seasonal low in mid-June, lichen intake increased to an annual high of 2.1 Kg/day in late August to generate a second peak in the cesium profile. Lichen intake declined sharply thereafter and remained

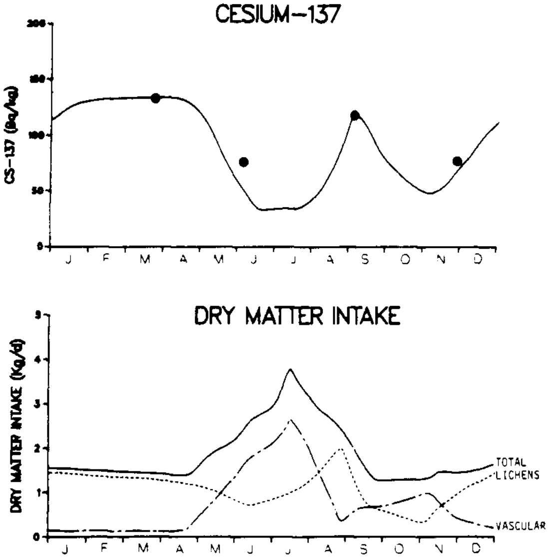


Fig.5. Simulated and observed radiocesium concentrations in skeletal muscle, and simulated ingestion rates when seasonal intakes were adjusted to best fit the observed radiocesium data.

low until November when it started to regain its winter value.

The simulation was repeated using seasonal intake values derived from empirical data (Figure 6). Dry matter intake was adapted from White and Trudell (1980) while dietary proportions of lichens and vascular plants were based on studies of the Porcupine caribou (Martell et al. 1986, Russell and Nixon 1988, Martell and Russell *in prep.*). In contrast to the first simulation, the dietary shift from lichens to vascular plants between winter and summer was pronounced. Additionally, lichen intake was elevated throughout the fall. Simulated cesium concentrations compared favorably with measured values for March, June, and September, but deviated by 80 Bq/kg in November because of sustained high lichen intakes. This resulted in a winter plateau extending from October to April.

In a third simulation, seasonal intakes were adjusted to yield a "conventional" profile depicting a gradual radiocesium incline in the fall prior to the winter plateau between February and April (Figure 7) . Simulated lichen intakes in this scenario are characterized by slow transitions between winter and summer values, constant rates throughout both winter and summers, and the absence of a fall peak.

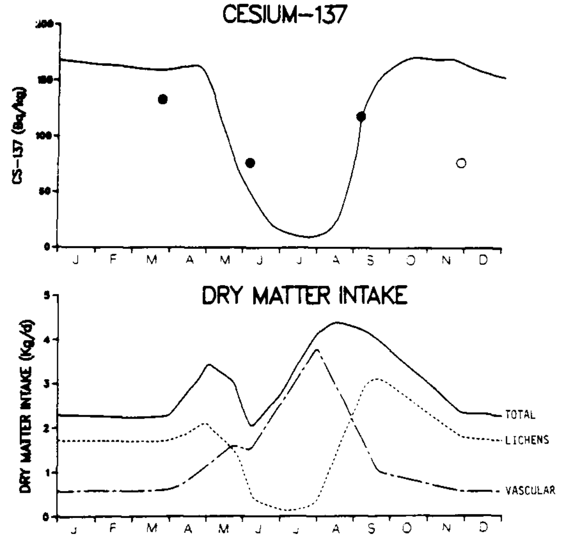


Fig.6. Simulated and observed radiocesium concentrations in skeletal muscle, and simulated ingestion rates when seasonal intakes were based on empirical data.

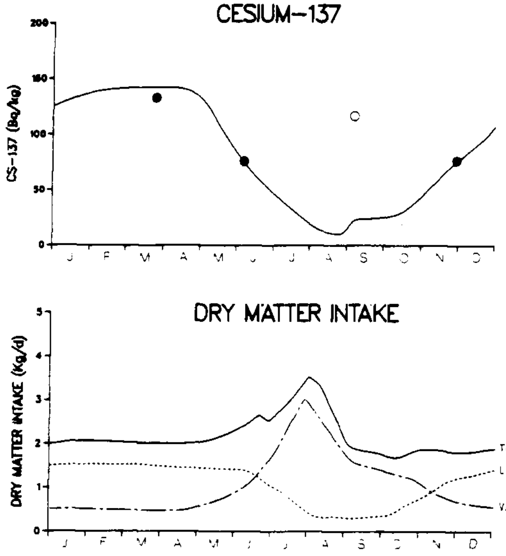


Fig.7. Simulated and observed radiocesium concentrations in skeletal muscle, and simulated ingestion rates when seasonal intakes were adjusted to yield a "conventional" cesium curve.

Discussion

Seasonal radiocesium concentrations measured in this study in caribou muscle from the Porcupine herd do not suggest any reason for health concerns. According to the National Council on Radiaton Protection and Measurements (1977), a radiocesium intake of 300,666 Bq/year results in the maximum permissable nonoccupational exposure for an adult human. In this study, mean radiocesium concentration in skeletal muscle peaked in September at 133 Bq/kg. At this concentration, an annual consumption of 2,260 kg of meat would be needed to reach the allowable intake limit. Even at 232 Bq/kg, the maximum radiocesium concentration found for any sample assayed in 1987, an annual consumption of 1296 kg of meat would be allowed. The radiation dose to an adult human with a daily consumption of 220 g of meat measuring 133 Bq/kg would, at the end of the year equal only 3.6% of the annual permissable maximum.

Simulated lichen intakes declined only modestly between winter and summer, and showed a distinct but transitory peak in late August when seasonal intakes were adjusted to provide the best agreement between simulated and observed radiocesium concentrations. Simulated intake patterns generated in this manner are therefore supported by measured cesium profiles; nonetheless, they should not be accepted as unequivocal in the absence of further validaton. The assumed timing and extent of elevated radiocesium levels directly contribute to the shape and chronology of the fall radiocesium peak. More importantly still, the assumption that animals from different collection dates share common radiocesium histories is both unverified and unverifiable. Results from the second simulation, in which empirical data were used to derive input values for seasonal intakes, suggest that this assumption may in fact be untrue. At present, however, the correctness of simulated scenarios can only be speculated on. Given the unvalidated assumptions of the model, simulation results are meant to be more thought provoking than predictive.

Acknowledgements

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Coping with the Chernobyl disaster: a comparision of social effects in two reindeer-herding areas

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Abstract: Lapland reindeer herders in the Vilhelmina and Jokkmokk municipalities of Sweden were interviewed in summer, autumn and winter 1987/88. The great variability in nuclear contamination between these areas has occasioned obvious but also unforeseen differences in the social effects for the Saami. The variability of contamination has also been compounded by the variability of compensation policy, variability of expert statements about risk, and also the change in state limits on Bq. concentrations set for meat marketability. This paper will illustrate the broad spectrum of Chernobyl-related social problems and the methods of coping with them.

Key words: *Rangifer tarandus*, Saami, Sweden, Lapland, anthropology

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This paper concerns socio-cultural issues following upon the Chernobyl nuclear disaster with regard to the Swedish Saami. Studies treating the social aspects of the Chernobyl disaster have been few, and yet they are essential if reasonable policies are to evolve for coping with nuclear contamination of our food chain. Such a focus reveals diverse unforeseen consequences deriving not only from the contamination itself, but also from the compensatory policies which it has occasioned. I have recently raised a number of these points with regard to assessment of low-dose radiation risk at the twelfth International Congress of Anthropological and Ethnological Sciences in Zagreb (Beach, forthcoming) and will have cause to recapitulate some of them here. In this paper I shall demonstrate the broad scale of Chernobyl-related social issues. While it will not be possible to examine all of the problems, I shall draw attention to some of the anomalies that can occur with the superimposition of ad hoc measures onto old regulations.

It should be noted at the outset that many of the topics raised here lend themselves easily to larger political debates and are controversial in a number of different contexts. My purpose, however, is to give the the views and experiences of my herding informants. While these views might not always be based on a fully correct knowledge or interpretation of the facts, the are nonetheless real and of social significance.

The data sampled here originate from interviews made in the field with herding families as part of a long-term study financed by the Bank of Sweden Tercentenary Foundation and administered under the Center for Arctic Cultural Research at Umeå University, Sweden. We have sought to record from the Swedish Saami reindeer-herding families themselves their fears, the damages they have sustained, and their efforts to deal with these problems. Both male and female research team members interviewd people in two main regions, one highly impacted by nuclear fallout (Vilhelmina), and one relatively lightly impacted (Jokkmokk). Care was taken to interview herders and family members of different sex and age as well as to include families with young children. Non-herding Saami, Saami handicraftsmen, and even non-Saami were also interviewd in order to gain insight into the herders' social context and possible cultural constraints. Interviews were conducted both in Vihelmina and Jokkmokk in summer 1987, autum 1987 and winter1987/88. The project will attempt to cover a five- year period with repeated follow-up interviews.

As background information a few essential facts deserve mention: The reindeer-herding area of Sweden is currently divided into 51 grazing districts called *samebys*. Membership in these *samebys* is tightly controlled both by regulations in the Swedish Reindeer Herding Act of 1971 and by the existing members themselves. Membership confers, besides the right to graze one's reindeer on *sameby* territory, also certain hunting and fishing rights. The right to herd reindeer in Sweden is almost exclusively reserved for those of Saami heritage. A *sameby*, therefore, defines both a territorial and a social unit.

Reindeer herding is centrally administrated under the National Board of Agriculture, to which is tied an advisory body with Saami representation. Regionally herding questions are handled under three provincial agriculture committees. The *samebys* all belong to the Swedish Saami Parliamentary Organization (SSR), which is the main political body of Saami in Sweden. In Sweden today, there are only about 900 active reindeer herders, with family members bringing the total of those directly dependent upon herding to approximatley 2,500 people. The reindeer stock in Sweden today is estimated at about 275,000 head. Reindeer herding is not, however, of major economic importance to the Swedish State. It is tolerated under normal circumstances and has been supported during the Chernobyl crisis largely as a concession to the cultural preservation of the Saami. The reindeer industry is hard pressed even in the best of times to assert itself against the heavy industrial exploitation of the grazing land.

In the early 1980s, the reindeer-slaughter company, Sameprodukter, servicing as much as 75% of the reindeer herding area, was reorganized and taken over predominately by Saami. SSR, the Saami political organization, bought controlling interest in the company. Although Sameprodukter is one of the largest and most modern of slaughter facilities active in the Jokkmokk area, it is not the only one. There are a number of other, smaller slaughter companies competing for the purchase of reindeer from the herders. The Vilhelmina area is almost entirely serviced by the large and fully modern slaughter facility of Lapplandsvilt. The different slaughter companies are capable of meeting different hygienic standards, and these differences in turn determine the extent to which the meat can be exported.

The following is a highly compressed account of the kinds of issues raised by the Chernobyl disaster which affect the livelihoods and traditions of the Saami:

In the wake of Chernobyl, contradictory statements and confusion were legion. As a result, Saami faith in politicians and administrative authorities seems to have reached a low point. Not only have different experts evaluated health risks differently, but in many instances herdes claim that administrative blunders have resulted in unnecessary reindeer losses.

Herders resent the "sacrifice" of their reindeer meat to preserve a contamination limit on marketability devised on the basis of risks to newborn infants and their consumption of milk (Labba, 1988). Most potential consumers of reindeer meat are not infants. Furthermore, since pre-Chernobyl reindeer often displayed Bq values over the post-Chernobyl state marketability limit (Hagberg, 1976), herders understandably ask why no limit was set previously if the pre-Chernobyl reindeer contamination really posed a health risk. If such pre-Chernobyl levels constitute no major risk, why then have so many reindeer been confiscated with such low levels following upon Chernobyl? There may be valid answers to some of these questions. My point is to show the confusion surrounding these issues.

In May of 1987, the marketability limit was raised by Statens Livsmedelsverk (SLV), the National Board of Foodstuffs, from 300 Bq/kg to 1500 Bq/kg for reindeer meat, game and inland fish, basic foodstuffs of the Saami, while the lower limit for the basic foodstuffs of the average Swede was maintained. According to the authorities, this measure was acceptable as the average Swede eats only 200 grams of reindeer meat per year (at least he did previous to Chernobyl) and, moreover, this would put more reindeer meat on the market. It is evident that many of the state's reactions to the complicated ramifications of this sudden and unique disaster have not been fully considered. Understandably, the Saami feel themselves to be discriminated against when, for example, their school children who normally eat a substantial amount of rendeer meat are now referred to meat with levels up to 1500 Bq/kg, while meat below 600 Bq/kg is selected out for export to Germany. Even though low-level meat was accessable to Saami children by various means, many resented the fact that a quality separation was made for export to small-quantity consumers but not for local, large-quantity consumers.

SLV sought to meet the obvious criticism for having established one health limit for the basic foods of the Swedish majority and another for the basic foods of the Saami minority by issuing a pamphlet of dietary recommendations (Statens Livsmedelsverk, 1987) to each herding family. In it, those with a high consumption of reindeer meat were advised to keep records of the quantity and contamination level of all the reindeer meat they ate, the dosage being a product of the two. As long as the yearly recommended dosage was not exceeded, the pamphlet did not discourage the consumption of meat with values up to 10,000 Bq/kg. Yet, at the same time, expert statements claimed the risks from low-dose radiation to be directly proportional to exposure, whether it be for an instant or over the years. The analogy was made to driving a car; the more one drives, the greater the danger of accident. (Note that this analogy should be broadened to include the risk to fellow "passengers" so as to encompass the possible risk of genetic disorder to the offspring even if the "driver" appeard to survive the "traffic" unscathed.) Some herders wonder: If it is not the Bq value itself but the product of Bq value times quantity consumed which is important, why should the tally for one year be significant rather than the compounded tally of Bq/kg times kg over a lifetime?

Obviously, confusion over the issue of health risk is widespread. Almost none of the herders interviewed bothered to keep records of the contamination values and quantities of the meat they consumed. Although they were well aware that it was Bq value times quantity which was important, many still treated the marketability limit as a health risk barrier, even if they would rather take the risks than respect it. The quintupling of what many tended to regard as the health risk limit was met with great cynicism by those who had previously had faith in the authorties. Had the initial limit been set at 1500 Bq/kg, the matter would have deen different. Due to the confusion, herders have fashioned their own Bq limits for the meat they would eat, based largely on general social consensus (neighbours, experts, media, the Norwegian limits etc.) and personal discomfort (economic, dietary and cultural).

Some of the problems seem to be inevitable consequences of the state's need to supervise inspection and enforce saftey standards. Members of herding families repeatedly complain over the loss not only of reindeer meat, but also of foods obtained from the blood and internal organs of the reindeer. These are of major importance to Saami identity. Foods prepared from the reindeer are loaded with traditions. The Saami who cannot slaughter and prepare food from his own reindeer according to his own special customs feels himself culturally impoverished. Herding parents fear that their children will miss the opportunity to learn these customs.

Herders in the hardest hit regions are often able to purchase frozen, low-level reindeer carcasses from further north, but although these provide meat, they do not provide blood and organs. Herders frequently complain that these reindeer, purchased from the slaughterhouses, are not handled or slaughtered to their liking. Many herders would accept the risks of greater contamination within bounds in order to slaughter and butcher their own household reindeer, rather than obtain cleaner meat from the north.

Slaughterhouses which had access to reindeer under the contamination limit would sometimes allow herders to make a simple exchange of "bad" meat for an equal amount of "good" meat. At other times, however, this would not be feasible. In either case, the testing itself would supposedly leave the herders several options of choice. Herders would be allowed to choose themselves whether or not they wanted to keep the meat of a bad reindeer for their own use—as long as it was not sold. But events proved that frequently the slaughterhouses could not guarantee such special treatment, and all reindeer over the limit, whether or not one was chosen by a herder for his own personal use, would be confiscated. Many herders complained that when they tried to collect the reindeer they had picked for their own household use, they found that it had been destroyed already, even if the test results showed it to have had a becquerel level as low as only 310 Bq/kg. Large-scale testing and compensation operations were hardly geared for the needs of the herding family to provide its own meat supply.

A leading cause of all the controversy is the fact that while the risks from various amounts of contamination consumed are scaled, they are not calibrated. Consumption of one kilogram of 600 Bq meat may be twice as dangerous as consumption of an equal amount of 300 Bq meat, but no one can yet provide a credible account of the risks to health involved with either dosage expressed, for example, in percentages of additional deaths. Expert statements cover the breadth of the spectrum from claiming there is almost nothing to fear and almost no precautions necessary, to predicting hundreds of additional cancer deaths. The social consequences of the Chernobyl disaster are therefore largely the result of opinions and fear—those of the herders and those of the state—without concrete foundations in biological fact. This is not to say that all such reactions are unreasonable given the situation, only that the facts are not available for reason alone to dictate a course of action.

Families with small children in regions of high contamination took extra care to ensure that their children ate meat with the lowest contamination they could obtain, usually, at levels under the state marketability limit. Even though some parents would eat meat they would not serve their children, others found it too difficult to keep menus divided and therefore joined their children in a low-level reindeer diet. In the early stages of the disaster, many herders took the precaution of preparing their food in such a way as to rid it of as much cesium as possible. To give but one example, the water in which reindeer meat was cooked was often discarded. This practice declined in many areas once the states's marketability limit was quintupled, freeing most reindeer for sale.

Other efforts to decontaminate reindeer meat attempt to lower cesium levels in the reindeer while it is still alive. These efforts involve the use of artificial fodder (even with cesium-reducing additives) and/or the freighting of entire herds by truck long distances to cleaner pastures. Such measures can involve major changes in land use and herding scheduling, besides much extra work and the extended separation of family members.

The effort to decontaminate the reindeer before slaughter has brought about considerable extra costs. Among these are expenses incurred through changes in reindeer management scheduling. Prior to Chernobyl, slaughterhouses would not accept rut bulls. Some herders have claimed that because of initial policy delays by the authorities, the September slaughter of bulls near full rut in their *samebys* was also delayed, with the result that hormone levels increased enough to render the meat unusable. In one of the particularly hard-hit areas, herders, realizing that their bulls would all contain a very high level of contamination at the usual autumn slaughter anyway and therefore unavailable to them as food even if bringing income from compensation, chose to postpone the regular slaughter of early rut bulls in September in order to hunt moose. Meat from the moose is not at all as contaminated as reindeer meat and therefore is more attractive to the herders as food (Labba, 1988:36).

Saami who, because of their need for funds, had acquiesced in the slaughter of animals doomed for becquerel confiscation, were prone to ignore the pre-rut slaughter schedule (no longer conceived of as time critical) when this came to interfere with their ability to supply themselves with another traditional food. Under the existing circumstances, it seemed absurd if meat were to be rejected by the slaughterhouses, because of hormone levels when it was already non-consumable from the becquerel perspective. In a hasty measure intended to make up for losses form delayed autumn slaughters, the Minister of Energy agreed in Sept. 6, 1986 to extend compensation to all "rut" bulls slaughtered, i.e. even to those bulls which had progressed too far in the rutting cycle to be saleable. This compensation would apply whether or not the meat would have passed becquerel safety standards.

Compensation policies have been disigned primarily to keep herders unharmed while pursuing their traditional work with the reindeer, as if nothing had happened. But the herders preferred to hunt the moose whose meat was far less contaminated than that of their reindeer. In the hard-hit areas, especially, moose meat has been one of the main substitutes for reindeer meat. Moose meat has always been a part of the traditional diet and has the advantage of being a subsistence commodity, frequently requiring no cash purchase. The herders knew that whether or not their bulls were slaughtered at the normal time or obtained too high a hormonal level for sale, they would still be barred from the market and confiscated on the grounds of their radiation contamination.

A recurring general issue of major importance concerning compensation policies is whether funds should be distributed simply to compensate for so called "becquerel meat" obtained through following a normal year's routine, or if it should in some way prioritize the production of good meat. This problem is complicated by consumer purchasing resistance against reindeer meat and the difficulty in selling even low-level meat. As a result, some slaughterhouses have already come to offer the herders less for their good meat than the herders can obtain from the compensation payments for their becquerel meat. Herders have commented that it would be smarter for them to feed their reindeer becquerels rather than the artificial fodder designed to decontaminate them.

Besides compensating for contaminated reindeer meat itself and the expenses connected with producing marketable meat, the goverment has also provided compensation for the destroyed fishing and berry picking harvests of the northern inhabitants, Saami as well as Swedes. Compensation of this sort, however, involves quite a different process from that related to reindeer meat. Whereas the herders are compensated for the unmarketable meat they produced, it would be senseless to require people to catch the contaminated fish or pick the contaminated berries, only to throw them away after establishing compensation demands. Instead, estimates of lost income or food value have been made on the basis of a person's previous harvest record. Those seeking such compensation are supposed to file for it, giving information about lost harvests. Often a standard sum in compensation is given each applicant, who, if he or she thinks it too little, can appeal the decision. To substantiate a case of high compensation demand, the authorities usually have requested the applicant to demonstrate his or her customary harvest size on the basis of the tax declaration of 1985. Many of my informants have accepted what they consider grossly inadequate compensation rather than subject themselves to what they regard as a rude inspection of their tax records.

Herders in different provinces, when comparing notes, have found that similar applications could result in vastly dissimilar compensation payments. Within each province, the strictness of the rules for distributing compensation varies according to the ratio of the total demand for compensation in relation to the amount of funds allocated to the province for that purpose by the central government. While a herder in the Norrbotten province might receive good compensation for the loss of his traditional catch of fish (even if small), a herder in Västerbotten with similar demands might receive nothing because the fishing is not considered his major source of income. Rather than administering a single policy for the entire country, so that similar demands would lead consistently to similar compensation, the central government has given the provinces the job. The provinces have not at all received the same amount of compensation funds or an equal proportion of compensation funds in relation to demands.

As a result of the Chernobyl disaster, herding households suffered not only a blow to their herding directly, but also to their herding lifestyle in general, a lifestyle to considerable degree dependent upon supplemental incomes from non-herding sources and non-herding subsistence resources. Besides the loss of fishing and berry picking, tourism has decreased. The earlier slaughter of reindeer has even made it more difficult to obtain reindeer antlers of a quality fit for handicraft work. In short, the economic flexibility of the family has decreased, and herders must weigh the trouble and humiliation of seeking compensation against taking greater Bq risks.

On the positive side, herders in the hard-hit areas have managed to cope with many of the problems of access to traditional foods of low contamination with help of a wide network of friends and family. Especially herding families of northern Saami origin have relatives spread throughout the Swedish herding districts due to the enforced relocation of northern Saami in the early part of this century. Saami in low-contamination areas have often sent fish, berries and even reindeer meat to their less fortunate relatives and friends. Herders in the hard- hit areas have not infrequently undertaken trips further north where they have been able to purchase a reindeer and slaughter and butcher it themselves according to traditional specifications. Even if such channels of food redistribution have not had heavy traffic, their influence can hardly be overestimated. The ability to obtain at least some traditional foods to prepare oneself according to customs means very much indeed, not least for the expression and practice of cultural identity.

Naturally, the Chernobyl disaster has also taken a psychological toll upon many herders who had come to feel themselves as wards of the state, subsidized by state compensation payments, people whose work was meaningless. With the change of marketability limit (which alone had freed most reindeer for the market) and the decontaminating efforts of artificial fodder and earlier slaughters (which have brought many of the reindeer in high contamination areas under the limit), most herders are no longer receiving compensation for their reindeer. As noted earlier, however, there is the danger that they will receive a relatively poor price for their meat due to purchasing resistance.

There has been a good deal of worry if, after the Chernobyl disaster, young Saami recruits to the herding livelihood will be as numerous as would otherwise have been the case. We have yet to come across any examples in our research areas of a decrease of Saami herders or Saami herding recruits because of Chernobyl. However, we have found young herders who have prudently decided to postpone major new investments in livestock or housing until they were more sure of the future.

Even in the hard-hit regions, herders now feel that the problems they face, although very likely long-lasting, can be dealt with. While many of their reindeer are still over the limit, they now know that their reindeer can be brought below the limit, albeit for short periods and at added expense. This expense is borne by the state, but herders need not feel that they are mere welfare recipents, for they can produce a quality product for human consumption.

Nonetheless, even though government expense for supporting the herding industry in this hour of crisis has decreased greatly, compensation to herders and slaughterhouses is still considerable. Herders are worried if compensation payments will impair the ability of herders to resist threats to the grazing lands by extractive industries such as the hydro-electric power industry and the timber industry? Will prolonged compensation place the herders in such a position of dependency that the herding livelihood will collapse once this compensation is removed? Many herders fear that the considerable support provided them by the state will in time cause their Saami rights to be looked upon as Saami privileges which can be removed (like compensation payments) by the state at will without due process (Beach, 1987).

A more permanent extra expense occasioned by alteration in the scheduling of herding events has been that brought about by early slaughter in southern Lapland. In the Vilhelmina area, the discovery that slaughters in late August might result in meat under the limit—in contrast to the high values recorded during the winter—causes earlier than normal slaughters. Currently, the relatively low Bq levels in the Jokkmokk area and the institutionalization of the raised marketability limit demand no changes in slaughter timing for the reindeer to clear the limit. Previous to the raising of the limit, however, many *samebys*, even in the more lightly contaminated areas, corralled their reindeer for autumn slaughters earlier than customary in order that the reindeer would be slaughtered before making the transition to the heavily contaminated lichen diet. In southern Lapland, the early slaughters will probably continue for many years to come. Such changes in scheduling have had unforeseen ramifications. In the Swedish mountain *sameby* herding cycle, the earlier it is in autumn, the further removed the reindeer are toward the west and the more spread out they are. Bringing these reindeer to slaughter has necessitated in many instances a far greater reliance upon air support, notably helicopters, than usual. This has added a sizable cost, one that was initially, at least, borne by the state.

A number of our informants indicated that the promise of compenstaion for the extra flying time needed has resulted in an overly carefree use of helicopters. They worry that, should this compensation continue for many years, the herding system would become far too helicopter dependent. Herders and reindeer would no longer know any other way. The emergency measure would become customary, and before long even a necessity, driving up the costs of herding. Even before Chernobyl, the over-use of technological equipment has been viewed as a growing problem by many herders, and some regard the compensation measures as aggravating the problem. Other herders do not see the use of modern equipment as a problem at all, but they are concerned that compensation policies will generate costly habits of use which will prove ruinous once state compensation ceases.

Of course, the added expense of rounding the herd up for early slaughter stems not only from increased use of helicopters, but also from reduced sales income. The earlier in autumn the bulls are slaughtered, the less they weigh. The herders and their Saami organizations have been negotiating with the government over compensation payment to cover the weight sacrificed for the sake of producing marketable meat.

The reindeer slaughter industry, too, has been affected heavily by Chernobyl. In the Jokkmokk area, where slaughterhouses are numerous and habitually in competition for reindeer, herders have been constantly discussing slaughterhouse policies. Although a herder will usually sell to whichever slaughterhouse is on the scene and gives the best price, herders have often expressed strong preferences and loyalties to particular slaughter companies. A number of herders have voiced the suspicion that government compensation to the slaughterhouses is being distributed in an unfair manner partly in an effort to promote restructuring of the slaughter industry according to state plans.

Due to the quirks of compensation policy to the slaughterhouses, considerable profits could be made from the slaughter of becquerel reindeer without much effort. Like the herders, slaughterhouses have also been compensated for the meat of the becquerel reindeer they have slaughtered, though at a much lower rate. As highly contaminated meat is destroyed, processing procedure at the slaughterhouses is unnecessary. Moreover, slaughterhouses have also received compensation for their reduced sales of processed meat sold as a delicacy product. Competition for becquerel reindeer became fierce, and slaughterhouses have been accused of using inequitable methods in the struggle. Some slaughterhouses have obtained large sums in compensation and support of their businesses, while others have received nothing. Those which have received funding are accused of using their compensation to gain an unjust advantage in the bidding for becquerel meat.

One slaughterhouse which was heavily dependent upon state aid offered a better price for becquerel meat than the usual governmeant rate of compenation, if in return the herders would refrain from inviting other slaughterhouses to attend their slaughter. Naturally this has caused a storm of protest by other slaughter companies and the herders supporting them. Was compensation payment to be utilized as a weapon in market wars between slaughterhouses? Moreover, if one slaughterhouse tried to meet the problems imposed by Chernobyl, for example by laying off personnel so as to minimize losses, should this company receive less compensation than another slaughterhouse that refused to cut back and therefore could demonstrate a larger loss incurred by Chernobyl? If the rule governing compensation payment is that it should simply cover loss, then any business which tried to cut its losses would be rewarded with less compensation. Incentive to improve the difficult situation would thereby be destroyed.

The differential payments to the different slaughterhouses have appeared quite arbitrary. The authorities are accused of helping a few big companies, whether inadvertently or by design while ruining the small companies' ability to compete. If this has been by design rather than by the blind following of insensitive regulation (and I have not been able to establish for certain which it is), perhaps it is motivated by a wish to rationalize the reindeer slaughtering business. Even so, while it may well be that the authorities deem it unnecessary to have so many competing companies given the scale of the reindeer slaughters, nonetheless one can as a matter of principle question whether disaster compensation payments should be slanted in such a way as to promote the rational restructuring of a business, favoring some against others.

Some herders worry that many of the small slaughterhouses will be forced from the field and that herders will lose the benefit of a competitive market for their reindeer. If competition in the slaughter industry should fall, the risk could grow that slaughterhouses might give the herders a lower price even for their good meat, under the pretence that purchasing resistance demanded it. But while it may well be that some resistance to the purchase of reindeer meat forces down the price the slaughterhouses can in turn pay the herders, it is practically impossible to know what part of a price drop is due to real purchasing resistance and what part is due to the slaughterhouses' desire for greater profit.

There is also cause for concern in the fact that Sameprodukter, one of the largest slaughter companies to receive massive state support in the form of Chernobyl compensation payments, is mostly owned by SSR, the Saami herders' major political organization. Just prior to the Chernobyl disaster, Sameprodukter seemed to be on the verge of bankruptcy. Now, some say as a result of large compensation payments, it has made a fast recovery. Owners of slaughterhouses which have received little to no compensation compared to Sameprodukter argue that the Swedish state, sworn to protect the Saami herders and the Saami culture from the ills of Chernobyl, can hardly afford to let Sameprodukter be a victim. But while the aid to Sameprodukter is generally applauded by the herders, many are worried if this economic link to thier political organization might not in some way come to compromise its other, political efforts for the Saami in its confrontation with the state. Sameprodukter itself claims that is has received no particularly favorable treatment, and surely one cannot expect it to refuse government compensation and risk financial ruin because of its connecton to the Saami political organization.

While both the state and the Saami can be relieved that the effects of Chernobyl now appear to be of a scale which can be absorbed by the flexibility of the government's budget, as well as by the herders' economy and by the Saami culture, I think it sobering to contemplate in closing the dilemma of principle in which this disaster has placed the Saami culture. It could have been worse. After all, the fallout from Chernobyl was by no means the first to reach Lapland, and the absorption properties of the lichen place the reindeer, and through them the Saami, in an extremly vulnerable position.

At first appearance one might consider that the demonstrated threat of nuclear fallout to the Saami culture through the reindeer would cause the Saami to seek a broader cultural base, one that would serve to hold them together even if the herding industry should be desperately crippled sometime in the future. At the same time, however, it is precisely because of this vulnerability of the Saami through their reindeer that they have been granted special compensatory policies over and above those bestowed upon other citizens. Should another, similar disaster occur, the Saami may well be best served in the short run by promoting even more the linkage between their culture and the practice of reindeer herding. In the long run, however, to absolutize this linkage could be fatal. The state can only do so much. If ever beset with long-lasting, wide-spread and high-level contamination at some future date, reindeer herding in Sweden will be in the hands of the consumer, regardless of any compensatory policies devised by the state. These can be but stop-gap measures. Of course, it is true that the importance of this practice to the Saami as a whole can hardly be overemphasized; yet there is more to Saami culture than reindeer.

In this first year of work with investigating the long-term social effects of the Chernobyl nuclear disaster for the Swedish Saami, our results cannot necessarily boast of long-term applicability. Many of the issues raised have concerned the worries of herders over some future possible development. While such things as worries, depressions, and the methods to cope with them do consitute social facts in themselves, deserving consideration on their own account, concrete social changes (sometimes the objects of worry, but sometimes unanticipated) will reveal themselves only with time. Will herder numbers decline further as a result of Chernobyl? Will the slaughter industry take on a new structure? Much further research is necessary to determine to what extent such developments materialize, what part Chernobyl has played in them, and what their consequences will be.

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Seasonal variation of cesium 134 and cesium 137 in semidomestic reindeer in Norway after the Chernobyl accident

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Abstract: The Chernobyl accident had a great impact on the semidomestic reindeer husbandry in central Norway. Seasonal differences in habitat and diet resulted in large variations in observed radiocesium concentrations in reindeer after the Chernobyl accident. In three areas with high values of cesium-134 and cesium-137 in lichens, the main feed for reindeer in winter, reindeer were sampled every second month to monitor the seasonal variation and the decrease rate of the radioactivity. The results are based on measurements of cesium-134 and cesium-137 content in meat and blood and by whole-body monitoring of live animals. In 1987 the increase of radiocesium content in reindeer in Vågå were 4x from August to January. The mean reduction in radiocesium content from the winter 1986/87 to the winter 1987/88 were 32 %, 50 % and 43 % in the areas of Vågå, Østre-Namdal and Lom respectively.

Key words: radioactivity, fallout

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Introduction

Reindeer eat lichens predominantly during winter, with lower intake during the rest of the year. The slow-growing lichens are predisposed to high levels of radionuclides, due to absorbing nutrients and nutrient analogues from water (rain) and air. Radiocesium concentrations in lichens do decrease with an effective half-time of 3 to 8 years (Martin and Koranda, 1971).

The rate at which elements are eliminated from ruminant animals is influenced by factors such as body size, age, sex, physiological condition and activity (Reichle, Dunaway, and Nelson, 1970). Cesium turnover in reindeer is two or three times faster during summer than in winter (Holleman, Luick, and Whicker 1971).

The seasonal change in habitat and diet in addition to the biological factors, resulted in large seasonal variation in observed radiocesium concentration in reindeer, in central Norway after the accident in Chernobyl. This study monitored the seasonal changes and yearly reduction in concentrations of cesium 134 (Cs-134) and cesium 137 (Cs-137) in reindeer.

Material and methods

Samples were collected between 1986 and 1988 from reindeer in three herds, all in Central Norway, which suffered high levels of radiocesium (Cs-134 and Cs-137).

The herds were located in Østre-Namdal (North Trøndelag), Lom, and Vågå (Jotunheimen).

Every second month about fifteen reindeer were slaughtered for measuring concentration of radiocesium (10 adults and 5 calves). Whole body counting of radiocesium activity or blood samples of about 10-30 living reindeer were also taken.

The measurement of Cs-134 and Cs-137 concentrations in skeletal muscle was done by a Canberra 35, 3×3 inch NaI-crystal at the National Institute of Radiation Hygiene. The skeletal muscle samples were taken from the front leg (*biceps brachii*) with wet weight about 400 grams. The muscle samples were counted for 1 to 10 minutes. The blood samples were counted by spectrometry, using a LKB Wallac, 1280 Ultragamma with a NaI (Tl) scintillator at the Isotope Laboratory, Agricultural University of Norway. The blood samples were 5 ml, mainly based on analysis of red blood cells (RBC) and were counted for 30 minutes. Whole body counting was done by a mobile equipment, a Canberra 10 plus with a 3 inch NaI (Tl) detector with a multichanal analyser. The measurements were made for one minute between the animals back legs.

Results

Cs-134 and Cs-137 concentrations in reindeer were lower in winter 1987/1988 compared to winter 1986/1987 in all three areas. In Vågå, Østre-Namdal and Lom the mean reduction of radiocesium in adult reindeer (>1 yr) from the winter of 1986/1987 to that of 87/88 was found to be 32% (53.0-36.0), 50% (46.0-23.0), 43% (25.5-14.5), respectively. The corresponding figures for calves were 42% (45.0-26.0), 45% (40.0-22.0) and 24% (18.3-14.0) (Figure 1). The figures in brackets are the mean values in kBq/kg, all adjusted to skeletal muscle values.

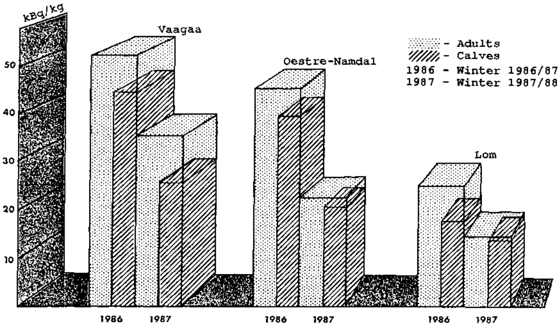

Fig. 1. Reduction of cesium 134 and 137 in reindeer (adults and calves) from Vågå, Østre-Namdal and Lom.

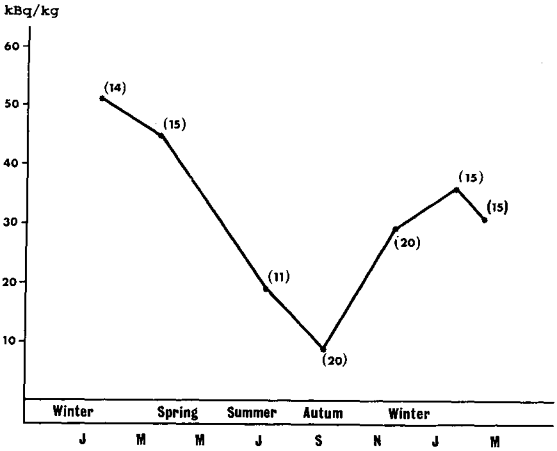

Fig.2. Seasonal variation of cesium 134 and 137 in reindeer (adults and calves) from Vågå. (In brackets - no. of samples).

Figure 2 illustrates the seasonal variation in the concentration of radiocesium in reindeer through out the year. All groups of animals are pooled together to show the main seasonal pattern for a reindeer herd as a whole. The values recorded range from 56.0 kBq/kg in January 1987, and the lowest 13.9 kBq/kg in September 1988.

In Lom the concentration of radiocesium in calves was about two times higher than in females (4.7 and 2.7 kBq/l, respectively) in July

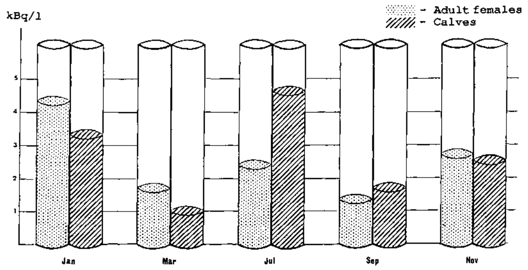

Fig.3. Cesium 134 and 137 in red blood cells (RBC) in reindeer females and calves at different seasons i Lom.

(Fig. 3). In November however, concentrations in calves and females were approximately the same. In late winter the relationship reversed, so that females had the highest values (4.8 and 3.3 kBq/l, respectively).

Discussion

The annual reduction of Cs-134 and Cs-137 in reindeer in the three areas investigated is greater than expected based on data from earlier studies (Martin et al., 1971, Reichle et al., 1970). However, the results are in accordance with other investigations of Cs-burdens in reindeer carried out in relation to the Chernobyl fallout (Skogland 1987, 1988). The main reason for this reduction of Cs-burden may be great reduction of radiocesium concentration in lichens and other plants during the first year after the reactor accident (Gaare 1988, 1989; Rognmo 1987).

The seasonal variation in the concentration of radiocesium in reindeer during winter was up to five times higher than in summer. The same pattern has previously been shown by Hanson, Whicker, and Lipscomp (1972). The high intake of lichens with a high concentration of radiocesium in winter (September to May) is obviously the main reason for the increase. The decrease in concentration of radiocesium in reindeer during summer was primarly due to decrease in radiocesium intake. Summerfood, namely deciduous shrubs, grasses and sedges, contains less radiocesium then do lichens. However, more rapid kinetics associated with the summer diet are likely to have contributed to a lower rodiocesium concentration in the animals. Holleman *et al.* (1971) observed that during the summer the kinetics of cesium are accelerated, being 2 to 3 times more rapid than during the winter.

Especially during summer, the results show a marked difference in radiocesium concentration, comparing adults and calves. Despite this, the data for these two groups are pooled together to form the basis for Figure 2. This is to show the main seasonal pattern for a reindeer herd as a whole.

The high radiocesium concentration values in suckling calves, compared to their mothers during summer may be caused by accumulation of radiocesium in reindeer milk (Eikelmann, unpub.). When suckling decreased in autumn, the concentration of radiocesium in calves declined to approximately the same level as their dams.

The results presented are preliminary, but are expected to show the main seasonal patterns in radiocesium accumulation in reindeer. Further studies will include other aspects of the radiocesium dynamics in reindeer.

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Modelling of radiocesium transfer in the lichen-reindeer/caribou-wolf food chain

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Abstract: The environmental contaminate radiocesium (cesium-137) has been shown to be of value as a marker in food selection and intake studies. Its greatest potential value as a food marker is in the subarctic/arctic regions, particularly in the lichen to reindeer/caribou to wolf food chain. A kinetic model describing the movement of radiocesium through the food chain has been developed using the SAAM computer program and is presented here. The program has been written so that the various paramenters affecting the transfer of radiocesium in the food chain can be altered more realistically to describe the system being modeled. The values of the parameters as given in this example are realistic for interior Alaska, however caution should be exercised in the application of the present results to regions that may be vastly different from the Alaskan interior without first evaluating the parameters and assumptions of the model.

Key words: Environment, fallout, transfer systems, cesium

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The computer program - SAAM and CONSAM

The computer program SAAM (Simulation, Analysis and Modeling) has been developed over a period of many years, primarily by the U.S. National Institute of Health. The program has been under continuous modification and is now available in a 'user interactive' form called CONSAM (conversational SAAM). SAAM and CONSAM will run on several computer systems including the Vax 11/780, DEC-SYSTEMS 10, UNIVAC, DEC 20 and the AT&T UNIX PC 7300. Information and tapes of the programs are available from:

Resource Facility for Kinetic Analysis
Center for Bioengeneering FL-20
University of Washington
Seattle, Washington 98195
U.S.A.

The computer program, version SAAM-29, was used in this study, however a later version, SAAM-30, is presently available.

In practice, the SAAM user writes a source input file in SAAM language which describes the model, and requests certain output. Output may be in the from of individual values, tabulated data or plots. A copy of the present source input file can be obtained form the authors.

The model - A description and the output

The transfer of radiocesium through the food chain is indicated in Figure 1. Radiocesium enters the reindeer/caribou via ingestion of contaminated forage and is subsequently transferred to the wolf. A two-compartment model is used to describe the kinetics of radiocesium in both

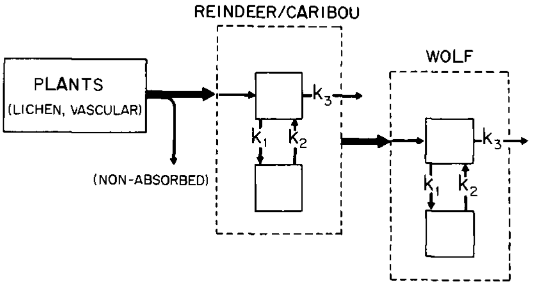

Figure 1. Radiocesium transfer in the lichen- reindeer/caribou-wolf food chain.

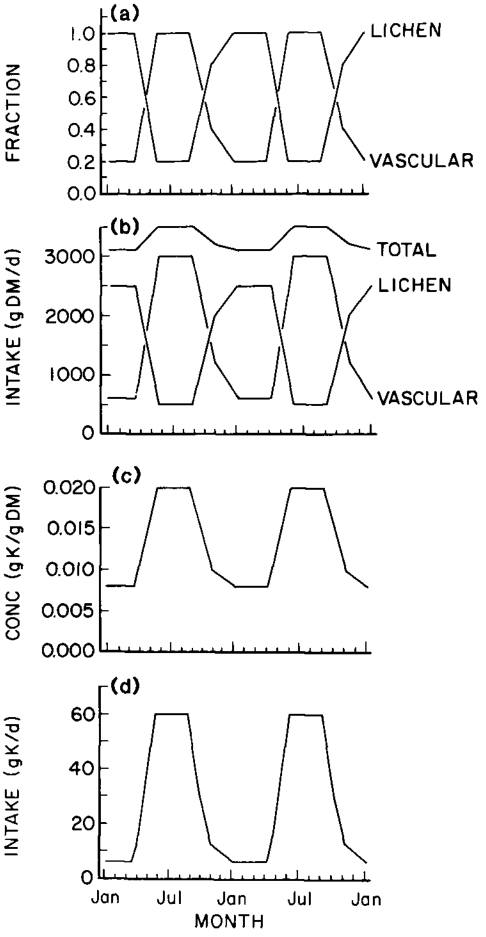

Figure 2. The potassuim intake rate of the reindeer-caribou and the input data that affect the potassium intake rate: (a) the fractional forage intake rate relative to the annual maximum intake for lichens and vascular plants, (b) the forage intake rates, (c) the potassium concentration in vascular plants and (c) the total potassium intake rate.

the reindeer/caribou and the wolf (Holleman *et al.* 1971; Holleman an Luick 1976).

Figures 2 - 5 show both input data and simulated output data of the model over a two year period. Input data can be altered in the program whereas simulated output data are the results from the execution of the program. It should be noted that the radiocesium concentration in the reindeer/caribou and wolf is arbitarily set to one initially (set to one instead of zero to prevent division into zero), which may be unrealistic but necessary since the actual values would be unknown. Therefore the initial part of the simulated output data, i.e., for 2-3 months, does not necesarily reflect what would normally be observed.

For the present simulation, the annual maximum intake rate of lichen and vascular plant by reindeer/caribou was assumed to be 2500 and 3000 g/d dry matter, respectively. The forage intake rate (fig. 2(b)) is the product of the annual maximum intake rate and the fractional intake rate relative to the annual maximum intake

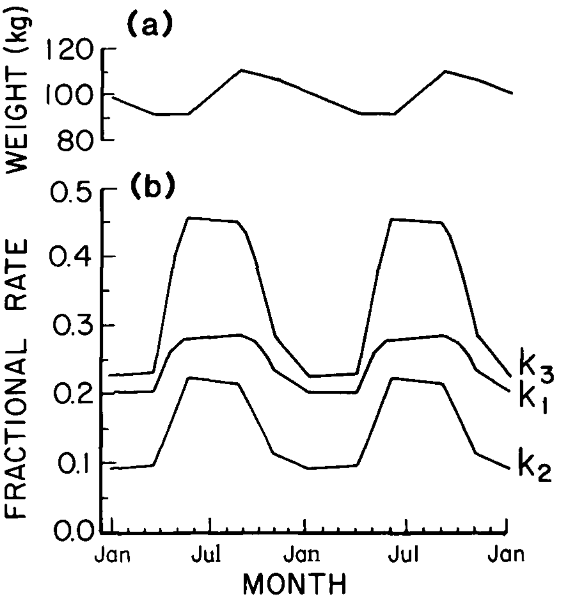

Figure 3. (a) Input data for the seasonal body weights and (b) the simulated output data for the seasonal kinetic parameters in reindeer/caribou.

rate (fig. 2(a)). The total potassium intake rate (fig. 2(d)) is the product of the forage intake rate and the potassium concentration in the respective forage (fig. 2(c) for vascular plants; 0.0005 g potassium per g dry matter for lichens).

In the present model the radiocesium kinetics in reindeer/caribou (fig. 3(b)) are dependent upon potassium intake rate and body weight (fig. 3(a)). The relationship between potassium intake rate and the kinetic parameters for reindeer/caribou (the k's - fractional rate parameters) are given in Allaye-Chan *et al.* (1990). The radiocesium kinetics for the wolf are assumed to be constant during the simulation.

The absorbed radiocesium intake for reindeer/caribou (fig. 4(a)) is the product of radiocesium concentration in the forage, the forage intake rate and the fraction of the radiocesium absorbed. In the present simulation the initial radiocesium concentration in lichen and vascular plants are assumed to be 0.1 and 0.005 Bq/g dry matter, respectively. The effective half-times of radiocesium in lichens and vascular plants are assumed to be 8.2 and 2.0 years, respectively. It was further assumed that 26% of the ingested radiocesium was absorbed (Holleman *et al.* 1971). Radiocesium concentrations in reindeer/caribou resulting from these assumptions are presented in figure 4(b).

The wolf was assumed to ingest 1000 g/d of

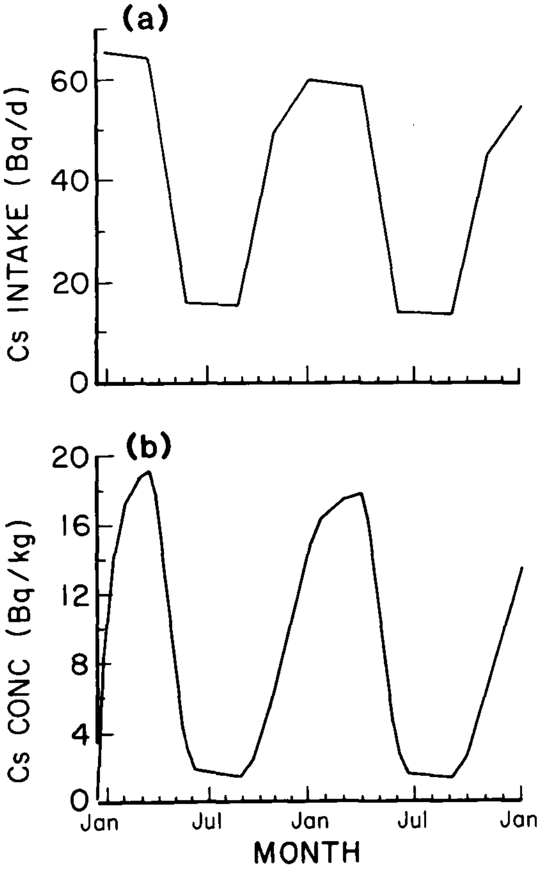

Figure 4. (a) Total radiocesium intake for reindeer/caribou and (b) the resulting radiocesium concentration in skeletal muscle of reindeer/caribou.

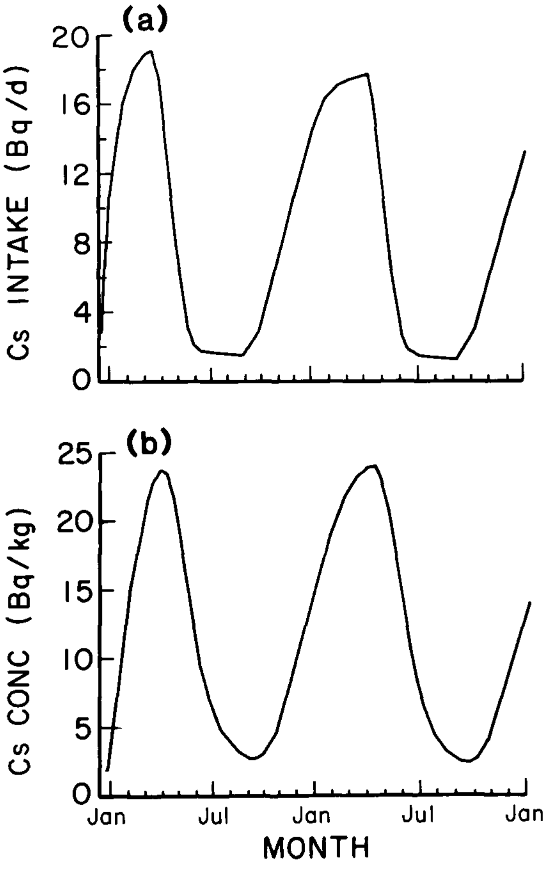

Figure 5. (a) Absorbed radiocesium intake for the wolf and (b) the resulting radiocesium concentration in skeletal muscle of the wolf.

reindeer/caribou muscle at the radiocesium concentration given in figure 4(b). All of the ingested radiocesium be the wolf was assumed to by absorbed. The resulting radiocesium intake rate for the wolf and the radiocesium concentration in the muscle of the wolf are given in figure 5.

Conclusions

The present model can be used to predict radiocesium concentrations in the reindeer/caribou and the wolf from known concentrations of environmental radiocesium. In this application the model could be used to evaluate the potential radiation dose from various levels of radiocesium in the environment. Also the model can be used to estimate food intake rates by reindeer/caribou and wolves from a knowledge of radiocesium concentrations in the study animal and in the respective food sources. In Alaska the model has been used to determine prey selection between caribou and moose for the wolf.

However, application of the model to other systems should include a careful consideration of the model's input data and assumptions to ensure that they are applicable to the system being modeled.

Acknowledgements

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Effect of Prussian blue (ammonium-iron-hexacyanoferrate) in reducing the accumulation of radiocesium in reindeer

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Abstract: Laboratory experiments. Prussian blue (Giese- salt) in doses of 50, 150, 300, 750 and 1500 mg was added to a daily ration of 1 kg reindeer feed (RF-71) and 0.25 kg lichen dry matter providing 8-10 KBq/d. Two reindeer calves were used per treatment, and the results compared to radiocesium accumulation in four control calves (no Prussian blue). Red blood cell activity increased in control animals from background levels to between 400 and 500 Bq/L and were still increasing after six weeks of observation. No accumulation of radiocesium could be detected in the calves treated with 300-1500 mg/d of Prussian blue. A moderate increase was observed at the lowest doses. Thus daily doses as low as 150 mg of the Prussian blue preparation practically prevented the absorption of radiocesium.

Field trials. Sodium chloride stones with 2.5% Prussian blue were provided to a herd with a body load of about 10 KBq/kg meat. After exposure to the stones for 24 d the average radioactivity in adult females was reduced from 10.5 to 6.6 KBq/kg (37%). Large differences in the intake of salt were evidenced by individual reductions in blood radioactivity varying from 0 to 70%. Salt eaters were easily distinguished by blue muzzles.

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Radiocesium metabolism in reindeer

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Abstract: Early in the era of atmospheric nuclear weapon tests, the reindeer was found to be an interesting animal concerning the transfer of environmental radioactive contaminants to man via the production of contaminated reindeer meat. The reason for the high transfer factors for some radionuclides is the feeding habits of the reindeer with a substantial intake of lichens, especially in the wintertime. One effect of the seasonal changes in feeding is also a considerable cyclic, seasonal variation in radiocesium content of soft tissues. The effective half-life of radiocesium was determined to about 30 days in an experiment where a herd of reindeer was moved form a high (>20 kBq/m^2 ^{137}Cs) to a low (<3 kBq/m^2 ^{137}Cs) contamination area. The fractional transfer of ^{137}Cs, during natural grazing, was determined to about 0.65 d/kg during wintertime on the low- contamination area and about 0.30 d/kg in summertime grazing in a more contaminated area. The radiation dose received by reindeers in Sweden after the Chernobyl accident was calculated to <200 mSv/a. The dose rate would be highest during the later part of winter but would not exceed 1 mSv/d.

Key words: reindeer, Chernobyl accident.

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Introduction

Radioactive pollutants from nuclear weapons tests were early detected in reindeer meat and the lichen-reindeer pathway was recognized as being interesting and important in the transfer of environmental radioactivity to man (Lindén & Gustafsson 1967; Miettinen 1967; Nevstrueva *et al.* 1967).

The reasons for this are mainly the feeding habits of the reindeer with a substantial intake of lichens high in radioactive contaminants (e.g. strontium, cesium and actinides) and a high transfer factor for radioactivity from reindeer-feed to meat. The grazing of lichens is high in wintertime, giving a substantial and typical seasonal variation in the radiocesium content of soft tissues with the highest concentration in late winter (Feb.-Mar.) (Lindén & Gustafsson 1967; NFA 1987). The disappearance of contaminants from the lichen plants is slow, which also adds to the long-term importance of reindeer meat as a potential contaminant of human foods (Westerlund *et al.* 1987).

Radioactive material, mainly ^{134}Cs and ^{137}Cs, from the Chernobyl nuclear power plant caused substantial contamintion of reindeer grazing areas in the middle part of Norway and Sweden. The total deposition in Sweden of the long-lived nuclide ^{137}Cs has been estimated to 3.4 PBq. Some 70,000 semi-domestic reindeer are normally kept by the local Sami families in the most contaminated ares. Wild game animals living in these areas have also been contaminated by radiocesium (Danell *et al.* 1989). A limited number of farmers have also been affected by contamination of their pasture mainly used for grazing of sheep and goats.

The level of radiocesium contamination, which was determined by aerial surveys already during the first month after the initial contamination and earlier studies of radiocesium transfer in reindeer (Ekman & Greitz 1967), showed that reindeer meat would contain ^{137}Cs well above the action level of 300 Bq/kg initially decided by the National Food Administration (NFA). The high radiocesium levels in reindeer meat will also persist for many years (Westerlund *et al.* 1987; Miettinen 1967). Several studies were therefore initiated in Sweden to find practical means to reduce the transfer of radioactivity to man from the reindeer forage - reindeer food chain.

The present study reports the results of moving about 5000 reindeer from their highly contaminated traditional winter grazing area in the middle part of Sweden to a less contaminated area further south where reindeer normally are not allowed to graze.

Material and methods

In late November 1986, the normal time for migration to the winter grazing area, about 5000 reindeer were moved by truck from the Gäddede area (lat. N 64° 15' - 64°55', long. E 12°) about 400 km south to Älvdalen (lat. N61°10', long. E 13°). The animals were allowed to graze in this area until late April 1987 when they were moved back to the normal spring grazing and calving area near Gäddede.

At monthly intervals, yearling bull calves were slaughtered both in the Älvdalen area and in the Gäddede area.

Samples were obtained form the flexor muscles of the fore limbs and from the ruminal content. All samples were analysed for radiocesium content and the ruminal samples were also analysed for potassium content by ^{40}K determination. Muscle samples were analysed as wet weight but plant material and ruminal samples were dried and analysed as dry matter (d.m.). To follow the seasonal changes of radiocesium in different plants, plant material was sampled in the area where the animals were grazing when slaughtered. These results will be presented elsewhere (Eriksson 1989).

The botanical composition was determined in the ruminal samples (Eriksson et al. 1981). The fractional transfer (f_m, d/kg) of ^{137}Cs from reindeer forage to meat was determined from the results of ^{137}Cs determination in meat and ruminal content.

Results and discussion

The average ^{137}Cs content of reindeer from the herd slaughtered in early November was 12 kBq/kg meat. Animals kept in the area throughout the winter had the same level or even increased levels in February - March when the highest levels normally are seen (Lidén & Gustafsson 1967; NFA 1987). These high levels are mainly due to the radiocesium contamination of lichens (e.g. *Cladina rangiferina)* which is the dominating feed in winter grazing conditions, which last from October to April in this area. Lichens grazed by these animals contain at least 10-15 kBq ^{137}Cs/kg d.m. (Eriksson et al. 1987).

The ^{137}Cs content of muscular tissue decreased, in this study, with an effective half-time of about 30 d when the animals had been moved to the low- contaminated area and were grazing lichens with a contamination level of <2 kBq/kg d.m. During the first week after tran-

Table 1. Measured content of ^{137}Cs in reindeer meat and calculated fractional transfer, f_m, of ^{137}Cs from natural grazing to meat. The daily potassium intake at different sampling times and the relative compositon of the ruminal contents are also shown.

Sampling time	^{137}Cs in meat kBq/kg	f_m d/kg	Daily K intake g/d	Lichen intake %	Vascular plant intake %
Nov	12	n.d.	n.d.	n.d.	n.d.
Jan	3	0.95	7	67	25
Feb	2.6	0.65	7	65	24
Mar	3.9	0.77	7	58	31
Apr	2.5	0.61	9	66	28
Jul	2.1	0.36	33	8	89
Aug	2.6	0.29	30	17	80
Sep	3.6	0.24	28	14	82

n.d. not determined

sportation of the reindeer the decrease was faster because they were fed uncontaminated hay in corrals.

The calculated fractional transfers, f_m, for different sampling times are shown in Table 1. Due to the seasonal changes in feeding habits of the reindeer its radiocesium metabolism will never be at steady state under natural grazing conditions. The calculated transfer factors therefore have to be evaluted together with the change in the body burden of radiocesium. The most reliable results will be seen in late winter and late summer, just before the major changes in forage selection occur (Eriksson 1989). The effects of these changes will be an overestimation of f_m in periods of decreasing radiocesium intake and an underestimation in periods of increasing intake, i.e. spring and autumn respectively, periods that are not specifically studied in this work. This effect is, however, indicated by the high f_m seen in January when these animals were still decreasing their body content of radiocesium after moving to the low-contamination area. If these effects are kept in mind the transfer of radiocesium to reindeer meat from a contaminated pasture can be estimated with reasonable accuracy if the radiocesium content of some specific forage plants are known. This type of information is valuable to the reindeer herders when planning grazing areas and slaughter times in a situation of substantial radiocesium contamination, such as after the Chernobyl accident.

The daily potassium intake of the reindeer, measured as ^{40}K, varies considerably through the year (Table 1). These variations reflect the different levels of potassium found in plants grazed by the reindeer. Lichens have a constant low potassium content throughout the year, about 2 to 4 g/kg d.m. (Åhman 1984) while most vascular plants which dominate summer feed intake have variable and in most cases substantially higher potassium levels, 20 to 35 g/kg d.m. (Hyvärinen et al. 1977; Wielgolaski et al. 1975). These differences are also confirmed by the present results, with a considerably higher potassium intake in the summer. The potassium intake of the reindeer in summer is similar to the intake of other herbivorous animals while the intake in winter is substantially lower. Earlier laboratory studies of cesium metabolism have not always shown clear effects of potassium suplementation within reasonable limits (Comar 1961) but in other studies increased potassium intake had decreased the body burden of radiocesium (Holleman et al. 1971). It is, however, possible that the considerable differences observed in potassium intake of reindeer can lead to effects on uptake, and f_m, of radiocesium under natural grazing conditions (Holleman et al. 1989).

The results of the botanical studies in this experiment will be reported in detail elsewhere (Eriksson 1989). The present study shows that natural grazing on low-contaminated pasture rapidly decreases the radiocesium content of reindeer and can be used as one effetive means of producing meat with, from a radiological point of view, acceptable levels of radiocesium.

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Elimination of radiocesium in contaminated adult female Norwegian reindeer

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Abstract: In an attempt to find practical solutions to the treatment of radiocesium contaminated reindeer, 8 adult female reindeer were fed naturally radiocesium contaminated lichen *ad lib.* for 35 days. The lichen contained on average 45 000 Bq/kg, and the food intake of lichen was on average 2 kg dry matter per day. Determination of radiocesium contamination was based on measurements of blood, after establishing that wet muscle contained 7 times more cesium than blood. In the experimental period accumulation of the isotopes ^{137}Cs, and ^{134}Cs combined was on average 400 Bq/kg wet muscle pr day. A daily oral administration of 250 mg ammonium-ferrohexacyanoferrate, (Giesesalt, Riedel-de Haën AG, Seelze, Germany), prevented net accumulation of radiocesium when reindeer were fed the above mentioned naturally radiocesium contaminated lichen *ad lib.*. The biological halftime of the cesium isotopes was determined to 25 days when reindeer were fed lichen, 10 days when they were fed RF-71, and 7 days when fed RF-71 *ad lib.* and orally treated with 250 mg Giesesalt pr day. Giesesalt mixed in artificial food, such as RF-71, seems to be very efficient in reducing the cesium burden of these animals. We have developed a constant releasing capsule (120 mm long and 21 mm diameter) containing Giesesalt, with an orifice of 15 mm. Four adult female reindeer have orally been given these capsules, which released on average 413 mg ± 286 mg pr day for 30 days. This prevented net absorption of radiocesium. In a separate series of experiments reindeer were given 2 g Giesesalt orally per day over a 2 month period without any ill effects.

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Systems ecology of radiocesium dispersal in forest landscapes and food

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Abstract: Persisting radiocesium in food of humans, reindeer, or other wildlife calls for research and assessments of the future. What trends in Cs are likely in forest and shrubland, as well as crops and pasture? Soon after Chernobyl fallout in 1986, Swedish berry plants, tree parts, organic and sandy soil were analysed. Now we can infer rates of transfer among a typical ecosystem's parts. Cs in food chains in Nordic woodlands seems likely to remain high for many years. I predicted such Cs would be removed to less available forms in soil minerals more slowly than Cs in Nordic crop systems, or in deciduous forest tagged with Cs-137 at Oak Ridge National Laboratory, Tennessee.* Cooler climate, partly evergreen plant habit, and many peat and sandy soils are among factors shared by Nordic countries that keep their Cs actively circulating in the ecosystem. Reindeer food chains in lichen woodlands (pine or birch) and seasonal pastures** seem important for testing improved modeling of natural processes of the system and predicting alternative scenarios, without waiting to see the real future. For this purpose, we need help in estimating lower and upper bounds for RATES: e.g. fractions per week of Cs in important parts (vegetation, consumers, residues, soils) moving to the other parts. Calculations using the resulting table (matrix) of sources and destinations would show net change (turnover) per week. Models combining many steps should imitate nature's redistribution of Cs. Displaying a range of possible future conditions and problems, and filling gaps in field or lab research, could clarify policy issues for reindeer and other ecological management.

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* J.S. Olson, Radiocesium in Swedish Forests, *Meddeland. fr. Växtbiol. inst. 1987:1*

** O. Eriksson *et al.,* Radioactivt Cs i Renbetet, *Medd. från Växtbiol. inst. 1987:2*

Studies on the ingestion of radiocesium from contaminated pastures in reindeer

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Abstract: Grazing experiment with two oesophageally fistulated reindeer were conducted during June to August 1987 in the Jotunheimen mountain range (1000-1400 m). Grazing in 4 different plant communities was compared: Mesotrophic birch forest dominated by heather, Oligotrophic community with poor snowcover dominated by heather and Dwarf birch, Oligotrophic community with moderate snowcover dominated by lichens and sedges and a snowbed community dominated by Least willow and lichens.

The radioactivity in food samples obtained from the fistula changed through the summer and differed between communities. from 8000 Bq/kg dry matter to 49000 Bq/kg dry matter. The major factor responsible for these changes was variations in the amounts of lichens ingested. Lichens beside mosses had the highest levels of radiocesium and consequently the amount of lichens consumed was the major single food item responsible for high intake of radioactivity.

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Radiocesium in lichens and reindeer after the Chernobyl accident

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Abstract: After the Chernobyl accident the sampling and measuring program of the Finnish Centre for Radiation and Nuclear Safety was intensified both for surveillance and research purposes. The deposition pattern of radionuclides was more complicated than from the global fallout after the nuclear weapons tests. The radioactive deposition was very unevenly distributed in Lapland, as also in the rest of Finland. Fortunately, the amounts of deposition in Lapland were only about one-tenth of the corresponding amount of deposition in southern Finland. In 1986-87 the mean concentration of Cs-137 in lichens and in reindeer meat increased to about the same level as in 1972-73 or to about 30 per cent of the maximum levels found in 1964-65 after the nuclear weapons tests. The activity concentrations in reindeer tissues vary according to season. In winter, reindeer eat considerable amounts of lichens with high radiocesium concentrations. In summer, lichens are replaced by other forage such as leaves from trees, green plants, etc. The ratio of Cs-137 concentration in reindeer meat between summer and winter is about 0.2. The mean concentration of Cs-137 in meat for consumption from the slaughtering period 1986-87 was 720 Bq/kg fresh weight. After that time concentrations started decreasing since no new fallout was deposited.

Key words: Cs-137, seasonal variation, Lapland

Rangifer, Special Issue No. 3, 1990: 55-61

Introduction

The radiocesium concentrations in lichens and reindeer were studied intensively in Finland (Miettinen and Häsänen, 1967, Rahola and Miettinen, 1977) as in other countries in the 60s and 70s (Åberg and Hungate, 1967) after the deposition of radioactive fallout originating in the atmospheric nuclear weapons tests. During the late 70s and the first half of the 80s samples from subarctic regions were taken and results reported were more sporadic than before. In Finland, the Finnish Centre for Radiation and Nuclear Safety has operated a laboratory at Rovaniemi on the Arctic Circle since 1970. This laboratory collected samples of lichens and other fodder plants eaten by reindeer, sampled reindeer tissues, fish and game in the 70s and early 80s (Rissanen et al., 1987). The intention of this sampling was to follow changes in radioactivity levels in the foodchain lichen-reindeer-man; this foodchain is the most efficient in radiocesium enriching in Lapland.

After the Chernobyl accident a more regular and intensified sampling program was started for both surveillance and research purposes. The radioactive deposition was very unevenly distributed in Lapland, as also in the rest of Finland. Fortunately, the amounts of deposition in Lapland were only about one-tenth of the corresponding amount of deposition in southern Finland (Arvela et al., 1987). Also in Norway (Bye, 1988, Gaare, 1986) and Sweden (Skålberg et al., 1987, Åhman et al., 1988) many investigations of lichens and reindeer were performed after the accident.

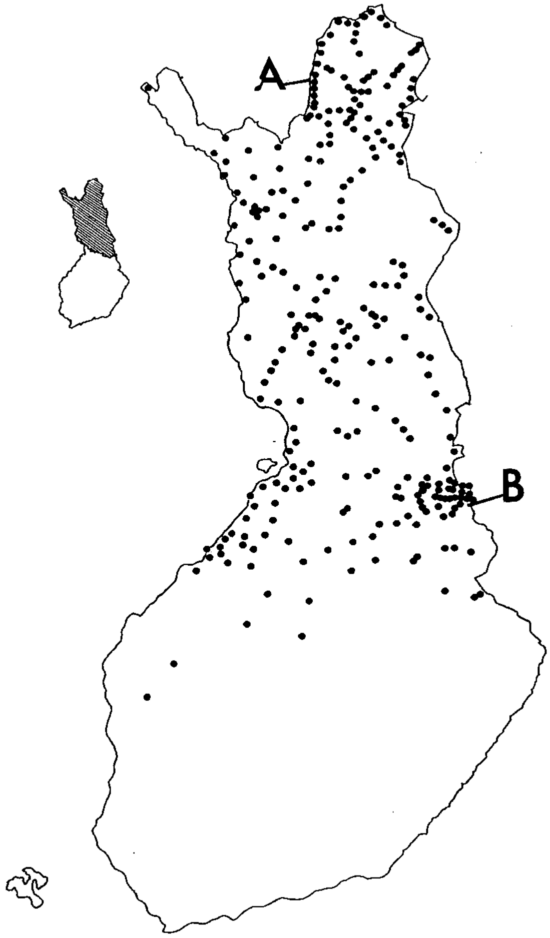

Fig. 1. Sampling locations for reindeer lichen in 1986 - 1987. All samples from the reindeer herding area (lined on the inserted map) are indicated but south of that area only the communities from which samples were taken. Results for the sample square collected from location A (Inari) are given in Table 1 and for those from location B (Kuhmo) in Table 2.

Material and methods

Lichen samples were collected by the Rovaniemi laboratory annually after the accident at Chernobyl. The collection locations for reindeer lichen are shown in Fig. 1. During 1986 and 1987 altogether 450 lichen samples were collected from the reindeer herding area and 200 samples south of this area. The species collected were *Cladonia stellaris*, *Cladonia mitis* and *Cladonia rangiferina*, the most important ground lichen species used as winter fodder by the reindeer (Fig. 2).

Fig. 2. 1) *Cladonia stellaris* a) whole, b) cleaved, 2) *Cladonia mitis* and 3) *Cladonia rangiferina*

After the Chernobyl accident about 11000 reindeer meat samples from all over Lapland were taken during the slaughtering season 1986-87 for surveillance and research purposes, and 4000 samples during the slaughtering season 1987-88. About 130 000 animals were slaughtered from a total of about 360 000 during each of these seasons.

All plant samples were dried and homogenized before the gammaspectrometric measurements. The meat samples were measured either fresh or dried and always homogenized. The measurements were performed with HPGe or GeLi detectors as described by Rissanen et al. (1987). All results presented are for plants given in Bq/kg dry material and for meat in Bq/kg fresh material.

Results

The Cs-137 concentrations in lichens collected in 1986 and 1987 from the reindeer herding area are presented in Fig. 3. The mean concentration in these lichen samples was 900 Bq/kg in 1986 and 800 Bq/kg in 1987, the concentrations varying from 200 to 2100 Bq/kg in both years. In Fig. 4, the Cs-137 concentration in lichen for the period 1961 to 1987 is presented. Only in Halla in a small corner (area V in Fig. 6) of the southeasternmost part of the reindeer herding district was the Cs-137 concentration in lichen higher, varying from 3 000 to 10 000 Bq/kg. Further south, Cs-137 concentrations even higher than 50 000 Bq/kg dry weight were measured, but fortunately no reindeer herding takes place at those locations.

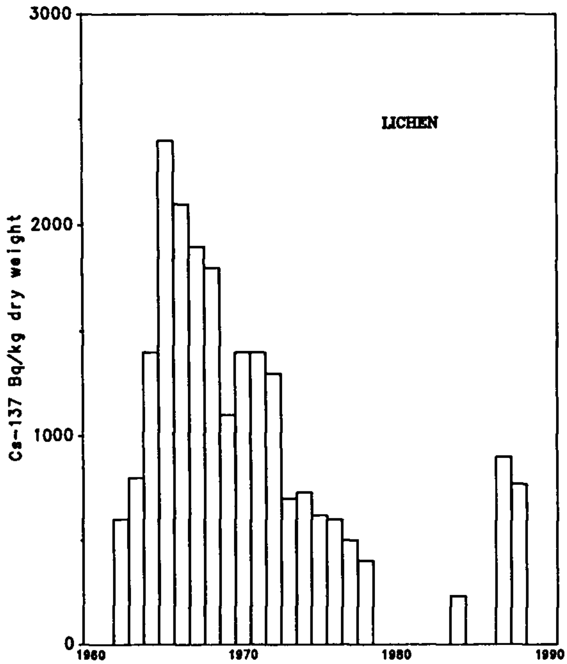

Fig. 3. Concentrations of Cs-137 (Bq/kg dry weight) in lichen collected in 1986 and 1987 from the reindeer herding area.

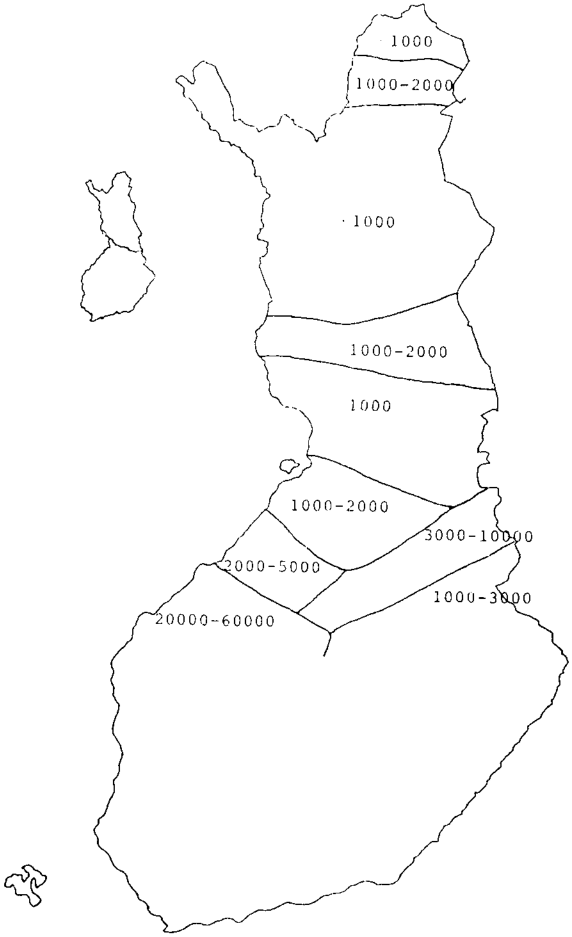

Fig. 4. Concentrations of Cs-137 (Bq/kg dry weight) in lichen from Lapland from 1960 to 1987.

In different lichen species collected from the same location, differences in activity concentrations could be detected as shown in Table 1 and 2. In *Cladonia stellaris* the activity was distributed so that the concentration in the top layer of the lichen was twice the concentration in the middle layer. The Cs-137 concentration in the whole lichen was about 70 per cent of that in the top layer. The amount of Cs-134 was 140 Bq/m^2 and of Cs-137 1200 Bq/m^2 calculated as a sum for all three *Cladonia* from Inari (marked A on map in Fig.6). The amount of Cs-134 was 3300 Bq/m^2 and of Cs-137 9200 Bq/m^2, calculated as a sum for all three *Cladonia* from Kuhmo (marked B on map in Fig. 6) to the south of the reindeer herding area. (Note: These figures include debris and top soil.)

Table 1. Measured Cs-134 and Cs-137 concentrations (Bq/kg dry weight) in different parts of three *Cladonia* species collected in 1987 at Muotkatunturi, Inari. The sampled area was 0.5 m^2.

Part of lichen	*Cladonia stellaris* ^{134}Cs	*Cladonia stellaris* ^{137}Cs	*Cladonia mitis* ^{134}Cs	*Cladonia mitis* ^{137}Cs	*Cladonia rangiferina* ^{134}Cs	*Cladonia rangiferina* ^{137}Cs
Top layer	340	1400	—[a]	—	—	—
Middle layer	130	610	—	—	—	—
Lower layer	89	450	—	—	—	—
Whole lichen	190	850	150	870	180	870
Debris[b]			54	510		
Top soil[b] 1-2 cm			0[c]	160		

[a] not separated into layers
[b] debris and top soil from the sampled area 0.5 m^2
[c] below detection limit

Table 2. Measured Cs-134 and Cs-137 concentrations (Bq/kg dry weight) in different parts of three *Cladonia* species collected in 1987 at Lipukkajärvi, Kuhmo. The sampled area was 0.25 m^2.

	Cladonia stellaris ^{134}Cs	*Cladonia stellaris* ^{137}Cs	*Cladonia mitis + rangiferina* ^{134}Cs	*Cladonia mitis + rangiferina* ^{137}Cs
Top layer	4100	11000	—[a]	—
Middle layer	2200	6000	—	—
Lower layer	1800	4800	—	—
Whole lichen	3000	8100	3300	8800
Debris[b]	1340	3600		
Top soil[b] 1-2 cm	200	730		

[a] not separated into layers
[b] debris and top soil (1-2 cm) from the sampled area 0.25 m^2

Cs-137 concentrations in reindeer meat since 1960 are presented in Fig. 5, the highest concentration, 2600 Bq/kg, being measured in 1964. The meat still contained 300 Bq/kg in 1985-86. After the Chernobyl accident in the winter of 1986-87 the level was 720 Bq/kg and

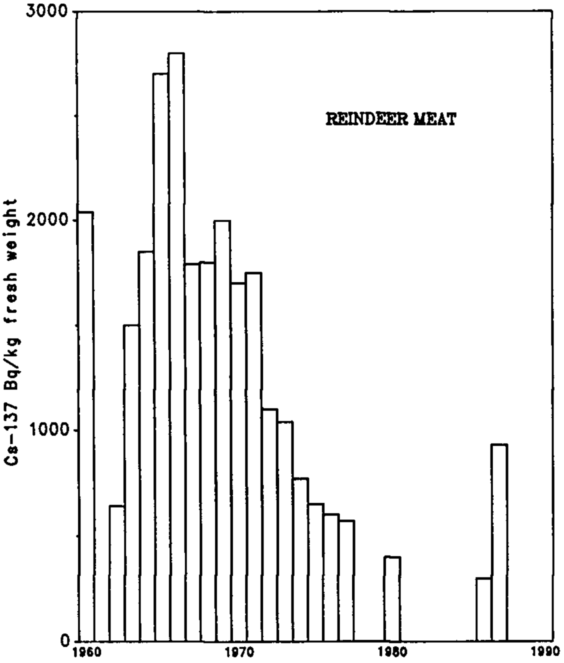

Fig. 5. Concentrations of Cs-137 (Bq/kg fresh weight) in reindeer meat in 1960 - 1987. The meat samples were collected during the first quarter of the year.

one year later 640 Bq/kg fresh weight. In the Halla area (area V in Fig. 6), the concentrations were higher and therefore samples were taken from each slaughtered reindeer for surveillance purposes.

The Cs-137 concentrations, Bq/kg fresh weight in reindeer meat, in the five areas (Fig. 6) of the reindeer herding district from June 1986 to March 1988 are presented in Fig. 6. The seasonal variation can be clearly seen in this figure. The Cs-137 concentration in summer is about 20 per cent of that of the winter maximum.

Discussion

The higher radiocesium concentrations in lichen in region V of the reindeer herding area result in higher radiocesium concentrations also in reindeer tissues. Only less than 1 per cent of all Finnish reindeer live in this region with a tenfold radiocesium deposition compared to the rest of the reindeer herding area. Samples from every reindeer slaughtered in area V were taken. Based on these sample measurements it was decided whether the meat could be delivered for consumption or not.

The activity concentrations in reindeer tissues vary largely from one season to another due to the composition of the diet of the reindeer. During winter, the semidomestic reindeer eat considerable amounts of lichen. Lichens contain higher amounts of activity than other forage. In summer, when the reindeer start eating tree leaves and green plants, the activity concentration in the meat decreases rapidly. In Finland, the main slaughtering period of reindeer is from October to January. From Fig. 6 it can be seen that this period is more favourable for slaughtering than would be the period December to March regarding activity concentrations.

After the Chernobyl accident the Cs-137 concentrations in reindeer tissues varied much more than before the accident depending on sampling location. This was a consequence of the unevenly distributed deposition and a similar variation could be found all over Finland. Thus it is important to have detailed knowledge of the factors influencing activity concentrations in sampled foodstuffs before drawing conclusions about the necessity for restrictive measures to protect the population from receiving unacceptably high radiation doses.

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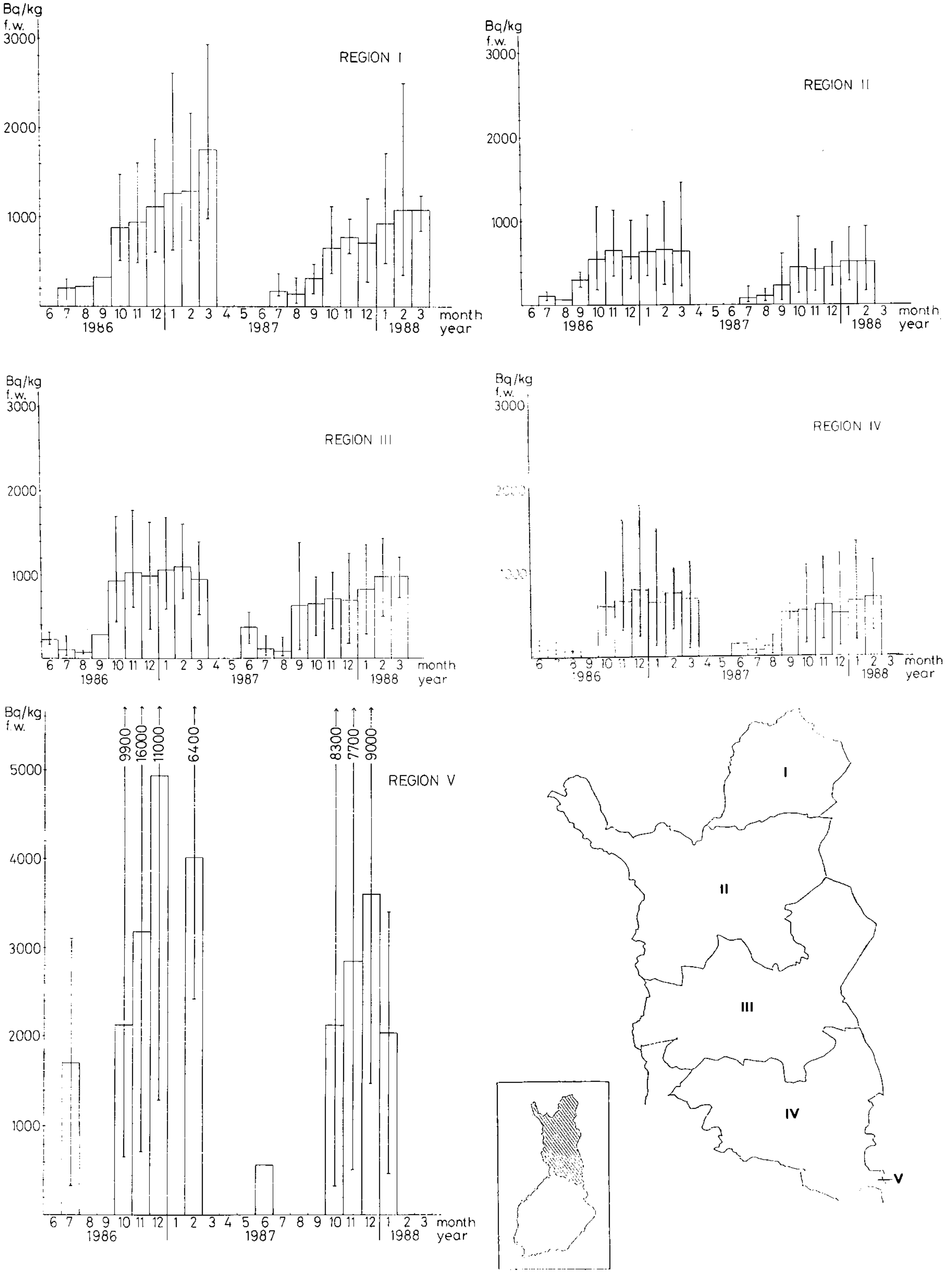

Fig. 6. Concentrations of Cs-137 (Bq/kg fresh weight) in reindeer meat from five different regions of the reindeer herding area from June, 1986 to March, 1988.

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Transport and recycling of radiocesium in the alimentary tract of reindeer

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Abstract: Transport of radiocesium between the body pools and the alimentary tract was studied in 7 reindeer calves. Comparisons were made between reindeer receiving the Cs- binder Prussian blue (Ammonium-ironhexacyanoferrate) and untreated animals.

The calves were fed lichens contaminated with ^{134}Cs + ^{137}Cs from the Chernobyl accident (about 10 kBq/day) for 4 weeks. Absorption and secretion of radiocesium, Na and K in the alimentary tract were calculated using ^{51}Cr-EDTA as a reference substance. Thirteen sections of the alimentary tract were sampled and analysed for radionuclides and chemical composition. In 4 animals, feeding with contaminated lichens continued until they were slaughtered, whereas in the 3 others the lichen feeding terminated 4 days before slaughter.

The activity concentration of Cs nuclides increased 5-17 - fold from duodenum to the distal colon, whereas the concentration of Na decreased and K remained almost constant. Radiocesium, Na and K were secreted into the rumen, the omasum and the abomasum, whereas Na and K also were secreted into the proximal small intestine. Prussian blue had no effect on Na and K recycling, but the flow of radiocesium from the abomasum to the anus and the fecal excretion increased markedly. In the 3 animals where feeding with contaminated lichens was disconutinued 4 days before slaughter, endogenous Cs was continuously recycled between the body pools and the alimentary tract. The net exchange of radiocesium between body pools and the alimentary tract was more than 4 times the amount ingested when lichens were fed. It is concluded that radiocesium is rapidly recycled between the alimentary tract and the other body pools. Cs-binders like ammonium-ironhexacyanoferrate may bind both endogenous Cs and Cs from feed.

Key words: Absorbtion, secretion

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Introduction

Reindeer require relatively large areas of plant growth to cover their energy requirements, and were therefore particulary susceptible to the airborne pollution of radiocesium from the Chernobyl accident. Radiocesium enters biological systems rapidly and is assumed to distribute in plant and animal tissues much like K. Within the reindeer body Na and K recycles rapidly between the alimentary tract and the other body pools (White *et al.* 1984. Staaland *et al.* 1986). As an alkali metal, Cs may be assumed to behave in a similar fashion, allowing an equilibration of endogenous Cs with freshly ingested Cs in the alimentary tract. Cesium binders of both the clay mineral (bentonite) and Prussian blue type (ammonium-ironhexacyanoferrates) have been used to reduce the radiocesium burden in farm animals an in domestic reindeer after the Chernobyl accident. Part of their effectiveness has been attributed to a possible binding of radiocesium which recycles from the body to the alimentary tract.

The biological half life of total body radiocesium is about 3 weeks in roe deer (Molzahn *et al.*1987), 1-3 weeks in reindeer (Holleman and Luick 1975) and 2-4 weeks in sheep and cattle (Howard *et al.* 1987; Goldman *et al.* 1965; Sansom 1966). Whole body estimates of Cs turnover do not, however, give information about cycling of radiocesium between the different cesium pools in the organism.

The purpose of the present paper is to study the patterns of secretion and absorption of radiocesium along the gastrointestinal tract of reindeer, and to locate the parts of the tract of interest for the binding of radiocesium to Prussian blue.

Material and methods

Seven male reindeer calves, 8-10 months old, were used. The animals were obtained from semidomestic herds in Southern Norway, and brought to the Agricultural University of Norway in September and November 1986. The reindeer were kept indoors (10°C) tied to their cribs from the time of arrival until slaughter. A commercial pelleted reindeer feed, RF71 with 4 percent $NaHCO_3$ added as a buffer, was used as the basic feed (Jacobsen and Skjenneberg 1979). In addition, the reindeer received lichens and at intervals some grass silage. The animals were fed twice a day. Before slaughter the body loads of ^{134}Cs + ^{137}Cs were brought up to 1-2 kBq/kg muscle tissue by feeding the animal about 320 g lichen DM/d for 4 weeks.

The lichens were collected in the Jotunheimen area of Southern Norway and were contaminated with radiocesium from the Chernobyl accident. The daily intake of ^{134}Cs + ^{137}Cs was about 9.9 kBq. In addition, 1 kg RF71 was given. The animals were divided into 3 groups. In 2 groups (I and II, Table 1) feeding with lichens continued until slaughter whereas in the

Table 1. Experimental design, feeding and treatments with ammonium-iron (III) hexcyanoferrate (II) (AFCF) and ^{51}CrEDTA. The treatments were carried out for 4 days prior to slaughter.

			Feed intake							
Group No.	Anim. No.	BW kg	Lichens g/d	RF 71 g/d	Total g/d	AFCF mg/d	^{51}CrEDTA kBq/d	^{134}Cs+^{137}Cs kBq/d	Na mmol/d	K mmol/d
I	653	54.5	319	880	1199	0	329	9.9	486	221
	1003	52.0	319	880	1199	0	329	9.9	486	221
II	831	47.0	319	880	1199	500	329	9.9	486	221
	15	38.5	319	880	1199	500	329	9.9	486	221
III	195	55.0	0	998	998	525	218	0	548	244
	11	49.5	0	998	998	525	218	0	548	244
	34	51.5	0	567	567	525	218	0	311	138

third group (III) the reindeer were fed RF71 only for 4 days prior to slaughter.

All animals were given ^{51}CrEDTA sprayed on the feed for 4 days before slaughter. Equal doses of ^{51}CrEDTA were given at 08.00, 16.00 and at 23.00 (Table 1). Group III were given 500 mg/d Ammonium-iron (III) hexacyanoferrate (II) (AFCF, Riedel de Haen, West Germany) commonly known as Prussian blue, sprayed on the morning meal. The group III animals received the daily dose of AFCF divided in equal parts sprayed on RF71 together with ^{51}CrEDTA and given 3 times per day.

On the fourth day all animals were killed by a shot in the head. Muscle samples for determination of radiocesium activity were taken from the hind leg. The whole gastrointestinal tract was immediately removed and divided into 13 different sections: (Fig. 1): rumen, reticulum, omasum, abomasum, small intestine (3 sections), caecum, proximal colon, spiral colon (2 sections) and distal colon (2 sections). The content in each section was weighed and samples for chemical analyses and measurements of radioisotopes were kept frozen until analyzed. Also samples of food were kept frozen and analysed for chemical composition and content of radioisotopes.

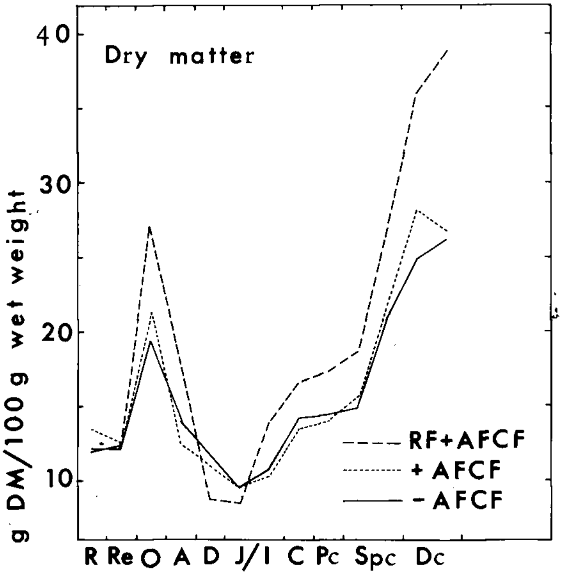

Fig. 1. Concentrations of dry matter along the alimentary tract of reindeer fed different diets and with and without treatment with Ammonium-ironhexcyanoferrate (AFCF); RF fed RF71 and given 525 mg AFCF/d (n=3); +AFCF fed lichens and RF71 and given 500 mg AFCF/d (n=2); -AFCF fed lichens and RF71 (n=2). R, rumen; Re, reticulum; O, omasum; A, abomasum; D, duodenum; J/I, jejunum/ileum; C, caecum; Pc, proximal colon; Spc, spiral colon; D, distal colon.

The activity of ^{134}Cs,^{137}Cs and ^{51}Cr in digesta food and muscle samples (300 g) were measured in 200 ml plastic vials using a Germanium detector connected to a Canberra 85 Multichannel Analyzer at the Isotope laboratory of the Agricultural University.

Alimentary contents and feeds were dried at 105°C for 24 hrs to determine dry matter content. The residues after ashing (625°C for 12 hrs) were dissolved in hydrochloric acid and diluted. Na and K were determined by atomic absorption spectrophotometry.

Samples of saliva were collected as previously described (Staaland *et al.* 1980). Na and K in saliva were determined by flame photometry and the content of radioactive Cs was measured in 5 ml samples in a LKB Wallac 1280 Ultrogamma Scintillation counter equipped with a 3 inch sodium- iodide detector.

The data were analysed by a model which assumes that a constant amount of ^{51}CrEDTA flows through each section of the intestine per day.

Based on the measurements of ^{51}CrEDTA concentrations into each section (M_i), and assuming that the ^{51}CrEDTA entry (M) into each section equals the amount ingested per day, the volume of wet mattter (M/M_i) per day passing through each section can be calculated. The amounts of ions, e.g. Na, K or radiocesium, leaving each section is calculated from this flow rate and local concentrations (C_i) (White *et al.* 1984).

The secretion or absorption in each section of the alimentary tract is thus the difference between flow into and flow out of the segment. Starting with the rumen, the net absorption or secretion is equal to the difference between nutrient or minerals in the food (Fo) and flow out of rumen. The sum of absorption or secretion in rumen/reticulum is the difference between food intake and flow out of reticulum. Similar calculations were carried out for each section of the alimentary tract. The cumulative exchange ($CABS_i$) therefore sums up the cumulative absorption or secretion from rumen through section i (i=1-13) of the alimentary tract Eq.1.

$$\text{Eq.1. } CABS_i = Fo - (M/M_i) * C_i$$

To visualize the activity of each site, the cumulative exchange ($CABS_i$) of Na, K and radiocesium between ingesta and body of the reindeer for each successive compartment were plotted graphically against the position of the compartment in the alimentary tract. This graph gives a visual documentation of cumulative exchange, i.e. absorption or secretion, of each element in each compartment of the tract. The approach is very sensitive to site-specific changes in nutrient exchange. The difference $CABS_{i-1}$-$CABS_i$, which can be read from the diagrams, gives the net secretion or absorption in each section.

Results

At the time of slaughter the combined concentrations of ^{134}Cs and ^{137}Cs in muscle tissues ranged from 822-2012 Bq/kg wet weight, whereas salivary activity was from 26-539 Bq/l (Table 2). Mean salivary concentrations of Na and K were 71 ± 25 and 11 ± 7 mmol/l. In the rumen and reticulum the dry matter content of ingesta was similar on all diets, whereas in the distal part of the alimentary tract animals fed a pure RF71 diet had a higher dry matter percentage than those fed a mixed RF71/lichen diet. No effect of treatment with AFCF on dry matter content was apparent (Fig. 1). The concentration of ^{51}Cr declined from the rumen/-reticulum to the abomasum and proximal small intestine. From then on a steady increase to the rectum was observed (Fig. 2). The combined activity of ^{134}Cs and ^{137}Cs followed basically the same pattern, except that an increase in acitvity was found in the omasum. The concentration gradient of ^{134}Cs + ^{137}Cs differed from that of Na and K (Fig. 2). Within the alimentary tract the stomachs dominated as the major pool for radionuclides and Na and K as well as water and dry matter (Table 3). However, relatively more of the total gastrointestinal pools of radionuclides than of Na, K, water and total digesta were found in the large intestine.

Table 2. Radiocesium in muscle tissue (Bq/kg wet weight) and in saliva (Bq/l) at the time of slaughter.

Group No.	Animal No.	Muscle	Saliva
I	653	1287	539
	1003	1806	x
II	831	822	159
	15	1285	119
III	195	1093	26
	11	1240	86
	34	2012	64

[x] Sample contaminated.

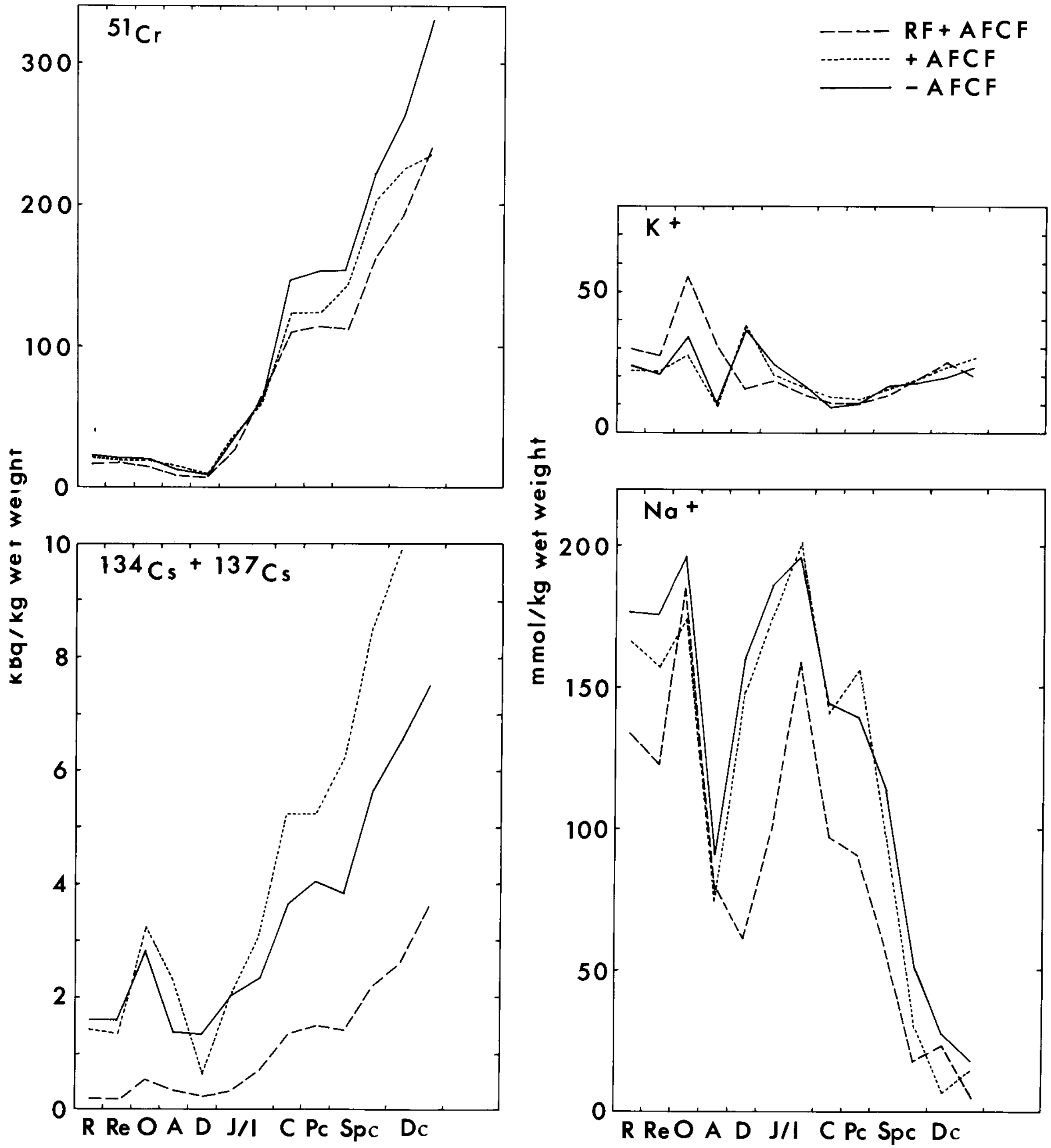

Fig. 2. Mean concentrations of ^{51}CrEDTA,^{134}Cs + ^{137}Cs, Na and K along the alimentary tract of reindeer fed different diets and with or without treatment with (AFCF). Abbreviations are given in Fig. 1.

The total pool of radiocesium in the alimentary tract for those animals continuously fed contaminated lichens exceeded that in the daily feed by 4.7 and 6.6 kBq in groups I and II, wheras alimentary ^{51}CrEDTA was 88, 90 and 124% of daily intake in groups I-III respectively (Tables 1 and 3). Patterns of absorption and secretion along the alimentary tract were calculated according to descriptions given above and White *et al.*(1984) (Fig. 3). The diagrams (as decribed above) express the cumulative absorption and secretion in relation to the amounts

Table 3. Distribution of material in the alimentary tract of reindeer (average and standard deviation). Group 1: Fed lichens and RF71, Group II: Fed lichens and RF71 and given AFCF, Group III:Fed RF71 and given AFCF. For further explanations see Table 1.

	Total alim. pool size			Stomach (% of total)			Small int. (% of total)			Large int. (% of total)		
Group No.	1	II	III	I	II	III	I	II	III	I	II	III
n	2	2	3	2	2	3	2	2	3	2	2	3
Total content (kg)	7.8	8.4	104 ± 1.2	83.1	85.1	88.4 ± 8.0	7.6	7.0	5.6 ± 0.8	9.3	8.0	6.0
Water (kg)	6.8	7.3	9.4 ± 1.5	83.3	85.1	86.6 ± 1.0	7.7	7.2	5.6 ± 1.1	9.0	7.7	7.8 ± 2.0
Na (mmol)	1324.6	1328.8	1341.4 ± 269.3	84.8	86.0	90.6 ± 1.9	8.4	8.1	5.8 ± 1.1	6.8	5.8	3.6 ± 0.8
K (mmol)	170.5	177.3	291.3 ± 39.3	87.4	87.8	94.2 ± 1.0	7.8	6.7	3.0 ± 0.4	4.8	5.5	2.8 ± 0.6
^{134}Cs + ^{137}Cs (kBq)	14.6	16.5	3.0 ± 1.2	70.9	67.2	55.7 ± 4.7	8.3	8.3	11.2 ± 1.7	20.8	24.5	33.1 ± 4.7
^{51}Cr (kBq)	295.2	289.7	268.8 ± 10.4	49.3	57.9	60.5 ± 4.3	9.6	9.1	10.4 ± 1.4	41.2	33.0	29.1 ± 3.1

ingested. Values above the zero line show a net absorption relative to the amounts in the feed, and values below the line a net secretion. Negative slopes on the curve show secretion into the gastrointestinal tract whereas positive slopes shows absorption. From the diagrams it therefore appeared that radiocesium was secreted into the rumen/reticulum and apparently also into the omasum and abomasum. Absorption mainly took place in the small intestine. The absorption was less efficent when the animals were given AFCF (Fig. 3).

Similar patterns were observed for Na and K, but these elements were also secreted into the duodenum in large quantities. No effect of AFCF on absorption of these elements was detected.

Irrespective of diet or treatment with AFCF, the larger part of radiocesium flowing out of abomasum (67-80%) was absorbed in the intestines (Table 4).

Discussion

The alkali metals Na and K are rapidly recycled between the body pools and the gastrointestinal tract. The exchangeable pool of Na in the reindeer was about 60 mmol/kg BW (Staaland *et al.* 1982). The exchangeable pool of a reindeer weighing 50 kg (Table 1) would therefore be about 3000 mmoles. In the present study, as a consequence of the buffer in the RF71, the daily intake of Na was high (500 mmol). Nevertheless it appeared (Fig. 3) that the net daily exchange of Na between the gastrointestinal tract and the tissues was of the same order of magnitude as the total exchangeable body pool and by far exceeded the daily amount in food. The total body burden of ^{134}Cs + ^{137}Cs was not measured. However, Holleman *et al.*(1971), found that 78.9% of Cs body burden was located to the skeletal muscles, and muscles constituted 40.7% of the total body weight. Using their estimates, the

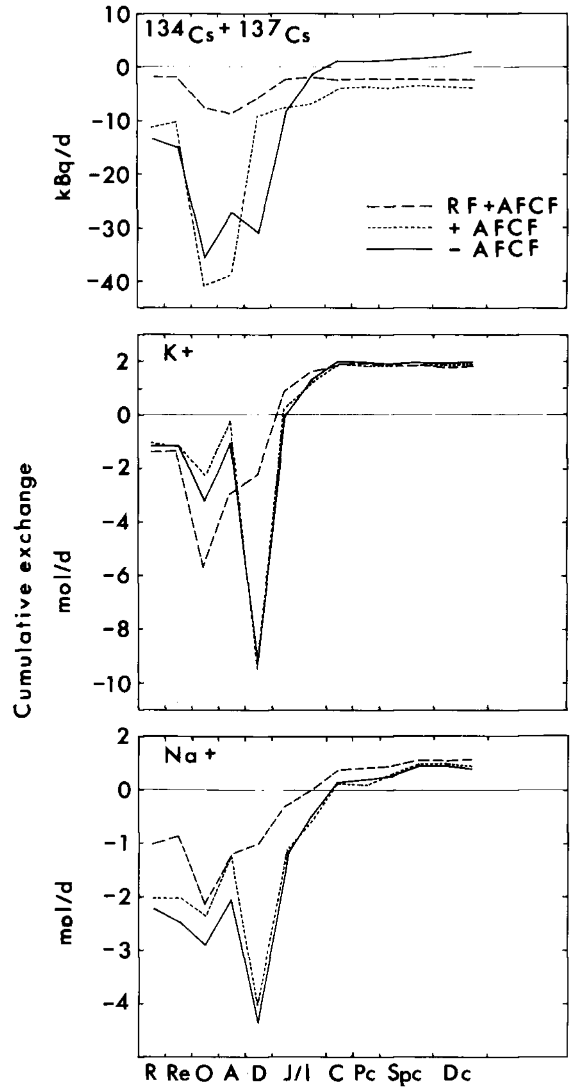

Fig. 3. Cumulative absorptions of radiocesium, Na and K in the alimentary tract of reindeer fed defferent diets and with and without treatment with AFCF. Negative changes indicate secretion and positive changes indicate absorption. Calculations for each element are made in relation to respective dietary intakes. Abbreviations are given in Fig. 1. For further explanations see text.

average body burden of radiocesium in our animals would be about 35 kBq. In the lichen-fed animals the daily flow of radiocesium out of the abomasum was 40-50 kBq, indicating a secretion of at least 30 kBq/d (Fig. 3, Table 4). The magnitude of net radiocesium exchange per day between the alimentary tract and the body therefore apppeares to be of the same order of magnitude as the total body pool of the animal.

After 4 days of feeding with only concentrate, the amount leaving the abomasum had declined to about 9 kBq/d, indicating a drastic reduction in the rate of radiocesium secretion to the upper gastrointestinal tract. A possible explanation of this may be a rapid decrease in the most readily available pools of radiocesium (Extracellular fluid and tissues with a rapid turnover of potassium). The present experiment does not allow us to draw any conclusions as to where this depletion occured.

The large recycling of alkali minerals, including Cs, contrasts to finding for bivalent and trivalent ions like Ca, Mg and P (White *et al.* 1984, Staaland *et al.* 1986). For these minerals small fractions only of the body pools seemed to be involved in exchange with the contents of the gastrointestinal tract.

Between radioactive Cs and Na and K there were differences with respect to the sits in the gastrointestinal tract where absorptions or secretions took place. All elements were secreted into the rumen/reticulum (Fig. 3). A major contribution is through saliva because of high concentrations and large volumes of saliva in ruminants (Table 3).

In addition, there was a large net secretion into the proximal small intestine of Na and K, whereas radioactive Cs apparently was secreted into the omasum and abomasum.

The method of slaughtering animals and the use of a non-absorbed marker to calculate absorption and secretion patterns in the gastronintestinal tract may not, however, be applicable in the omasum. Here, this method is most likely invalidated because of the preferential movement of the liquid phase of the ingesta through this organ (Engelhardt and Hauffe 1975, Faichney 1975, White *et al.* 1984). Irrespective of these errors there was an apparent large flow of radioactive Cs from abo-

Table 4. Nutrient flow and mean digestion of alkali elements in the alimentary tract of reindeer ± S.D. Group I: lichens and RF71; Group II: lichens and RF71 and given AFCF; Group III: RF71 and given AFCF. For further explanations see Table 1.

	Na			K			^{134}Cs+^{137}Cs		
Group No.	I	II	III	I	II	III	I	II	III
n	2	2	3	2	2	3	2	2	3
Intake (MMol/d or Bq/d)	4861	486	469 ± 137	221	221	209 ± 61	9876	9876	0
Leaving abomasum (mmol/d or Bq/d)	2605	1777	1818 ± 391	334	243	494 ± 70	37203	49008	8857 ± 7020
Leaving ileum (mmol/d or Bq/d)	1025	1126	540 ± 99	88	88	49 ± 9	12128	17108	2396 ± 629
Fecal output (mmol/d or Bq/d)	19	33	9 ± 15	23	35	21 ± 8	7522	14098	2953 ± 1344
Net absorption (mmole/d or Bq/d)	467	463	539 ± 15	198	186	188 ± 57	2354	-4222	-2953 ± 1344
Mean apparent dig. (% of intake)	96	95	98 ± 3	89	85	90 ± 1	24	-43	—

masum to duodenum (Table 4). Absorbtion of Cs and K seemed to be completed when the digesta reached the caecum, whereas Na also was absorbed in the large intestine (Fig. 3). There were also marked differences in absorption and secretion patterns between feeding regimens. The animal fed only the pelleted rations had secretion and absorption patterns in the proximal part of the intestine which differed from those also receiving lichens in the diet. These findings agree with previous studies (White *et al.*1984, Staaland *et al.*1986).

In the present study a close connection between the secretion of Cs and K was not apparent in the gastrointestinal tract since Cs mostly seemed to be recycled into the stomachs and K into the small intestine. In provious studies, Holleman and Luick (1975) observed reduced biological half life for Cs in reindeer in early summer. They explained this observation by increased intake of K from new growth of green vegetation in spring. A reduction in body retention of Cs has also been observed in rats following a very high increase in the intake/l of K (Wassermann and Comar 1961), but the effect of adding K to the diet of naturally Cs contaminated sheep was negligible (Hove and Ekern 1988). Further studies are therefore needed to explain the relationship between K and Cs excretion in animals.

The stochiometry of the chemical reaction between radiocesium and AFCF is not known since the concentrations of cold Cs in the digesta were unknown. However, the reaction seemed to be specific in the alimentary tract since there apparently was no effect of AFCF on the other alkali elements. According to our findings, the main function of the Cs binder is to inrease the alimentary flow of radioactive Cs by keeping Cs bound to a large molecule that cannot absorbed (Table 4). The increased flow rate is mainly achieved in the proximal part of the gastrointestinal tract and is maintained throughout the small and large intestine to the rectum (Fig. 3).

The large flow of radiocesium measured by the present method must to some degree represent a rapid recycling between the plasma pools and the gastrointestinal contents. Intracellular radiocesium shows a half life which is by no means compatible with the high gastrointestinal fluxes of radiocesium. It may therefore be expected that the fraction of the total body pool avilable for exchange with radiocesium will be rapidly reduced after a few days of treatment with AFCF or other cesium binders.

In the distal part of the alimentary tract very little Cs was secreted or absorbed. The addition of AFCF to the feed during the last 4 days before slaughter enabled the animals to greatly increase their fecal output of radiocesium. The negative net absorption in Table 4 showed that AFCF actually was instrumental in reducing the body burden of radiocesium during lichen feeding.

The effect of AFCF on radiocesium seems therefore to be an increased flow through the alimentary tract and increased rectal flow during AFCF administration. AFCF apparently binds part of the radiocesium in the stomach and keeps this element bound through the alimentary tract and thus prevents its absorption. This again cause a net fecal loss instead of a net absorption of radiocesium from the alimentary tract.

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Zeolite and bentonite as caesium binders in reindeer feed

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Abstract: The effects of zeolite and bentonite on the accumulation and excretion of radiocaesium (Cs-137) in reindeer were studied in two feeding experiments. Six animals in each experiment were given lichens contaminated with radiocaesium from fallout after the Chernobyl nuclear power plant accident. In addition, they were fed pellets containing bentonite (Experiment I) or zeolite (Experiment II). Two animals, controls, in each experiment received no caesium-binder. The activity concentration of radiocaesium in blood was used to evalute the radiocaesium level in the body. Faeces and urine were collected to measue the excration of radiocaesium.

The animals in Experiment I were depleted of radiocaesium before the start of the experiment. After three weeks, with an intake of 17 - 18 kBq Cs-137/day, the controls had reached activity concentrations of radiocaesium in blood corresponding to 4 - 4.5 kBq Cs-137/kg in muscle. Reindeer fed 23 or 46 g of bentonite per day stabilized at values below 0.8 kBq/kg in muscle. In Experiment II, the reindeer started with radiocaesium activity concentrations in blood corresponding to 2 - 4.5 kBq Cs-137/kg in muscle. After four weeks of feeding, with an intake at about 8.5 kBq Cs-137/day, controls had increased their radiocaesium values by an average of 40%. Reindeer receiving 25 or 50 g zeolite per day decreased with 18 and 45%, respectively. Net absorption of radiocaesium from the gastro-intestinal tract was calculated at 50 - 70% in animals receiving no caesium-binder. Reindeer fed bentonite had an absorption below 10% while those fed zeolite absorbed around 35%.

Key words: radiocesium, radioactivity, fallout, Chernobyl

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Introduction

In large parts of the reindeer herding area of Scandinavia, lichens - the main winter feed for reindeer - are highly contaminated with radiocaesium (Cs-134 and Cs-137) from the Chernobyl fall-out (Figure 1). In contaminated areas reindeer have a high intake of radiocaesium from September to April. Radiocaesium is easily absorbed from the gastro-intestinal tract and accumulates in soft tissues, resulting in high activity concentrations of radiocaesium in the muscles. Reindeer meat that is sold for human consumption in Sweden is not allowed to contain more than 1500 Bq Cs-137/kg. In many

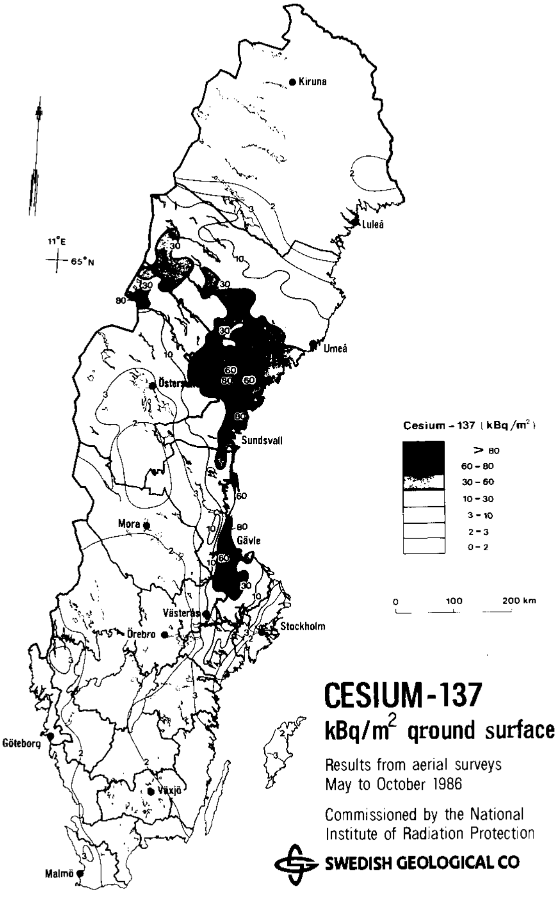

Figure 1. Ground cover of Cs-137, kBq/m^2 over Sweden. The amount of Cs-137 per m^2 corresponds roughly to the amount of Cs-137 per kg of dry lichens.

areas reindeer meat can reach values 10 to 30 times this during the winter.

The biological halflife of radiocaesium in reindeer is relatively short. With no radiocaesium intake the body content of radiocaesium is halved in 1 - 4 weeks (Holleman *et al.* 1971, Blix 1988, Åhman 1988b). A high intake of potassium has been shown to increase excretion of radiocaesium in sheep (Mraz 1959) and reindeer (Hove *et al.* 1987).

Holleman *et al.* 1971 found the shortest halflives (6.7 days) in June - July when metabolic rate was high and potassium intake was about 10 times higher than in the winter.

During the last two winters feeding has been used in Swedish reindeer management as a means to reduce radiocaesium in reinder before slaughter. For practical and economical reasons, and also not to risk the health and wellbeing of the animals, it is important to keep the time of feeding as short as possible. One way of doing this is to add a caesium-binder to the feed given to the reindeer. When feeding reindeer outdoors, in corrals, there will always be some vegetation available and there is also the possibility of soil-eating. An efficient caesium-binder can prevent most of the ingested radiocaseium from being absorbed. Radiocaesium from the body pool secreted into the gastrointestinal tract may also be restricted from reabsorption.

Since the 1960's caesium-binders have been used in animal studies. Hexacyanoferrate (Giese-salt, Prussian blue) were used as caesium-binder to rats by Nigrović (1965) and to rat, pig and cattle by Giese (1971). In Norway hexacyanoferrate has been given to reindeer with good results (Blix 1988, Hove *et al.* 1988). Hexacyanoferrate is not, however, allowed in animal feed by the Swedish authorities. Van den Hoek (1976 and 1980) used bentonite, a clay consisting mainly of montmorillonite, as caesium-binder to sheep and cattle. With 10% of bentonite in the concentrate ration, absorption of radiocaesium from the gastro-intestinal tract was less than 5%. Pellets containing bentonite (2.5%) have also been used in practical reindeer feeding in Sweden during the winter of 1987/88. Bentonite, however, increases water consumption considerably (Åhman 1988a), which is a serious draw-back in reindeer feeding. More recently zeolites, a group of tectosilicate minerals, have been used in animal feed. Of the zeolites, chabazite, mordenite and also clinoptilolite have high affinity to caesium. Mordenite has been shown to accelerate radiocaesium excretion in sheep and goats (Forberg *et al.* 1988). Clinoptilolite significantly reduced absorption of radiocaesium in sheep (Philippo *et al.* 1988). Zeolites have also been used as dietary supplements to improve health and productivity in many domestic animals (Mumpton & Fishman 1977).

The aim of this study was to investigate the effect of bentonite and zeolite on radiocaesium absorption and excretion in reindeer fed lichen contaminated with radiocaesium from the Chernobyl fallout.

Material and methods

One feeding experiment with 6 male reindeer calves was performed during January and February 1987 (Experiment I) and another during April and May 1988 (Experiment II). The animals were fed lichens contaminated with radiocaesium (30 - 45 kBq Cs-137/kg DM) and pellets with bentonite, Experiment I, or zeolite (mordenite), Experiment II. In each experiment two reindeer were fed the same pellets without any caseium-binder added. Both experiments were made as parts of more comprehensive studies (Åhman 1988b and Åhman 1988c).

The animals were kept individually in outdoor pens. They were fed twice a day. Daily food and water consumption was registered and the animals were weighed once a week.

Feed consumption and intake of Cs-137 in the two experiments are shown in Tables 1 and 2. Daily radiocaesium intake varied somewhat depending on varying radiocaesium content and ray matter in the lichens. Samples of lichens were taken continuously for the analyses of dry matter and radiocaesium content and the average daily amount of radiocaesium provided to the reindeer was calculated.

In Experiment I the animals were given 17 - 20 kBq of C-137 daily. During the first three weeks two animals (Group I) got no bentonite, two (Group 2) got 23 g of bentonite/day and two (Group 3) got 46 g/day. During the following two weeks all animals got 27 g og bentonite/day.

In Experiment II the amount of Cs-137 given to the reindeer was 8 - 9 kBq/day during the first four weeks, followed by 1 kBq/day during 10 days. Two reindeer (Group 1) got no zeolite,

Table 1. Daily consumption of lichens and pellets in Experiment I. Intake of Cs-137 and bentonite per day.

Period (1987)	Lichens (DM) per day	Cs-137 per day	Pellets (91% DM) per day	Supplements of bentonite per day Group 1	Group 2	Group3
Jan. 16-29	500 g	17-20 kBq	750 g	–	23 g	46 g
Jan. 30 - Feb. 6	500 g	17-20 kBq	850 g	–	23 g	46 g
Feb. 7-20	500 g	17-20 kBq	900 g	27 g	27 g	27 g

Table 2. Daily consumption of lichens, hay and pellets in Experiment II. Intake of Cs-137 and zeolite per day.

Period (1988)	Lichens (DM) per day	Hay (87% DM) per day	Cs-137 per day	Pellets (91% DM) per day	Supplements of zeolite per day Group 1	Group 2	Group 3
April 22- May 19	280 g	110 g	8-9 kBq	980 g	–	25 g	50 g
May 20-29	35 g	180 g	1 kBq	1410 g	–	25 g	50 g

two (Group 2) got 25 g/day and two (Group 3) got 50g of zeolite/day during both periods.

Blood samples were taken in order to monitor radiocaesium content of the body. Faeces and urine were collected for determination of the daily excretion of Cs-137. In Experiment I, collection was made on four occasions, each time during two days from one of the reindeer in each of the three goups and during the following two days from the other reindeer in each group. During collection the reindeer were kept indoors in cages. Faeces were collected in a bag connected to a harness put on the animal. Urine was collected in a vessel beneath the cage.

In Experiment II collection of faeces was made during two or three days on two occasions. Unfortunately the reindeer had begun to grow large antlers which made the cages too small for them. However, faeces could be collected with the reindeer in an indoor pen. Urine could only be collected from three animals during the first collection period and from one during the second. During the period with low radiocaesium intake collection of faeces was made from three animals during one day. From one animal also urine was collected.

In Experiment I Cs-137+134 in whole blood and in urine (20 ml samples) was measured in a well scintillation (NaI) detector at the Department of Radioecology, Swedish University of Agricultural Sciences. The amount of Cs-137 was calculated as total amount of Cs-134 and Cs-137 times a factor 0.69. Cs-137 in lichens, hay, and faeces was measured by means of Ge hyperpure detectors at the same department. In Experiment II the corresponding samples were measured either with a NaI(TI) or a Ge detector at the Department of Nuclear Chemistry, The Royal Institute of Technology, Stockholm.

Results

The reindeer in Experiment I maintained their body weight, 49 kg on average, throughout the experiment. In Experiment II, body weights increased by 8 kg, from a mean of 44 to 52 kg, during the experiment.

Animals given bentonite in Experiment I had higher water consumption than controls, especially during collection periods when the reindeer were kept indoors in cages (cf. Åhman 1988a). We found no such effect of zeolite.

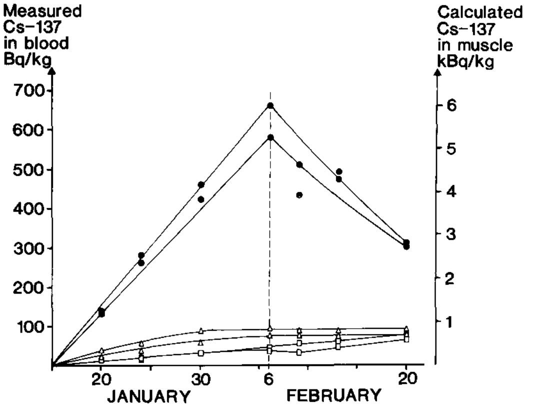

Figure 2. Cs-137 in blood and muscle (calculated: 9 x Cs-137 in blood) from reindeer in Experiment I. The reindeer were fed lichens giving 17-20 kBq Cs-137/day. During the first period, January 15 to February 5, Group 1 (●) got no caesium-binder in their feed, Group 2 (△) got 23 g of bentonite per day and Group 3 (□) got 46 g per day. From February 6 all reindeer got 27 g of bentonite per day.

The changes of Cs-137 activity in blood are shown in Figures 2 and 3. In Experiment I the animals started with a Cs-137 activity at zero level. In Group I (controls) Cs-137 activity in blood increased rapidly to about 600 Bq/kg without levelling in three weeks. Those getting benetonite reached 70 - 90 Bq/kg (Group 2) or about 40 Bq/kg (Group 3).

When the feeding of bentonite continued with 27 g bentonite per day to all animals, the level of Cs-137 in blood of controls decreased to about half the maximum value (Figure 2). In

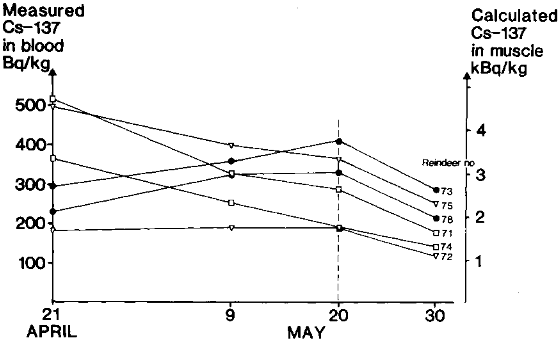

Figure 3. Cs-137 in blood and muscle (calculated: 9 x Cs-137 in blood) from reindeer in Experiment II. Group 1 (●) got no caesium-binder in their feed, Group 2 (▽) got 25 g of zeolite per day and Group 3 (□) got 50 g of zeolite per day. During the first month, April 21 to May 19, the reindeer were fed lichens giving 8-9 kBq Cs-137/day. From May 20 the reindeer were given 1 kBq/day.

Group 2 radiocaecium activity concentration in blood did not change while for animals in Group 3, that got less bentonite than before, the values increased to the level of Group 2 (70 Bq/kg).

In Experiment II the animals started at higher levels of radiocesium in blood (200 - 500 Bq Cs-137/kg, Figure 3). In controls the levels increased by about 100 Bq/kg (40% on average) in four weeks. One animal in Group 2 remained on 200 Bq/kg throughout the four weeks, while in the other radiocaesium activity decreased slightly. The average reduction in Group 2 was 18%. Group 3, getting the higher dose of zeolite, decreased by 45% on average. During the ten last days of the experiment, when the reindeer got only 1 kBq of Cs-137/day, blood-Cs decreased by 30 - 40%. No effect of the zeolite was discernible during this phase of the experiment.

Excretion of Cs-137 with faeces and urine in the two experiments is shown in Figures 4 and 5. In Experiment I (Figure 4), total excretion in Group 1 (controls) increased from zero to about 11 kBq/day in one week. After three weeks the excretion was about 14 kBq/day with 20 - 35% of Cs-137 being excreted with urine. In reindeer receiving bentonite (Groups 2 and 3), excretion of Cs-137 reached a maximum level at about 18 kBq/day in less than two weeks. The amount of Cs-137 excreted with urine in these groups was 0.3 - 1.0 kBq/day which is 2 - 5% of total excertion of Cs-137.

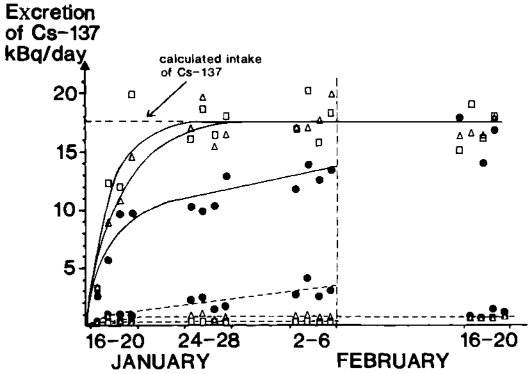

Figure 4. Daily excretion of Cs-137 in Experiment I. Exretion in urine (----) and total exretion, urine + faeces (——), in Group 1, controls (●) and in reindeer receiving bentonite; Group 2, 23 g/day (△) and Group 3, 46 g/day (□). From February 6 all reindeer got 27 g of bentonite per day.

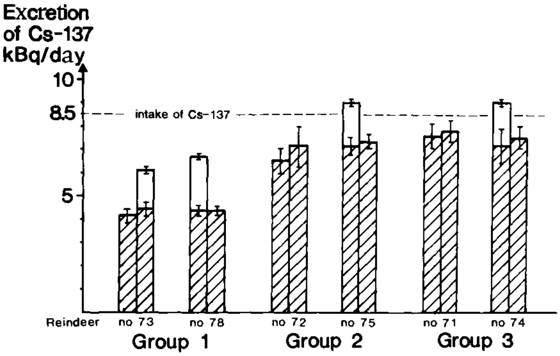

Figure 5. Excretion of Cs-137 in Experiment II. Daily excretion in faeces ▨ and urine □ during two periods, April 25-28 and May 16-20, (mean ± S.D.) in controls (Group 1) and in reindeer receiving 25 g zeolite/day (Group 2) or 50 g zeolite/day (Group 3).

When all animals were given 27 g/day of bentonite, the total excretion of Cs-137 with faeces and urine in Group 1 (controls) increased. After 10 days it was at the same level as in Groups 2 and 3 (18 kBq/day). The share of Cs-137 excreted with urine decreased. In Groups 2 and 3 the total excertion did not change significantly. The franction excreted with urine increased somewhat in Group 3.

Figure 5 shows the excretion of Cs-137 in Experiment II. Excretion with urine was measured on one occasion in four of the animals. For the remaining two, only excretion with faeces was measured. For controls (Group 1), excretion with faeces was 4 - 4.5 kBq/day and with urine about 3.5 kBq/day (about 36% of total excreted Cs-137). For reindeer fed zeolite (Groups 2 and 3) the excretion with faeces was 6.5 - 7.8 kBq/day. Excretion with urine was 1.9 kBq/day (21% of total excreted Cs-137). When intake of radiocaesium was reduced to 1 kBq Cs-137/day the excretion with faeces (measured in one animal of each group) was 1.5 - 1.8 kBq/day. There were no significant differences between the groups during this period. Excretion with urine, measured in one of the controls (no 73), was 1.6 kBq/day (50% of total excretion).

Discussion

In the experiment there were fluctuations in the daily intake of radiocaesium due to variations in radiocaesium content of the lichens. The exact lichen intake was also difficult to estimate, since leftover lichens were spilled out in the pen and trampled down.

An estimation of the daily intake could be made by measuring daily excretion of radiocaesium when the animals were at steady state. In Excperiment I, the average excretion of Cs-137 in Group 2 during the periods February 2-6 and 17-20, when the animals in this group had constant radiocaesium levels in their blood (Figure 2), was 17.4 ± 1.4 kBq/day (Figure 4). This value, we believe, gives a good estimate of the daily intake. In Experiment II one animal in Group 2 (no 72) had constant radiocaesium activity concentration in the blood during the first phase of the experiment (Figure 3). In this animal, only excretion of radiocaesium with faeces was measured (Figure 5). Assuming that the part excreted with urine is the same as for the other animals in Group 2 and 3 (21%), the total excreted Cs-137 will be 8.5 kBq/day, which thus should be equivalent to the daily radiocaesium intake.

In these experiments, the radiocaesium activity concentration of blood was used to measure the level of radiocaesium in the body. It has been shown that the activity concentration of radiocaesium in muscle is 7 to 10 times the concentration in blood (Åhman, B 1986, Åhman, G. 1986, Blix 1988, Eikelmann 1988). The lower factor applies to animals that are increasing their levels of radiocaesium (Åhman, B. 1986). This seems logical since blood transporting radiocaesium to the tissues should have a higher concentration relative to tissue than blood draining radiocaesium from the tissues. In this report we have used the factor 9 when calculating radiocaesium in muscle. For animals at or near steady state this factor should give a good estimate of radiocaesium in muscle. The factor 9 is probably too high for controls (Group 1) in the beginning of Experiment I, when these animals were increasing their radiocaesium levels rapidly. The factor 7 might give a better estimate of radiocaesium in muscle in this group.

In Experiment I, the controls (Group 1) had, after three weeks of estimated daily intake at 17.4 kBq Cs-137/day, reached blood values corresponding to 4.0 - 4.6 kBq/kg in muscle (7 x Cs-137 in blood). By feeding these animals bentonite (27 g/day), we were able to revert the rapid incerase of radiocaesium in the body into a decrease, althrough the animals had the same radiocaesium intake as before. Reindeer given bentonite throughout the experiment (Groups 2 and 3) seemed to approach radiocaesium levels corresponding to concentrations in muscles at 0.5 - 0.8 kBq/kg. This is well below the current limit for reindeer meat sold in Sweden (1500 Bq/kg).

The conditions of Experiment II differed form those in Experiment I in various respects. The animal were in a growth period, also with some practical problems as a consequence. They were fed less lichens and more hay and pellets. The estimated radiocaesium intake was 8.5 kBq Cs-137/day. The starting level of radiocaesium in the body was much higher than in Experiment I. Also the individual variations were larger. On average, however, the radiocaesium levels in blood of the controls increased by 40% from April 21 to May 20, while reindeer fed zeolite, Groups 2 and 3, decreased with 18% and 45%, respectively.

Excretion of Cs-137 was measured also in another part of Experiment I, when the reindeer had no radiocaesium intake (cf. Åhman 1988b). The relation between the activity concentration of radiocaesium in blood and the excretion per day was calculated. In reindeer receiving no caesiumbinder the amount of Cs-137 excreted with faeces was about 5 times

Table 3. Calculated net absorption of Cs-137 from the gastro- intestinal tract in Experiment I. Estimated radiocaesium intake was 17.4 kBq Cs-137/day.

Rein-deer no.	Day	Cs-137 in blood Bq/kg	Estimated excretion in faeces from body deposits kBq/day	Measured excretion in faeces kBq/day	Not absorbed Cs-137 from the feed kBq/day	Not absorbed Cs-137 from the feed % of intake	Absorbed % of daily intake
Group 1 - controls			(5 x blood)				
19	Jan 26-28	361	1.80	10.1	8.3	48 %	52 %
	Feb 4-6	572	2.86	10.3	7.4	43 %	57 %
21	Jan 24-26	328	1.64	7.8	6.2	36 %	64 %
	Feb 2-4	602	3.01	9.4	6.4	37 %	63 %
							59±6 %
Group 2 - 23 g bentonite/day			(10 x blood)				
27	Jan 26-28	48	0.48	15.5	15.0	86 %	14 %
	Feb 4-6	72	0.72	18.3	17.6	101 %	-1 %
	Feb 16-18	72	0.72	16.0	15.3	88 %	12 %
28	Jan 24-26	65	0.65	17.3	16.6	96 %	4 %
	Feb 2-4	89	0.89	16.2	15.3	88 %	12 %
	Feb 18-20	89	0.89	16.4	15.5	89 %	11 %
							9±6 %
Group 3 - 46 g bentonite /day			(10 x blood)				
23	Jan 26-28	28	0.28	17.0	16.7	96 %	4 %
	Feb 4-6	38	0.38	16.7	16.3	94 %	6 %
26	Jan 24-26	22	0.22	17.2	17.0	98 %	2 %
	Feb 2-4	41	0.41	18.3	17.9	103 %	-3 %
							2±4 %

the amount of Cs-137 in one kg of blood. For reindeer fed bentonite, the factor was 10. To calculate the absorption of radiocaesium from the feed, we estimated faecal excretion of radiocaesium from body deposits and compared it to the measured daily excretion in Experiments I and II. The results of these calculaions are shown in Tables 3 and 4. (Blood values for the actual day are taken from the graphs shown in Figures 2 and 3.) These calculations are based on factors that are somewhat uncertain. The estimated radiocaesium intake greatly affects the calculation, especially if the absorption is small.

According to the calculations, controls, (Group 1) in Experiment I had an average net absorption from the gastro-intestinal tract of 59% (Table 3), while the absorption in Groups 2 and 3, receiving bentonite, was 9 and 2%, respectively. The relation between Group 1 and Group 2, with about 6 - 7 times more radiocaesium absorbed in controls than in those fed bentonite, is in accordance with the results discussed previously. The true absorption in Group 3 is most likely larger than the calculated 2%. With a radiocaesium intake at 18 kBq/day (instead of the estimated 17.4 kBq) the absorption will be 5%.

Table 4. Calculated net absorption of Cs-137 from the gastro- intestinal tract in Experiment II. Estimated radiocaesium intake was 8.5% kBq Cs-137/day.

Reindeer no.	Day	Cs-137 in blood Bq/kg	Estimated exretion in faeces from body deposits kBq/day	Measured excretion in faeces kBq/day	Not absorbed Cs-137 from the feed kBq/day	% of intake	Absorbed % of daily intake
			(5 x blood)				
Group 1 - controls							
73	Apr 26-28	313	1.56	4.2	2.6	31 %	69 %
	May 17-20	414	2.07	4.5	2.4	28 %	72 %
78	Apr 26-29	277	1.38	4.4	3.0	35 %	65 %
	May 17-19	257	1.28	4.4	3.1	37 %	63 %
							67±4 %
Group 2 - 25 g zeolite/day							
72	Apr 26-29	182	0.91	6.5	5.6	66 %	34 %
	May 17-20	187	0.94	7.1	6.2	73 %	27 %
75	Apr 26-28	462	2.31	7.1	4.8	56 %	44 %
	May 17-20	284	1.42	7.3	5.9	69 %	31 %
Group 3 - 50 g zeolite/day							
71	Apr 26-29	431	2.16	7.6	5.4	64 %	36 %
	May 17-20	290	1.45	7.8	6.4	75 %	25 %
74	Apr 26-29	319	1.60	6.2	4.6	54 %	46 %
	May 17-20	203	1.02	7.4	6.4	75 %	25 %
							34±8 %

In Experiment II (Table 4) the average absorption in Group 1, controls, was 67%. The calculated absorption in reindeer fed zeolite, Group 2 and 3, was about half of this, 34% at an average.

The caesium binding characteristics of the zeolite and bentonite were studied *in vitro*, in solutions of KCl and NH_4Cl and in rumen fluid from reindeer (Forberg 1989). Caesium had a higher affinity to the actual quality of zeolite than to the bentionite, indicating that some factor had reduced the efficiency of the zeolite when it was given to reindeer. Artificial mordenite had a somewhat higher affinity to cesium. Artificial mordenite was also shown to be very efficient in experiments with goats and sheep (Forberg *et al.* 1988). It was, however, judged too expensive for practical application on reindeer.

The natural zeolite was ground, before it was mixed into the pellets, until 73% by weight passed through a 32 μ m sieve when wet. Par ticles of this size are not expected to settle in the gastro-intestinal tract. However, agglomeration might reduce the efficiency of zoelite and may be an explanation for the inferior effect.

Conclusions

Bentonite is a caesium-binder efficient enough to be used in reindeer feeding in heavily contaminated areas of Sweden. With 2% of bentonite in the total food, absorption seems to decrease to about 15% of the absorption when no caesium-binder is added. At an intake of about 20 kBq Cs-137/day, 2% of bentonite in the food should be sufficient to keep radiocaesium levels in muscles below the limit 1500 Bq/kg. Since bentonite increases water requirements, it is important that the reindeer have access to drinking water. This could be a problem especially at low temperatures. Also, due to its unspecific binding of minerals and electrolytes, it is important to keep the bentonite dose at a moderate level.

The zeolite used in our study binds caesium less efficiently than bentonite. When the reindeer were given 2 or 4% of zeolite in their feed, absorption decreased to about 50% of the absorption without caesium-biner. Zeolite, however, does not have the negative effects of bentonite on water balance. Further studies are required to find a more efficient from of zeolite than the one we have used.

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Consequences of the Chernobyl accident for reindeer husbandry in Sweden

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Abstract: Large parts of the reindeer hearding area in Sweden were contaminated with radioactive caesium from the Chernobyl fallout. During the first year after the accident no food with activity concentrations exceeding 300 Bq/kg was allowed to be sold in Sweden. This meant that about 75% of all reindeer meat produced in Sweden during the autumn and winter 1986/87 were rejected because of too high caesium activites. In May 1987 the maximum level for Cs-137 in reindeer, game and fresh-water fish was raised to 1500 Bq/kg. During the last two year, 1987/88 and 1988/89, about 25% of the slaughtered reindeer has had activities exceeding this limit.

The effective long-time halflife or radiocaesium in reindeer after the nuclear weapon tests in the sixties was about 7 years. If this halflife is correct also for the Chernobyl fallout it will take about 35 years before most of the reinder in Sweden are below the current limit 1500 Bq/kg in the winter. However, by feeding the animals uncontaminated food for about two months, many reindeer can be saved for human consumption.

Key words: Cs-137, half life, feeding

Rangifer, Special Issue No. 3, 1990: 83-88

Introduction

A few days after the nuclear power plant accident in Chernobyl it was evident that reindeer herding areas in Sweden had been hit by appreciable radioactive deposition. Ground radiation measurements showed the highest levels in Southern Västerbotten, Northern Jämtland and Northwestern Ångermanland. Levels ranging from 60 to 80 kBq Cs-137 per m^2 were found in the worst affected areas (Figure 1), being 40 - 50 times the levels during the mid-sixties of ground radiation from the nuclear weapon tests (Lidén & Gustafsson 1967).

Measurements of activity concentrations of radiocaesium in reindeer have been made in Sweden since 1961. Some values are shown in Table 1 (Åhman 1986). In Finland measured activity concentrations of Cs-137 in reindeer meat in the winter 1985/86, before the Chernobyl accident, was 300 Bq/kg on an average (Rissanen et al.1987). The level of radiocaesium in reindeer varies during the year, with high values in the winter when the reindeer eat lichens and

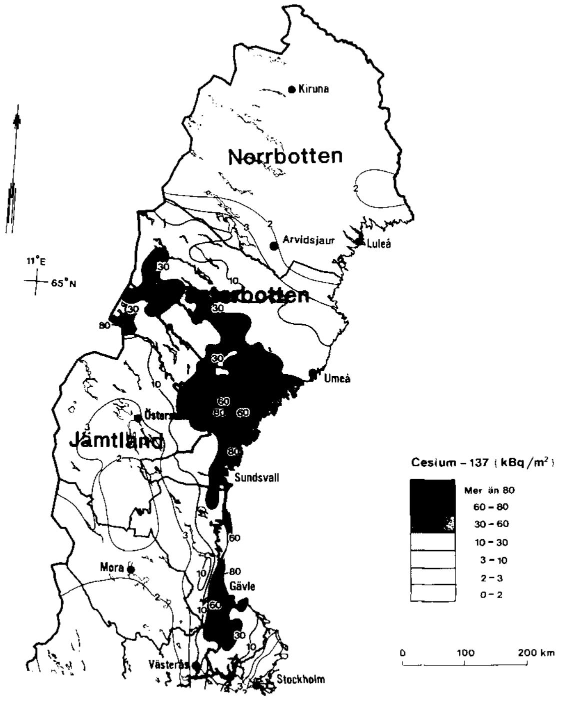

Figure 1. Ground radiation of Cs-137, kBq/m^2. Results from areal surveys, May to October 1986. Commissioned by the National Institute of Radiation Protection. Swedish Geological CO.

Table 1. The activity concentration of Cs-137, kBq/kg, in reindeer meat in the autumn and winter 1964/65, 1974/75 and 1985/86 (from Åhman 1986).

Year	Cs-137, kBq/kg Autumn	Winter
1964/65	0.5-1	2-4
1974/75	0.3	1-2
1985/86	0.1	0.3

low values in the summer when they eat mainly green plants (grass, leaves, etc.) that are not so high in activity concentrations of radiocaesium (Lidén & Gustafsson 1967; Åhman et al. 1988).

The first year after Chernobyl, 1986/87

Soon after the Chernobyl accident an action level of Cs-137, 300 Bq/kg, was set by the National Institute of Radiation Protection in Sweden for all food, including reindeer meat, to be sold for human consumption. The Swedish Government declared that compensation would be paid for costs and loss of income because of the Chernobyl fall-out. According to this general promise the reindeer owners are paid for rejected reindeer meat, lower body weight and cost of labour when the time of slaughter has to be changed and also for costs when feeding reindeer to lower the radiocaesium content. The slaughter companies are refunded by the state for costs involved in slaughtering animals which are rejected.

During June and July 1986 a total of 102 reindeer were slaughtered and samples were taken from muscle, blood, rumen content, etc. for analyses of radioactive caesium (Åhman 1986). Some results are shown in Table 2. From an additional 132 live animals, blood samples were taken. The aim of the studies was to get an overview of the situation in different Saami (Lapp) villages and support for predicting radiocaesium levels in meat at the time of slaughter.

Table 2. Activity concentrations of Cs-137 in reindeer meat in June and July 1986 (6-10 samples from each area).

Area	Cs-137, kBq/kg in meat June	July
Norrbotten		
middle	0.1-0.2	—
southern	0.4-1.9	0.1-0.3
Västerbotten		
middle	—	0.7-1.6
southern	3.1-6.6	1.8-4.3
Jämtland		
northern	5.4-7.6	0.9-3.2
southern	1.7-2.6	0.1-1.6

From these investigations it was clear that the majority of reindeer to be slaughtered in Jämtland and Västerbotten during September would

Table 3. Number of reindeer accepted for human consumption (<300 Bq Cs-137/kg in meat) and number rejected, from Norrbotten, Västerbotten and Jämtland in July 1986 to April 1987 (from Lantbruksnämnden i Jämtland län 1987 and Nilsson 1988).

	July–Sept.		Oct–Dec.		Total	
	accepted	rejected	accepted	rejected	accepted	rejected
Norrbotten	19013	2731	6902	32268	25915 (43%)	34999 (57%)
Västerbotten	134	5644	3	11217	137 (1%)	16861 (99%)
Jämtland	0	2342	1131*	12169	1131 (7%)	14511 (93%)
Total	19147	10717	8008	48837	27183 (29%)	66371 (71%)

* animals fed in corrals

be rejected because of Cs-137 levels exceeding 300 Bq/kg. A large proportion of the reindeer meat from Norrbotten was predicted to be below 300 Bq/kg. Slaughter during the autumn and winter season 1986/87 revealed, however, that almost 60% of the carcases from Norrbotten were above 300 bq/kg and were rejected (Table 3). A few villages in Norrbotten were advised to slaughter earlier than normal, before the radiocaesium values started to increase because of high lichen intake. A couple of thousand carcasses were saved for human consumption in this way.

In Västerbotten only 137 reindeer (1%) were below 300 Bq/kg and the rest were rejected. In Jämtland about 1100 reindeer were taken into corrals and fed during January to March and thus saved for human consumption. During the slaughtering season 1986/87, 71% of all reindeer that were slaughtered in Sweden had activity concentrations of Cs-137 in meat exceeding 300 Bq/kg. The remaining 29% had values below 300 Bq/kg and were accepted for human consumption.

In samples taken after Chernobyl, Cs-137 from the sixties can be estimated by using the relation between Cs-134 and Cs-137 (Åhman 1986), since the Chernobyl fallout contained one-third of Cs-134 while the contamination from before Chernobyl is only Cs-137. Old Cs-137 estimated in this way was 0.06 - 0.25 kBq/kg in reindeer from Norrbotten during October and November 1986.

The second year after Chernobyl, 1987/88

In May 1987 the decision was taken by the National Food Administration to raise the action levels of Cs-137 in reindeer, game and fish from 300 to 1500 Bq/kg (see also Johanson, K.-J. in this publication). The increase of maximum level of Cs-137 had the effect that virtually all of Norrbotten and also a few villages in Jämtland were classified as 'safe' areas (all reindeer were considered to be below the new limit of 1500 Bq Cs-137/kg in meat and no analyses had to be made, except for a few test samples) during the bull slaughter in September of 1987. For the remaining part of the year, Norrbotten exept the southernmost Saami villages were classified as safe.

In several villages in Jämtland reindeer were fed in corrals during the winter 1987/88. A total of 5500 reindeer were fed pelleted feed supplemented with 2.5% bentonite and 0.25% potassium. These animals were also given hay. The addition of bentonite to bind radiocaesium was considered necessary, as the reindeer had access to some pasture with high radiocaesium content in their corrals. They could also eat contaminated soil. The addition of potassium was made to speed up the degradation of caesium in the body.

From two Saami villages in Västerbotten and Jämtland (Vapsten and Frostviken mellersta), 10000 reindeer were transported to Älvdalen in nothern Dalarna. In this area the radiocaesium contamination was not so high (1-2 kBq/kg DM in lichens, Eriksson et al., 1987). It was still not sufficiently low to reduce the levels of radiocaesium in the animals below 1500 Bq Cs-137/kg and about 2500 reindeer selected for slaughter had to be fed in corrals for some weeks. The other animals were transported back to their calving range in April.

During 1987/88 a total of 68000 carcasses (72%) were accepted for human consumtion, out of 95000 slaughtered reindeer (Nilsson 1988). Figures from some Saami villages are shown in Table 4. Among those that were accepted, 5000 animals had been slaughtered early (before the normal bull slaughter in September) and 5500 had been fed in corrals during the winter. The remaining 57500 had not been treated in any special way.

Table 4. Activity concentration of Cs-137 (kBq/kg) in reindeer meat from some slaughters in the autumn of 1987.

Reindeer from	Date	No. of animals	kBq/kg $\bar{x} \pm SD$	Per cent <0.3	Per cent <1.5
Norrbotten					
Jåkkåkaska					
Prinskullen	Aug 25	10	0.1	100	100
Tjapsåive	Sept 14	7	0.2	85	100
Sågudden	Dec 14	22	0.7 ± 0.1	0	100
Västra Kikkejaure					
Dolpek	Nov 17	118	1.2 ± 0.5	0	93
Solberg	Dec 15	60	0.6 ± 0.2	0	100
Västerbotten					
Umbyn					
Biellojaur	Aug 20	377	0.5 ± 0.3	5	99
”	Sept 5	172	1.1 ± 0.5	0	90
”	Sept 19	244	1.0 ± 0.5	0	92
”	Oct 25	244	3.6 ± 1.1	0	0
Vilhelmina norra					
Gielas	Sept 5	333	1.0 ± 0.4	0	86
”	Sept 15	218	3.9 ± 1.1	0	0
”	Oct 21	127	8.5 ± 3.5	0	0
Jämtland					
Hotagen					
Vinklumpen	Aug 23	112	0.8 ± 0.2	0	100
”	Sept 8	184	1.4 ± 0.5	0	71
”	Nov 30	163	6.0 ± 1.4	0	0
Mittådalen					
Flatruet	Sept 16	10	0.8 ± 0.2	0	100
Lossen	Nov 28	114	1.9 ± 0.4	0	16

Prospects for the future

If there is no additional fallout the levels of radiocaesium in reindeer in the future will depend mainly on the effective half-time of radiocaesium in lichens. Lidén and Gustafsson (1967) estimated this half-time to 11 years. If grazing was taken into consideration they predicted the yearly decrease of radiocaesium in reindeer meat to be 10 - 15%, which corresponds to a effective half-time of 7 years. Holleman (1973/74) estimated the effective half-time of Cs-137 in lichens to be 8.3 years. From figures given by Westerlund et al., (1987) on Cs-137 in reindeer meat from 1965 to 1983, we have calculated the effective half-time of Cs-137 to be 7 years.

Even in one of the most contaminated Saami villages (Vilhelmina Norra in south Västerbotten) the values are below 1500 Bq/kg in July and August (Figure 2) but already in the beginning of September they start to increase rapidly. Before mid-September, the normal time for bull slaughter, most reindeer have passed the limit 1500 Bq Cs-137 in meat. If the half-time of radiocaesium in most plants grazed by reindeer in late summer is the same as in lichens, it will take at least until the year 2000 before most of the reindeer in Vilhelmina Norra are below 1500 Bq/kg at the normal time for bull slaughter.

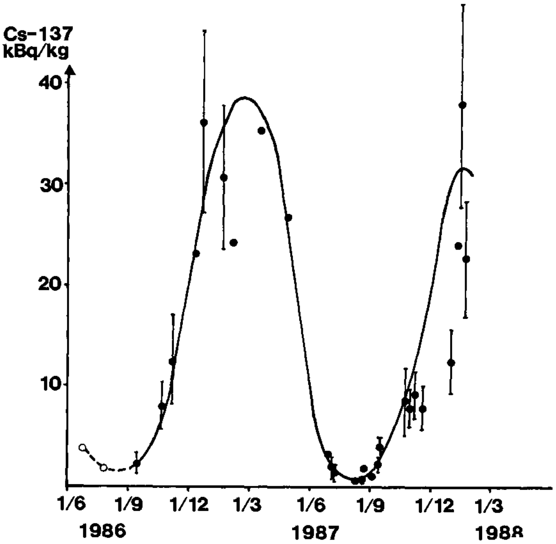

Figure 2. Yearly variation in activity concentration of Cs-137 in reindeer from the Saami village Vilhelmina Norra (south Västerbotten) from June 1986 to February 1988 (kBq/kg in meat).

In the winter the highest activity concentrations of radiocaesium in reindeer in Vilhelmina Norra, as in the rest of southern Västerbotten and the most northern part of Jämtland, are at a level of 40 kBq Cs-137/kg in meat. It will take 5 half-times, 35 years, before most of the reindeer are below the 1500 Bq/kg level in the winter. In northern Västerbotten and and middle Jämtland, were the activity concentrations are at a level of 10 kBq Cs-137/kg in the winter, it will take about 20 years before all reindeer fall below the 1500 Bq/kg limit.

If no measures are taken to reduce radiocaesium levels in reindeer before slaughter, nearly 30000 carcasses per year will be rejected during the next two years. Economically, early bull slaughter is the most efficient messure. Loss of income because of lower body weight and costs for extra labour amount to 20 -30% of the value of the meat. It is, however, often difficult and some times impossible to round-up reindeer for slaughter in August. For this reason, most of the bull slaughtering will have to be done at the ordinary time in September.

There is great interest among the reindeer herders to move animals to areas with low radiocaesium contamination. Moving animals outside the normal pasture land for reindeer creates several legal and economical problems.

Lowering radiocaesium levels in reindeer by feeding had been used with success in most Saami villages in Västerbotten and Jämtland. To achieve a good live weight before slaughter the feeding has to be continued for 8 to 10 weeks. The half time for radiocaesium in reindeer that are fed is normally 15 - 17 days. This means that most reindeer can be saved for human consumption by feeding. The total cost for feeding during 10 weeks is, however, almost as large as the price paid for the meat produced. New types of feed and new techniques that reduce the costs will be tried during forthcoming years.

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Range Ecology

Key note adress:

Reindeer lichen productivity: Problems and possibilities

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Abstract: Reindeer lichens are important in the structure and function of tundra and taiga ecosystems, as exemplified by cover values, biomass, mineral content, and effect on other ecosystem components. They are particularly important for winter ecology of reindeer and caribou which largely really on them. Growth measurement is difficult due to the very slow rate and the methods that have been used are not sufficiently documented, precise, or appropriate. Use of carbon dioxide exchange models, coupled with models of lichen microclimate and water relations, based on microclimatic data are suggested as alternatives for land managers. The assumptions of such models are discussed and the performance of mixed species lichen mats and of the lichen CO_2 environment and its effect on lichen CO_2 exchange.

Key words: pastures, growth

Rangifer, Special Issue No. 3, 1990: 91-98

The importance of reindeer lichens

Many studies from tundras and taigas have shown that reindeer lichens are very important ecosystem components in terms of their biomass and nutrient store. Rencz and Auclair (1978) and Auclair and Rencz (1982) have shown that 20% of the biomass, 25% of the nitrogen, and 12% of the phosphorus of and open lichen woodland in northern Quebec is to be found in a lichen mat which covers 97% of the forest floor. Tundras may have equally high lichen biomass values as lichen woodlands. In a range survey of the Seward Peninsula, Alaska, Swanson et al. (1985) found up to 760 g m^{-2} of live lichen biomass on lichen lowland tundras and up to 1436 g m^{-2} on upland lichen slopes. The total biomass amount is obviously dependent on a varitety of factors including microclimate, time since burn, and grazing history, but it is clear that in terms of biomass and nutrients, the reindeer lichen can dominate the ecosystem.

Reindeer lichens may also strongly control the fluxes of energy and matter in the ecosystem. It has been shown (Kershaw and Rouse 1971, Kershaw and Field 1975, Cowles 1984) that the lichen mat significantly reduces soil temperature while increasing soil water retention by reflecting much of the incident solar radiation. Lichens may signigicantly affect the nutrient dynamics of the ecosystem by forming a filter between above and below ground system components and thus perhaps both reduce the rate of nutrient release and intercept some of the released nurients before they reach the soil (Cowles 1984). Lichens have also been purported to inhibit growth of neighboring vascular plants through the release of allelopathic chemicals (Brown and Mikkola 1974) but Cowles (1984) demonstrated that the overall effect of the lichen mat in northern Quebec on black spruce growth was positive while seedling establishment was negatively affected. Clearly, reindeer lichens can be considered significant controllers of ecosystem fluxes.

However, it is as reindeer/caribou winter forage that the importance of reindeer lichens is best recognized. The winter forage availability appears to be the most significant factor affecting herd size. The availability of the forage is primarily a function of snow characteristics and forage biomass. In a comprehensive literature study Eriksson et al. (1981) cite many studies demonstrating that lichens constitute a significant portion of the winter diet of reindeer/caribou wherever there are any lichens available. These studies, which are based on composition of fecal pellets, stomach contents, fistula samples, and visual observations of foraging animals indicate that lichens account for 15% to 90% of the food. Further it is held that animal condition is improved with access to lichens. Spectacular fluctuations in reindeer/caribou population numbers have often coincided with range depletion and weather hazards, such as the population crash of reindeer on St.Matthew Island, Alaska in 1964 (Klein 1968).

Most important reindeer forage lichens are fruticose, either growing on the ground, such as the genera *Cladonia*, *Cladina*, *Cetraria*, and *Stereocaulon* or as epiphytes on trees such as the genera *Usnea*, *Bryoria*, and *Alectoria*. Management of these lichens is important as they are susceptible to overgrazing (Swanson et al. 1986) which may result in reduced total lichen availability and changes in lichen species composition to less paltable ones (Klein 1968, Oksanen 1978). The lichen mat is also brittle when dry and is therefore sensitive to trampling by animals (Pegau 1970) and vehicles (Carstairs 1976). Finally, fires often destroy the lichen mat, leading to a long successional sequence with a horn lichen phase preceding the reindeer lichens (Swanson et al. 1985). Important winter range can thus be damaged in various ways and needs to be managed properly if reindeer/caribou management is desired.

Growth measurements

For management to be successful the lichen growth rate needs to be known and its relationship to extrinsic and intrinsic factors needs to be established.

There are difficulties in establishing the growth rate of lichens, primarily because they grow so slowly. Accurate changes in lichen diameters of crustose, foliose, or squamulose lichens can be monitored (Hale 1974, Lawrey and Hale 1977), but fruticose lichen mats are more difficult (Andreev 1954). Andreev (1954) reviewed work and methods up to 1952 and suggested a method that has since been widely used (e.g., Scotter 1963, Pegau 1968, Skuncke 1969, Lechowicz 1983). He correctly criticized the method by Tengwall (1928, as cited in Andreev 1954), which was based in changes in lichen height in reference to fixed points above the lichen canopy, pointing out the possibility of snow compressing the mat and of the "fixed " points moving.

Andreev (1954) referred to the method of Gorodkov (1934, as cited by Andreev 1954), which involved measuring growth above a permanent marker of indelible ink or a string but which was discontinued on favor of using "inherent growth markers". The idea of inherent growth markers was proposed by Salazkin (1937, as cited by Andreev 1954) and further developed and modified by Igoshina (1939, as cited by Andreev 1954) and Andreev (1940, as cited by Andreev 1954).

Salazkin's method was based on the assumption that forking of the thallus of *Cladonia* and *Cladina* lichens is a yearly event and therefore can be used as a growth marker (Fig. 1). Salazkin proposed that the yearly production equall-

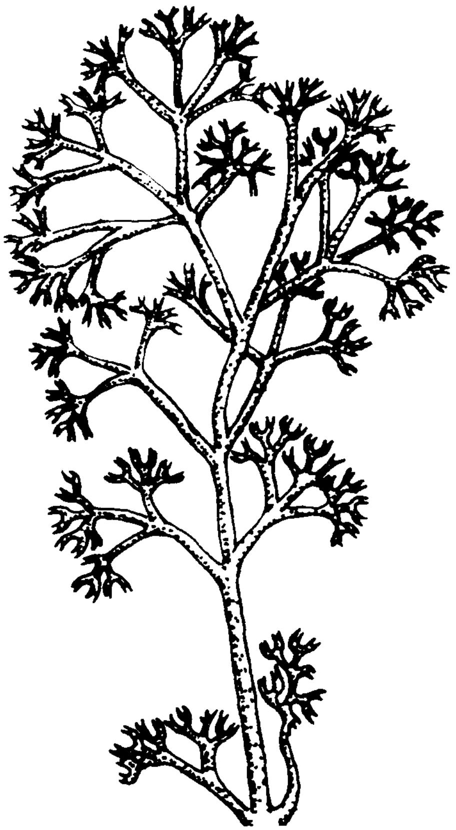

Figure 1. The branching patttern of *Cladina stellaris* (syn. *Cladonia alpestris*). This forking has been assumed to be a yearly event and has been used as an innate growth marker. Adapted from Brehmer in Thomson (1984) and Kärenlampi (1970).

ed the length of the uppermost interval that had stopped elongating, while Igoshina felt that the average of all intervals should be used. Andreev, also used the average interval, but used only the "living" part of the thallus. As results from the marking method of Gorodkin were found to be similar to results from the inherent growth marker method as used by Salazkin, the latter method was considered proven. To cite Andreev (1954), "If branching did not occur every year but (for example) every second year, the amount of annual growth would be half the lenght of a ring that had finished growing. If branching occured more often than once a year, for instance twice a year, the amount of annual growth would be twice as large as the length of a ring. Since experimental data do not disclose such differences, it must be concluded that the podetium of fruticose lichens branches, as a rule, once a year". Note that there is an implicit assumption that branching is a temporally regular event.

There are, therefore, two crucial assumptions on which Andreev's method rests, yearly forking, and a clear demarcation of the live to dead interface. Neither of these can be considered sufficiently demonstrated, although Skuncke (1969) states that Swedish *Cladonias* branched roughly once a year. Andreev specifically states that once growth of an interval has ceased it is no longer alive, rejecting Elenkin's claim (1922, as cited by Andreev 1954) that the fungus may still be alive, without offering experimental proof to the contrary.

Another method for determining growth rates is monitoring growth of thalli in containers (Kärenlampi 1971, Gaare pers. comm.) or growth of transplanted thalli. The question here is, to what extent the conditions in the containers are known, ecologically meaningful, and extrapolatable. Toxic chemicals in the boxes may reduce growth initially (Goodall pers. comm.), and/or CO_2 concentration around the thalli may be important (Sonesson, pers. comm.) and changed by the presence of the containers insulating the lichen from the ground. Still largely unexplored for growth monitoring purposes, the use of radioactive markers such as strontium and cesium from fallout or experimentally administered should be explored (Feige et al. 1988).

Assuming that both Andreev's growth method (only applicable to *Cladina* and *Cladonia* and other growth methods are valid, they are still not sufficiently precise to allow predictions or evaluate effects of weather changes or habitat conditions (Kärenlampi 1971). As the growth is very slow the time interval must be large (a year) and even year to year fluctuations are difficult to detect. There is consequently a great need for an alternative approach.

Carbon flux

There have been many studies of vascular plant productivity where growth analyses and CO_2 exchange have been used separately or in combination. There is a general agreement or corrrelation between the two methods, but it has proven difficult to measure the natural exchange of all parts and the total flux is generally obtained by extrapolation of laboratory conditions to the field (see Mooney 1972). There have been demonstrations of leaching from foliage, stems, and roots (Barber and Martin 1976, Smith 1976) and fine root turnover is largely unknown (Persson 1978). In spite of these problems, productivity of vascular plants is frequently modeled based on CO_2 exchange of the parts.

Lichens with their relatively simple structure represent in this way a much easier organism to study as they have no below ground parts. Therefore, the exchange of the whole thallus can be assessed together. What then, do we know about reindeer lichen carbon flux? How much of what we know is relevant to reindeer lichen productivity in the field?

In order to be able to model and thus extrapolate the CO_2 exchange data to a variety of weather and habitat condition several assumptions will have to be true.

1. *Carbon dioxide uptake represents the predominant mode of carbon capture; the fungus is not also saprobic.*

The author is not aware of any confirmed reports of saprobic carbon uptake of naturally grown lichenized fungi. Some, normally lichenized fungi, can be grown saprobically isolated from the phycobiont (Ahmadjian 1974), but the nutritional needs of lichenized fungi are assumed to be fulfilled by the phycobiont. Despite the importance of this concern, it has not received sufficient attention and needs study.

2. *There is no significant leaking of organic substances form the thallus or, alternatively, such leaking is quantifiable and can be modeled.*

A study of *Hypogymnia physodes* (Farrar 1976) indicated losses of carbohydrates during the drying/wetting cycles. A study by Cooper and Carroll (1978) identifies the epiphytic lichen *Lobaria oregana* as the major source of polyols in leachates from the canopy of Douglas fir in Oregon. Ribitol was the most abundant ingredient. In an experiment with *Cladina stellaris* (author's unpublished data) exposed to $^{14}CO_2$ there was no leaking of labelled substances; the loss was only through respiration. This type of experimentation needs to be repeated with more reindeer lichen species and losses, if found, must be quantified.

3. *The extrinsic and intrinsic controls of CO_2 flux are well known and quantifiable. Preferably these controlling factors should be few.*

The environmental physiology of lichen thalli is well established and relatively simple. Basically, lichens are metabolically active only when moist. Dry, they are inactive and brittle. Following showers, dew fall, or condensation of upwardly moving soil moisture, activity starts with a burst of CO_2 loss. The thallus starts photosynthesizing if incident radiation allows and the rate is primarily determined by the thallus water content and temperature. As the thallus dries out the photosynthetic rate may first increase until optimum water content is reached and subesquently fall as the internal water potential drops (Fig. 2). The reduction of the photosynthetic rate by supraoptimal water contents has been shown to be caused by increased diffusion resistance of the saturated thallus (Lange and Tenhunen 1981). The rate of drying is purely governed by physical conditions as lichens, lacking roots, do not possess active mechanisms of water uptake, and lacking stomata have no significant dynamic effect on evapotranspiration.

Although, there are concerns (Green and Snelgar 1981, Lange and Tenhunen 1981) over experimental methods in which CO_2 drawdown analysis is used (e.g. Larsson and Kershaw 1975), there are several other data sets de-

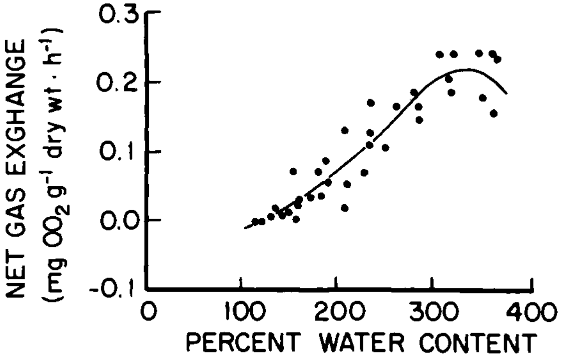

Figure 2. Net photosynthesis in relation to thallus water content in *Cetraria cucullata* from the Seward Peninsula. The measurements were made at optimum temperature and saturating irradiance.

monstrating the multivariate response surfaces of lichen photosynthesis (e.g. Carstairs 1978, Lechowicz 1978, Kappen and Redon 1978). One possible complication to the extrapolations of such data sets to natural condition, is the unknown CO_2 lichen environment and the scarce information of the interaction of CO_2 and other extrinsic and intrinsic factors. Clearly, there is a need to characterize reindeer lichen CO_2 environments and analyze lichen CO_2 gas exchange responses to these.

Lichens do not appear to be nutrient limited (Skuncke 1969, Carstairs 1978) as application of fertilizers did not result in change in growth or photosynthesis. Intrinsically, there are seasonal changes in CO_2 exchange of thalli (e.g. Carstairs 1978) and thalli of different size classes (ages?) have different rates of net CO_2 exchange (Sveinbjörnsson 1987). The exact mechanisms for these have not been fully explored.

4. *The lichen environment can be characterized and related to macroclimatic conditions with appropriate transfer functions.*

Reindeer lichens may be found scattered or in mats of varying expanse, thickness, and composition. These habits profoundly affect their environment as do other physiognomic features of the vascular plant vegetation and the general landscape topography. The thickness of the lichen mat, with dead lichen mulch below the coherent lichen, affects, as mentioned above the intrinsic CO_2 exchange capacity. It also profoundly influences the operational environment of individual thalli (Fig. 3).

Considering lichen mats as reindeer winter ranges, it is perhaps not very relevant to understand the functioning of the thickest mats with much attached dead lichen tissue and mulch as these represent underutilized degenerating range stanges (Andreev 1954) which would not exist with prudent management. However, even small amounts of attached dead tissue can significantly moderate the rapidity and severity of the drying/wetting cycles. On cool clear nights with little wind, infrared radiation loss from thallus tips reduces their temperature, while warmer moist air from the soil and the

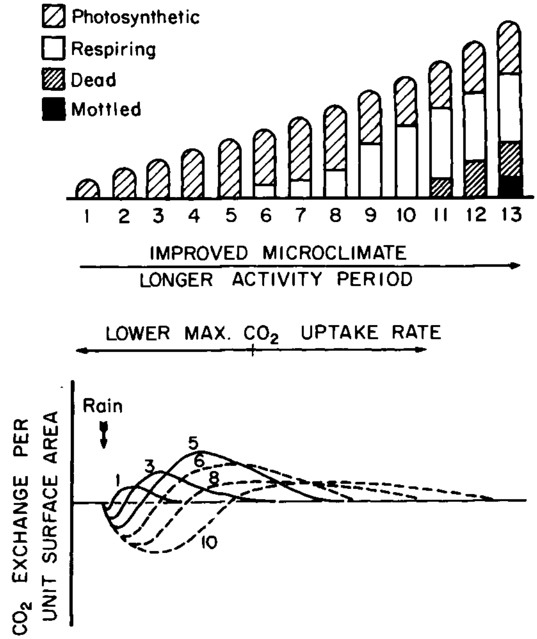

Figure 3. A hypothetical change in net CO_2 flux of lichen mats of different developmental stages. As the lichen mat gets thicker it improves it's own microclimate. Thus, the photosynthetic periods become more prolonged while the maximum rate of photosynthesis starts decreasing once the photosynthetic zone has reached maximum size.

ground rises through the mat. As it diffuses through the upper parts of the lichen thalli, the water condenses on them increasing their tissue water content significantly and rendering them capable of greater photosynthetic rates in the early morning hours. This phenomenon has been found both on low peat mounds on Nunivak Islands (Fig. 4) and in paper birch/white spruce forests in south central Alaska, but would logically be expected to occur most frequently in habitats with little wind movement. This upward movement of water, beneficial as it is to the lichen photosynthesis, which takes place in the uppermost part of the thallus, is not without costs. As mentioned above thicker mats have lower maximum rates than thinner ones, pressumably because they contain attached nonphotosynthetic tissue (Kärenlampi 1970, Carstairs 1978, Sveinbjörnsson 1987) (see Fig.3).

Monospecific lichen mats have been characterized in terms of boundary layer resistance as a function of wind speed as well as internal thallus resistance to water loss (Lechowicz 1976, Collins and Farrrar 1978, Green and Snelgar 1981, Link et al. 1985). Light penetration in such mats has also been studied (Kershaw and Harris 1971). Humidity, temperature, and drying rates all have been monitored in lichen woodland mats (Carstairs 1976, Kershaw and Field 1976). But just as different species have different gas exchange and water relations it is logical to assume that mixed mats may not simply be the sum of the parts. As an example, the dark brown, *Cetraria islandica* absorbs more solar radiation than the faintly yellow *Cetraria cucullata*, and as resistance characters are identical in these species,the former dries out faster than the latter (Sveinbjörnsson and Resnick *in prep.*). It does not necessarily have to be that these differences persist in mats of these two species as they may be differentially exposed to radiation and as thermal conductance and convection may be different depending on exact composition of the lichen canopy.

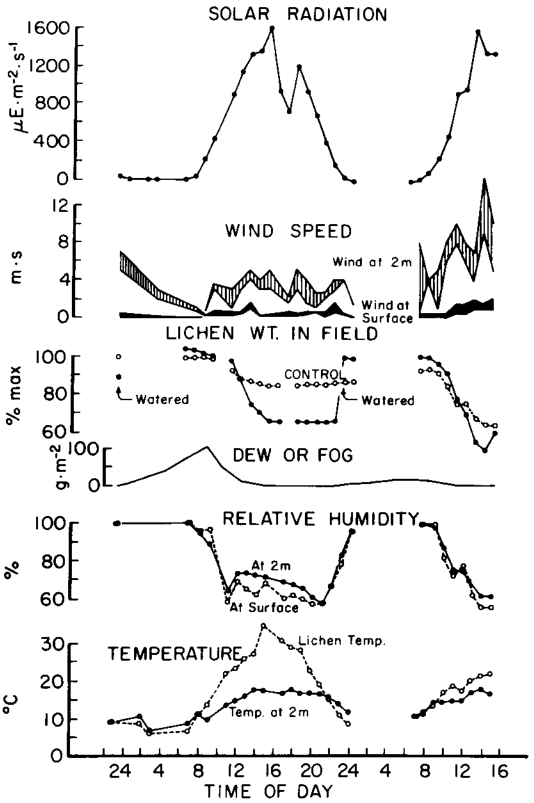

Figure 4. Microclimatic conditions and lichen water content on a peat mound edge near the airport on Nunivak Island, Alaska. Note the high humidity and dew deposition at night and early morning in spite of considerable wind speeds.

Models of lichen biophysics (Hoffman and Gates 1970) and physiology exist; some are simply regression models based on laboratory or field data (Lechowicz 1976, Lange et al. 1977, Paterson et al. 1983), while others attempt to take a more synthetic mechanistic approach (Link et al. 1985). A mathematical model of lichen mats biophysics also exists (e.g. Lechowicz 1976), although it has not been verified in situ. Thus, the framework exists for a combined model of lichen biophysics and physiology based on laboratory and field measurements. The use of well constructed models, with robust transfer functions relating macroclimate and lichen condition coupled with existing physiological models, can be used to evaluate the productivity of lichen ranges following verification in the field.

The lichen resource is utilized by the reindeer/caribou both in accordance within their behavioral constraints, and in intensive management, the directions of the manager. Lichen-reindeer interactions have been modeled (Bunnell et al. 1973) but with more behavioral and management input these models may now be improved. The time is ripe for a concerted effort to join these parts into one realistic model with range management as a guiding goal. Thus, the range manager may be provided with a tool to maximize use and minimize abuse of this valuable resource.

Acknowledgements

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Impact of soil scarification on reindeer pastures.

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Summary: During recent years, soil scarification has become a standard procedure for improving seed beds after logging. Around 57 000 ha were treated, primarily through harrowing and ploughing, in the counties of Västerbotten and Norbotten during 1985.

The positive effects of scarification, from a forestry point of view, are improved access to plant nutrients, raised soil temperatures and reduces surface moisture.

The aim of the present study was to describe long-term changes in the ground vegetation following scarification.

Harrowing affects 45-55% of the plant cover while ploughing affects 65-90%.

10 years after ploughing and harrowing about 20% of the surface is still without vegetation.

Real long-term effects remain in dispute. It has been claimed that ploughing, at least, may lead to irreversible changes.

Key words: Forestry methods, harrowing, ploughing

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Introduction

All types of soil scarification after final felling of forest stands aim to support germination of tree seeds and establishment of tree plants and their further development.

The silvicultural effects of different kinds of site preparation are well documented (Mälkönen, 1987; Pohtila, 1977; Söderström, 1975, 1976, 1988; Örlander, 1986). Scarification influences soil temperature, soil moisture, competition from surrounding vegetation, nutrient circulation and hydrology and ultimately, also plant growth (Bäcke *et al.* 1986). However, there are few experiments or published studies which describe effects of scarification on the ground vegetation (i.e. the field-and bottom layers).

The aim of this investigation was to study the long-term effects of harrowing and ploughing, especially on plant species that are grazed by reindeer.

Reindeer are herded over almost all of the two northernmost counties in Sweden, Norrbotten and Västerbotten, and in a considerable

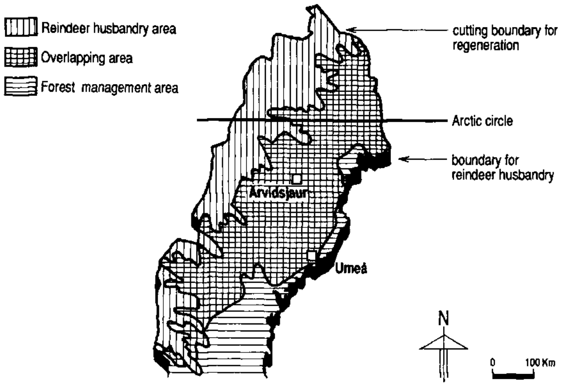

Fig. 1. Areas of interest to forestry and to reindeer husbandry in northern Sweden (Mattson, L. 1981).

part of the county of Jämtland (Fig. 1). Most of the winter range lies below and east of the cutting boundary for regeneration (Fig.1). In this part of Sweden, logging is the major industry.

According to the Forestry Act, all logged areas have to be reforested either artificially by planting or sowing, or naturally from seed trees. (Only Scots pine, *Pinus sylvestris*, is left as a seed tree, because of the risk of wind-throws which would occur if spruce trees, *Picea abies*, were left solitary. The current trend is to treat the ground after logging in most sites (Skogsvårdstyrelsen, 1987). Harrowing is by far the most common practise but mounding is increasingly used (Fig. 2).

During the last eight years the total annual scarification area in the northernmost county, Norrbotten, has totaled 27 000 ha. Of this area 20% is ploughed (Fig. 3). There is, however, a great variation between counties, different districts and ownership categories within counties (Fig. 2).

Study area

The study area is located between latitude N 63°and 68°in N Sweden. It belongs to the northern boreal vegetation zone according to Ahti *et al.*, (1968). The study objects are situated between 300 and 580 m a.s.l. The growing season lasts 130-150 days. The temperature sum for the whole region is less than 800°C with an threshold value of +5°C (Odin *et al.*, 1983). The annual precipitation is 450-550 mm, of which 35-45% falls as snow (Atlas över Sverige, 1971).

Methods

Based on information from the National Forest Enterprises of Sweden, a number of regeneration stands were defined. The aim was to find as comparable areas as possible from biotic and abiotic viewpoints.

The scarification methods which so far have been studied are ploughing and harrowing. Because of the differences in construction, in the degree of disturbance capacity, ect., between the earlier and the existing scarifiers, we have concentrated on regeneration areas, which were cultivated with the most frequently used machines and models still utilized.

The soil moisture and the thickness of the humus layer primarily determine the method to be used. We decided to choose areas with me-

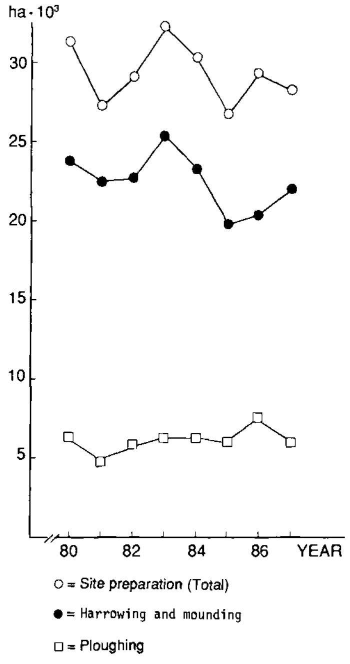

Fig 3. Site preparation during the period 1980-87 in the county of Norrbotten (Source: The National Board of Forestry.)

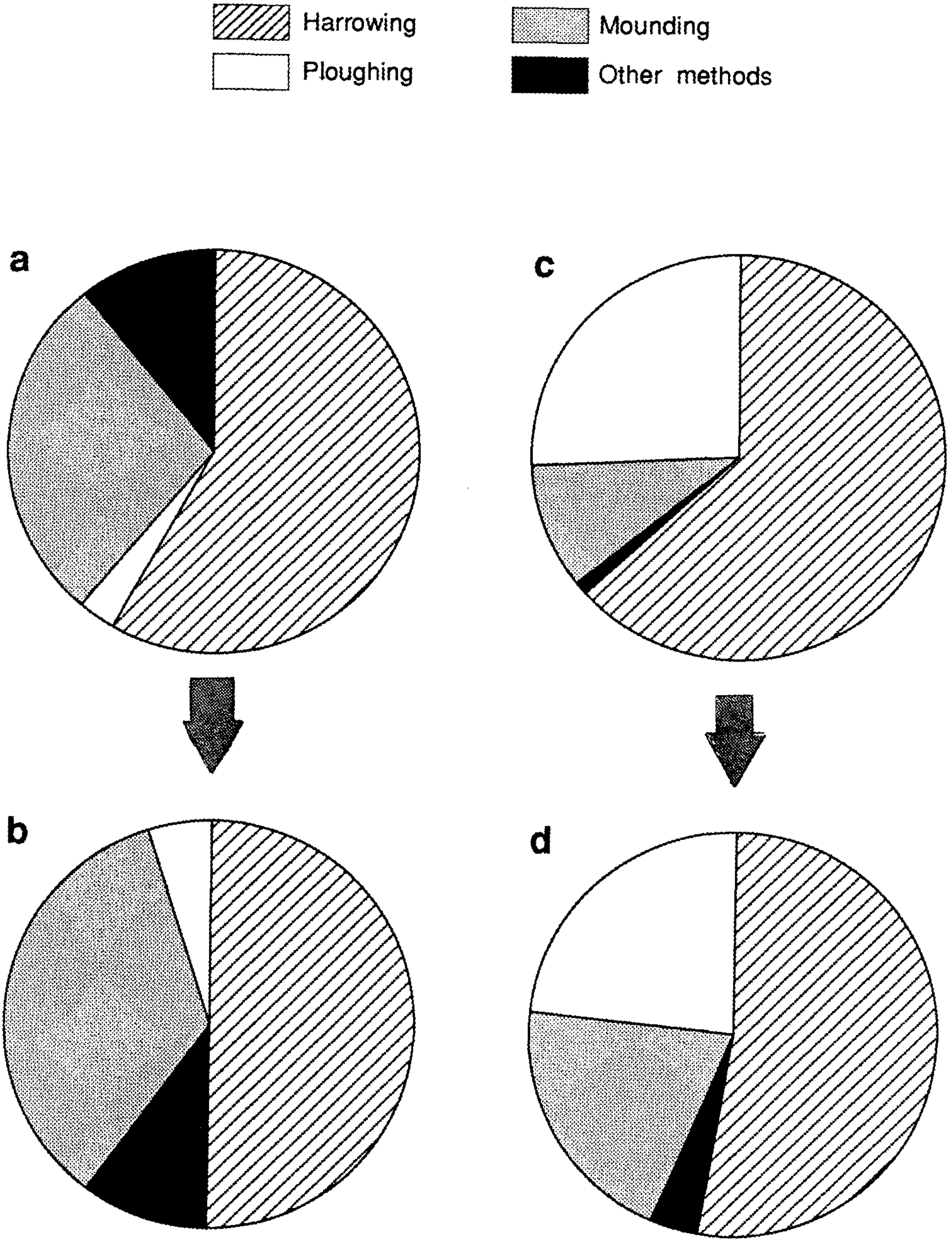

Fig. 2. The percentage distribution of different site preparation methods in 1987 and prognoses for 1991/92 in the two northernmost counties of Västerbotten and Norrbotten. Values apply only to state-owned forests. (Source: The National Forest Enterprise of Sweden).
a= Västerbotten 1987 b= Västerbotten 1992
c= Norrbotten 1987 d= Norrbotten 1991

Photo 1 a,b. The main site preparation methods to be used are harrowing and ploughing. A) deep cultivator (=plough), B) scarifier of harrow type. (Photo: O.E.)

Photo 2. Harrowed pine stand with seed trees. Harrowing is the most common site preparation method in Northern Sweden. (Photo: O.E.)

Photo 3. With modern scarifiers the degree of disturbance and the depth of furrow is adjustable. (Photo: O.E.)

sic soil moisture types dominated by sand to fine sand moraine, because these types dominate within the reindeer area.

As we could not study a limited number of sites over a long period of time we instead had to select our investigation areas in an age series, based on year of treatment. A number of control sites, *i.e.* mature forest stands comparable to the logged ones before logging and situated quite close to them, were also chosen and inventoried; accordingly we are using a static method (Austin, 1977).

In each investigation area the relative frequencies of the different subsections - tilt, shoulder, ditch bottom and intact ground - were recorded. The standing crop of the ground vegetation on each subsection was calculated.

A number of parallel transects, at a 45° angle to the dominating plough course, were distributed across the sites. A number of sample plots were systematically placed along these transects and in each plot the following measurements were made:

1. In the 1 m^2 plots the cover of each plant species or plant group, both in the whole plot and in the respective subsection within the plot, were estimated and the proportion of each subsection was estimated.
2. On every subsection a vegetation sample (500 cm^2) was taken in order to quantify the standing crop. The samples were brought to the laboraory, where they were dried, sorted and weighed.
3. From the centre of each plot a 10 m measuring tape was laid out at right-angles to the predominant plough course and along that tape the length each subsection occupied was measured.
4. The height differences between the intact ground level and the manipulated subsections, top of tilt and shoulder, and bottom of ditch, were measured.

Preliminary results and discussion

The material presented below is preliminary and, in many ways, also incomplete. Some data from an earlier pilot study are also included (Eriksson, 1985).

Physical features

The proportion of intact ground on recently ploughed areas varied between 13-22% and on harrowed areas between 48-56%. The values obtained on the ploughed areas agree well with those reported by Kellomäki (1971) and Ferm & Pohtila (1981) from ploughed areas from different parts of Finland. Eriksson (1985) also obtained similar values in his investigation carried out near Jokkmokk in North Sweden.

The heights of the tilts varied form 17 to 27 cm on ploughed areas and from 14 to 15 cm on the harrowed areas in relation to the intact ground. There was, however, no clear reduction in height with time, probably because so few stands have been investigated.

Development of the vegetation

The proportion of litter, mineral soil and humus decreased from 48% to 17% during a period of eleven years on harrowed sites (Fig. 4 a,b) and from 75% to 10% during twenty years on ploughed sites.

The ground vegetation developed rapidly during the first years, but later the changes were somewhat slower. Ferm & Pohtila (1981) found a similar trend in their study. Many factors may affect this process: soil moisture, type of soil, temperature sum, tree layer, etc.

The control stands (mature stands) represent the hypothetical situation before site preparation. According to Sjörs (1980), succession may be irreversible. It is, thus, not certain that the prepared stands return to the same composition in the long run. In fact, the desirable long-term effect of scarification is to increase the forest production. If that is true, this long-term effect should then also be seen on the ground vegetation. Twenty years is, however, too short a period of time to determine whether succession will lead to another composition in the mature second growth stand.

It seems to take more than twenty years in ploughed areas (Fig. 4 b) before the soil is covered by ground vegetation. The time period is probably a little shorter on harrowed areas (Fig. 4a). The total percentage cover of dwarf-shrubs was lower than the mature stand 11 years after ploughing and 16 years after harrowing. The opposite effects were observed for the sum of grasses and herbs (Fig. 4 a,b). The dominant dwarf-shrubs in the study stands were *Vaccinium myrtillus*, *Vaccinium vitis- idaea*, *Vaccinium uliginosum* and *Empetrum hermaphroditum*. *Deschampsia flexuosa* was the most common graminoid. Herbs such as *Chamaenerion angustifolium*, *Linnea borealis*, *Solidago virgaurea* were quite rare. *Pinus* and *Picea* plants, *Salix spp. and Betula pubescens* were the most frequent shrubs. Lichens in the study stands were of rare occurrence.

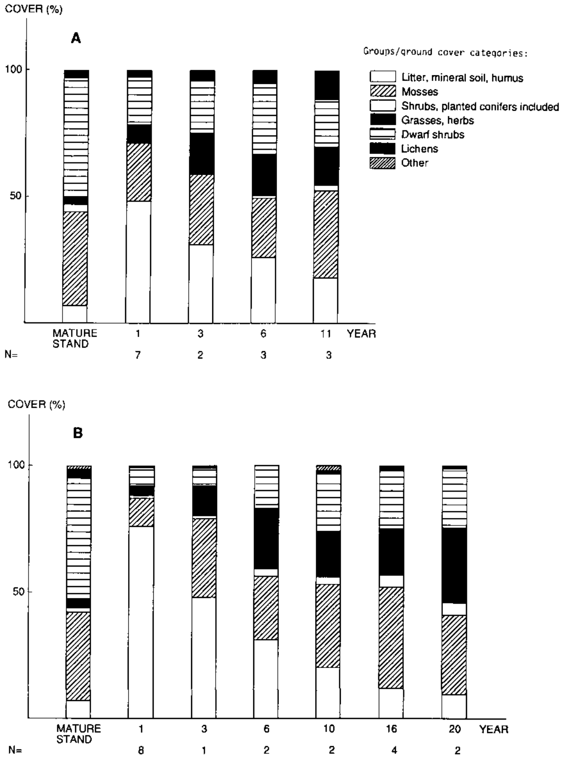

Fig. 4. Harrowed sites of different age. Cover (%) of 7 different groups/ground cover categories on sites of different ages after soil scarification. A = harrowed sites, B = ploughed sites N = number of investigated stands.

The abundance of *Empetrum hermaphroditum* and *Vaccinium myrtillus* decreased after ploughing (Fig. 5). Eleven years after the scarification their coverage was reduced by 10-15% compared to the control sites (Fig. 5). Mosses common in mesic forest types, like *Pleurozium schreberi* and *Hylocomium splendens,* had also decreased. *Deschampsia flexuosa,* which had a coverage of only a few per cent in mature stands, increased to a coverage of about 15-30% in areas which were scarified eleven years earlier. *Vaccinium vitis-idaea* had an irregular development.

Pioneer mosses and mosses which are common in dry sites like *Polytrichium piliferum* and *Ceratodon purpureus,* had a coverage about 30-35% higher than the mature forest eleven years after site preparation.

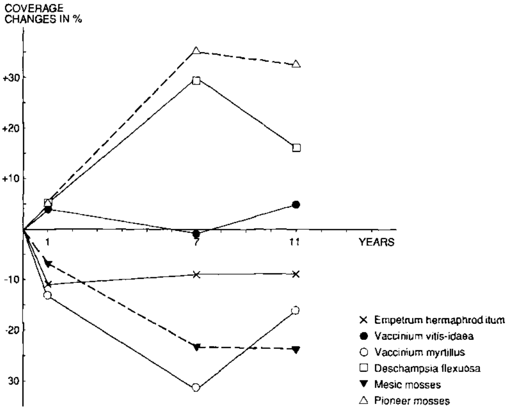

Fig. 5. Relative changes of different species/groups during 11 years (n=3x(20+20)) on ploughed sites compared to mature, control stands.

The differences in cover are significantly different from the cover values in the mature stands for all species and species groups already seven years or, as for *Vaccinium vitis-idea,* after ten years. Ingelög (1974) decribes the same kind of vegetation changes after clear-cutting without site preparation.

The vegetation on different subsections

The succession of the vegetation on the different subsections differs from the vegetation development in the whole area. After eleven years *Deschampsia flexuosa, Vaccinium myrtillus, Empetrum hermaphroditum* and the mesic forest mosses are more abundant on the intact ground than on the other subsections. On the ditch bottoms the pioneer mosses dominate. *Vaccinium vitis-idaea* is more abundant on tilts than on the other subsections. These trends agree very well with those described by Ferm & Pohtila (1981).

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The effects of stand characteristics on reindeer lichens and range use by semi-domesticated reindeer

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Abstract: The study was carried out in Kuusamo (66°15'N, 29°05'E) and Inari (68°30'N, 28°15'E), northern Finland, where 24 and 22 Scots pine stands were studied respectively. Clear-cutting (logging residue) caused a decline in lichen biomass for some few years, but otherwise the age of the stand had no effect upon lichen biomass. Instead, a positive correlation was found between litter/logging residue and the mean height of lichens; in Kuusamo, logging residue decreased significantly with the age of the stand. Grazing pressure in terms of fecal group density increased with the age of the stand. The preference of old forests came visible also as a lower mean height of lichens, which eliminates the possibility that the preference of old forests is associated only to the use of arboreal lichens. In Inari, grazing pressure sharply increased after the stand had reached the age of 100 years despite scarce litter/logging residue and fair lichen ranges in younger forests; there prevailed a negative correlation between stand density and grazing pressure. It has been suggested that there might be three main reasons for reindeers preferring old forests: 1) hardening of the snow (because of winds) on clear-cut areas, 2) logging residue preventing digging for the food beneath the snow, and 3) poor visibility in young pine stands (Inari) which might increase predation risk.

Key words: Ecology, forestry

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Introduction

In Fennoscandia, a major proportion of semi-domesticated reindeer (*Rangifer tarandus L.*) confine themselves in winter in coniferous forests where timber is commonplace the main forest product. The impacts of wood production on winter ranges can be described briefly as follows:

1. Clear-cutting on fresh mineral soils adds *Deschampsia flexuosa* improving range conditions in autumn and early winter (Sulkava and Helle, 1975; Helle and Saastamoinen, 1979; Mattila, 1981).
2. Cutting reduces arboreal lichens *(Usneaceae)*, since forests with abundant sources of them are normally older than 100 years (Mattila, 1979); arboreal lichens are used mainly in late winter when ground vegetation is not available to reindeer because of deep or hard snow.
3. Reindeer lichens *(Cladonia ssp.)* are the most

important component in the winter diet of reindeer. However, the opinions on the effects of forestry on lichen biomass and lichen use by reindeer are some what conflicting. Mattila and Helle (1978) and Mattila (1981, 1988) stated that in Finnish reindeer management area there is no significant difference in lichen biomass in young (<70 yrs.) and older forests. On the other hand, there exists evidence that reindeer likely graze in old forests (R. Helle, 1984; Helle and Aspi, 1985). The question on availability of reindeer lichens is coming more important with the reduction of arboreal lichens caused in northern Finland by cuttings and air pollution (Kautto et al., 1986; Mattila, 1988; Helle et al., 1989).

This paper deals with that obvious discrepancy between absolute (total biomass) and relative (biomass available to animals) lichen resources (see Andrewartha and Birch, 1954). Our hypothesis is that forestry practices influence, by altering and modifying stand and site characteristics, habitat selection of reindeer and thus effect on the actual lichen use. It claimes that the impacts of forestry can not be evaluated only on the basis of lichen biomass. The hypothesis was tested by measuring the main characteristics of lichen vegetation and quantifying grazing pressure by reindeer in same areas, and relating them to stand and site characteristics.

Material and methods

Study area

The study was carried out in Kuusamo (66°15'N, 29°05'E) in the herding association of Alakitka and in Inari (68°30'N, 28°15'E) in the herding association of Ivalo. In Kuusamo 24 and in Inari 22 sample areas, located on poor mineral soils (*Calluna-Cladina* type) in pine forests, were studied in 1983 and 1984. The size of the sample areas was 1 ha, and they were selected for the study on the basis of the estimated age of the stand in order to obtain a representative sample from forests of various age.

Sampling

Percent cover of various plant species and litter (including logging residue) was estimated from 15 randomly selected plots each of which 0.25 m^2 in size in each sample area.

The density of the stand and grazing pressure in terms of fecal group density were determined by the method of plotless sampling (e.g. Greig-Smith, 1964; Pielou, 1977), i.e. by measuring the distance from a random point to the nearest item.

From lichens (including *Cladina* species and *Stereocaulon spp.)* the mean height of the living thallus was measured by the accuracy of 1 mm. Lichen biomass was calculated on the basis of percent cover and height of lichens using formulas presented by Mattila (1981).

Density of trees and fecal groups was calculated using Pielou's (1977) formula

$$\tilde{\lambda} = \frac{n-1}{n} \cdot \frac{1}{\bar{w}} \qquad (1)$$

where w is the squared distance ($w = r^2$) from the random point to the nearest item and n is the number of observed values (15 in this case).

The method requires that the items are randomly distributed. The test of randomness was made after Greig-Smith (1964) and it showed that the distribution of trees and fecal groups did not differ significantly from random distribution.

Fecal group density as an index of grazing pressure

One of the basic weaknesses of fecal counting method is that the rate of decomposition of fecals is dependent on soil characteristics and vegetation. Because all the sample areas were situated on the same forest type, this problem might not be serious in this study. That was tested by using a following procedure. The distance from the centre of the sample plot was measured separately to the nearest fresh (< 1 year) and old (> 1 year) fecal group in 16 sample areas in Kuusamo in order to determine the average decomposition time for fecal groups.

If the grazing pressure in a known area is constant, the circle of radius, which contains at least one fresh item, is every year:

$$(2) \qquad r_f = \sqrt{1/\lambda}$$

were the Poisson parameter λ denotes the mean number of items per circle of unit radius (see Pielou, 1977). If the fecal groups are observable only one year, then the distance from the random point to an old fecal group is the same as the distance to a fresh group. Generally, if fecal group is observable t years, then distance to an old group is:

$$(3) \qquad r_t = \sqrt{1/(t \times \lambda)}$$

Thus the ratio between old and fresh group in the stand is:

$$(4) \qquad r_t/r_f = (\sqrt{1/(t \times \lambda)})/(\sqrt{1/\lambda})$$

and the age (t) of the fecal group is found to be:

$$(5) \qquad t = 1/(r_t^2/r_f^2)$$

If the sample areas younger than 10 years are excluded, the average time that fecal groups are visible accounts to 4.9 years, and the rate of decomposition is not dependent on the age of the stand (Fig. 1). In young stands (< 10 yrs.) many old but only few fresh fecal groups were found giving seemingly an indication of a very slow rate of decomposition. However, the result is an obvious artefact. Very likely, the abundance of old fecal groups is associated to normal winter feeding behaviour of reindeer: they gather in late winter to logging areas to feed on arboreal lichens from fallen trees (see Helle and Saastamoinen, 1979). Therefore, densities in young forests are obvious over-estimates, which should be taken into account when interpreting the results.

Results

General features of study areas

The means for the main characteristics of the study areas are given in Table 1.

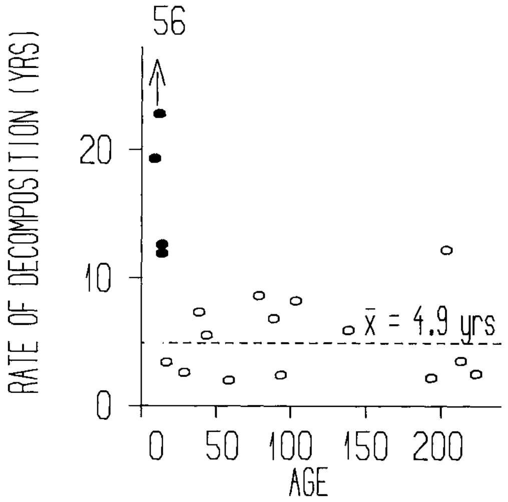

Fig. 1. The rate of decomposition of fecal groups in stands of various age.
● = stands < 10 year; o = stands > 10 year

The lower percent cover of lichens in Kuusamo is largely a result from heavier grazing pressure. In the late 1970's, the lichen range area per reindeer older than one year (close to animal number of winter herd) amounted in Kuusamo to 19 ha and in Inari to 68 ha. That explains also the lower mean height of lichens as well as the smaller proportion of *Cladonia stellaris* (0.3% vs. 33.7%, calculated from percent cover), whose poor resistence to heavy and frequently repeated grazing is well-known (Ahti, 1961).

Also percent cover of mosses and litter was greater in Kuusamo. Most of litter in young stands was logging residue in both study areas. Material from Kuusamo comprised of younger regeneration areas, which might explain the abundance of logging residue.

Reindeer lichens

The characteristics of lichens were not dependent on the age of the stand in Kuusamo, whilst in Inari the mean height of lichens correlated negatively ($r = -0.521$, $p < 0.05$, $df = 20$) and percent cover positively ($r = 0.445$, $p < 0.05$, with the age of the stand. One should note, however, the drastic decline in lichen biomass in Kuusamo immediately after clearcutting (Fig. 2), when about 60% of the ground was

Table 1. General characteristics (mean ± standard error) of the sample areas in Kuusamo and Inari.

	Kuusamo		Inari	
	x̄ ± S.E.	Range	x̄ ± S.E.	Range
Age of stand, yrs.	76 ± 16	0.5—230	99 ± 12	12—230
Trees per ha	1846 ± 415	140—8554	1521 ± 270	285—5138
Lichens:				
percent cover	24 ± 2	7—41	55 ± 2	38—67
mean height, mm	13.7 ± 0.7	9.3—20.5	22.1 ± 0.7	15.3—27.2
Biomass, kg/ha	232 ± 26	47—452	480 ± 27	137—703
Percent cover of:				
Mosses	10 ± 2	0—47	2 ± 1	0—9
Dwarf shrubs	13 ± 2	6—38	21 ± 2,	8—33
Litter (including logging residue)	15 ± 3	4—60	5 ± 1	0—14

covered by logging residue. The most harmful effects of logging residue seem to be over in some few years, which is obviously associated to dropping-off of needles from the branches. Material from Inari comprised only of older regeneration areas, but a corresponding reduction in lichen biomass just after clear-cutting i expected, because stand densities (and volumes) are quite similar to those in Kuusamo. It is interesting to note that in Inari the observed age-specific trends in mean height and percent cover of lichens counterbalanced each other, because of which lichen biomass was not dependent on the age of the stand.

Percent cover of lichens correlated in Kuusamo with litter/logging residue negatively ($r = -0.411, p < 0.05, df = 22$), but the mean height and biomass were not influenced by stand and

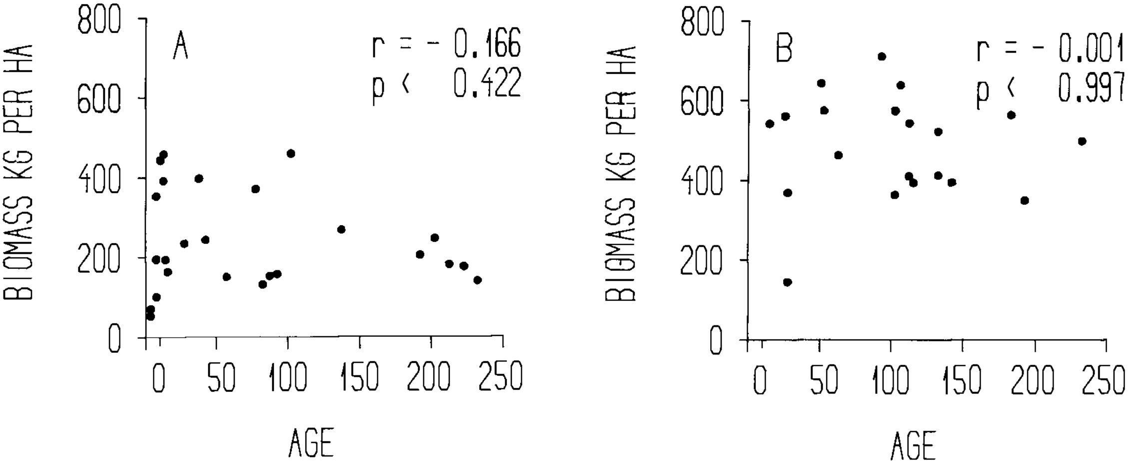

Fig. 2. The age of the stand and lichen biomass in Kuusamo (A) and Inari (B).

range characteristics. In Inari, the mean height of lichens correlated positively with mosses ($r = 0.521$, $p < 0.05$) and dwarf shrubs ($r = 0.423$, $p<0.05$) and lichen biomass with litter/logging residue ($r = 0.424$, $p<0.05$). A significant negative correlation occurred between percent cover of lichens and litter/logging residue ($r = -0.480$, $p< 0.05$), dwarf shrubs ($r = -0.457$, $p < 0.05$) and mosses ($r = -0.537$, $p< 0.05$).

The correlations between percent cover and mean height of lichens and ground vegetation (including litter/logging residue) were studied also at the level of the single sample areas.

In Kuusamo, percent cover of lichens was negatively correlated ($p < 0.05$) with litter logging residue in 8 sample areas, of which 7 were located in stands younger than 15 years. A positive correlation between mean height of lichens and litter/logging residue prevailed in 8 sample areas, from which 7 were in stands younger than 35 years.

In Inari, a negative correlation between percent cover of lichens and litter/logging residue existed in 3 sample areas, from which 2 were located in stands younger than 50 years. The correlation between mean height of lichens and litter/logging residue appeared significantly positive in 5 sample areas without any clear association to the age of the stand. The effects of mosses and dwarf shrubs on the reduction of lichens were occasional.

Distribution of grazing

Fecal group density increased with the age of the stand in both study areas (Fig. 3). It correlated negatively with mean height of lichens in both study areas (Fig. 4), in addition to which a negative association between fecal groups density and litter/logging residue occured in Kuusamo ($r = -0.414$, $p<0.05$, $df = 22$).

The relationship between fecal group density and lichen biomass appeared to be quite similar in both areas (Fig. 5). Especially in Inari, fecal group density remained quite low in young forests despite of fair lichen biomasses; it showed a clear increase after the stand had reached the age of 100 years. In Inari, a negative correlation was found between stand density and fecal group density (Fig. 6).

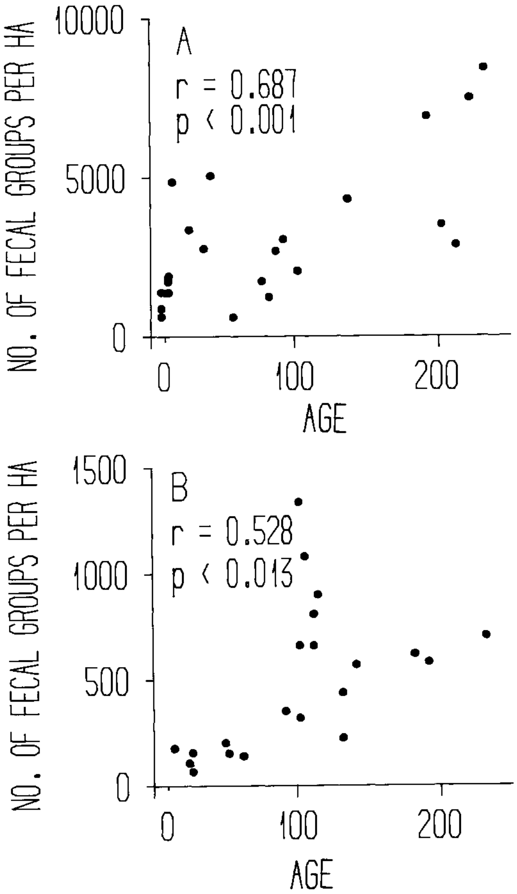

Fig. 3. The relationship between the age of the stand and grazing pressure in Kuusamo (A) and Inari (B).

Discussion

The behavioral responses of animals to variation in their food resources are commonly described by means of the concept of functional response (Holling, 1959). In several herbivorous mammals, food intake increases linearly or exponentially as the function of plant biomass (Alldeen and Whittaker, 1970, Batzli et al., 1981; Short, 1985; Spalinger et al., 1988). Similar relationship is found also in reindeer in summer (Trudell and White, 1981; 1980, Skogland). In this study (Fig. 5), however, that relationship differed from the theoretical pre-

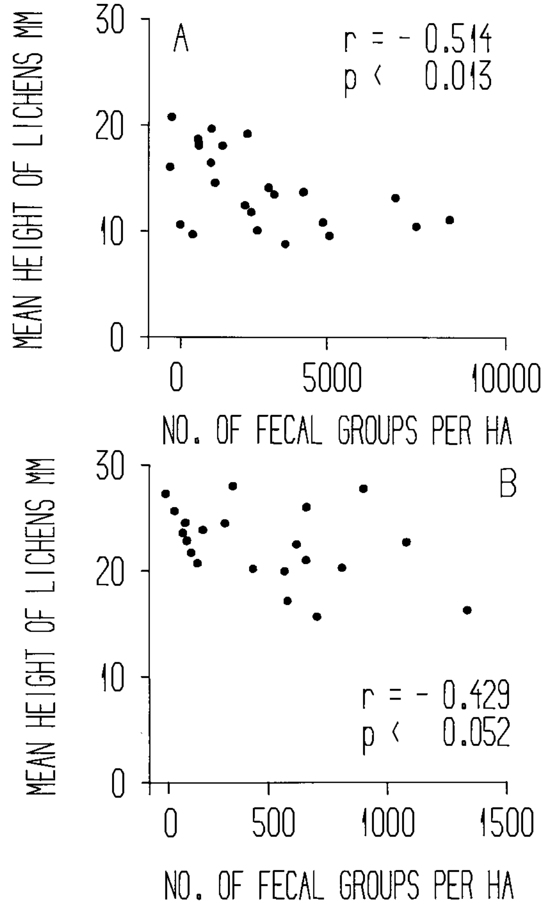

Fig. 4. The relationship between grazing pressure and the mean height of lichens in Kuusamo (A) and Inari (B).

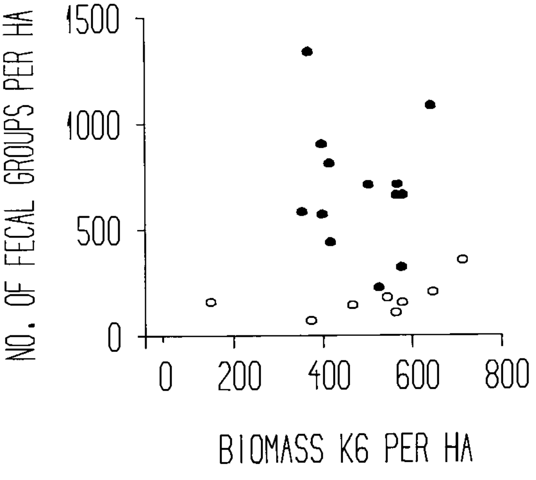

Fig. 5. The relationship between lichen biomass and grazing pressure according to the age of the stand in Inari.
o = stands<100 years; ● = stands>100 years

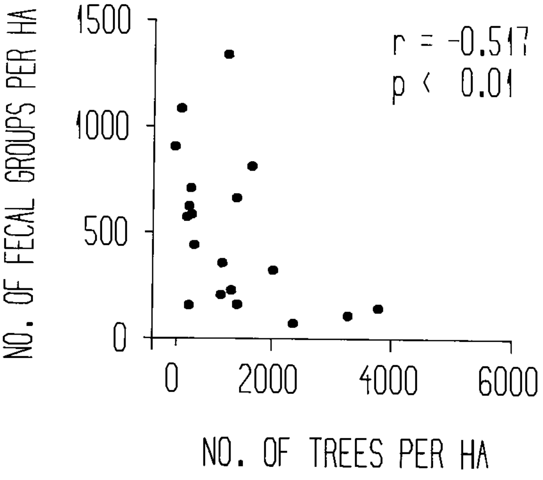

Fig. 6. The relationship between stand density and grazing pressure in Inari.

dictions as well as the earlier empirical findings indicating that lichen use by reindeer is influenced also by other factors than lichen biomass only.

In Kuusamo, reindeer tended to avoid clear-cut areas and seedling stands, whilst in Inari grazing pressure remained at a low level till the stands had reached approximately 100 years age. Of course, reindeer do not determine stand age, but their habitat preferences are dependent on stands and site characteristics associated to the stand age.

At the first glance, the preference of old forests seems to fit well in feeding behaviour of the reindeer. In easy snow conditions reindeer dig lichens for their food, but revert later in winter upon arboreal lichens, which occur most abundantly in old forests)Mattila, 1979). However, that can not explain the negative correlation between the age of the stand and mean height of lichens; it is a clear indication of light lichen use in young forests. An alternative explanation is that lichens grow faster in young forests than in old ones. Indeed, there exist results that *C. rangiferina* grows fastest in young dense pine stands and *C. mitis* in small seedling stands (Helle et al., 1984). However, the differences are too small to cause any clear negative relationship between the age of stand and mean height of lichens as found in this study.

Eriksson (1976) found that the snow hardens in a clear-cut area more likely than in the shade of forests. There exists, however, no evidence that the snow conditions in young forests are in general less favorable than in older ones.

Especially in Kuusamo, a negative correlation between litter/logging residue and fecal group density occurred and a positive correlation was found between litter/logging residue and mean height of lichens. These facts support the idea that logging residue is a major factor for the low preference of young forests. It is easy to understand that large-sized dry branches and crowns on the ground prevent effectively the reindeer to obtain lichens by digging beneath the snow; the greater is percent cover of logging residue, the smaller the actual availability of lichens.

In Inari, the avoidance of young forests was even more striking than in Kuusamo despite lower percent cover of logging residue. That suggests that there might exist also other factors than possible unfavorable snow conditions and logging residue which influence range selection. It can be hypothesized that good visibility of the range would be of importance, especially in areas where reindeer are used to live partly in open fell terrain as they do in Inari. Good visibility is known to play an important role in habitat selection of barren-ground caribou *(Rangifer t. groenlandicus)* (Pruitt, 1959; Henshaw, 1970) and wild forest reindeer *(Rangifer t. fennicus)* (Helle, 1981), because it obviously reduces predation risk. If seedling stands are excluded, visibility is, no doubt, associated with the age and especially the development class of the stand, because density of trees will decrease and lower branches self-prune with the succession of the forest.

The three hypotheses presented here can be tested with simple field experiments. These should compare lichen use by reindeer (1) in clear-cut stands with and without logging residue, (2) in young stands with different thinning regimen and (3) study snow conditions in different treatments and their possible effect on lichen use.

Practical remarks

High preference of old stands may effect negatively on productivity of the range. Helle et al. (1989) showed that there prevails, in general, a strong positive relationship between lichen range area per reindeer and percent cover of lichens ($y = 10.9 + 0.577 x$, where y = percent cover of lichens and x = lichens range in ha per reindeer, $r = 0.849$, $df = 12$, $p < 0.001$). The function predicts that a 2-fold and 3-fold increase in animal density result in a 38% and 51% reduction, respectively, in percent cover of lichens by the long run. Extensive forest renovation has thus a detrimental effect on the condition of lichen ranges in old stands.

Now one may argue that lichens gain a corresponding benefit in young stands counterbalancing the losses elsewhere. The present results do not support that; the mean height of lichens was greater in young stands, but not percent cover. Recovery from the obvious mechanical destruction caused by cutting may take time, and later, in dense sapling stands, reindeer lichens are not capable to compete with mosses (especially *Pleurozium shreberi*) (Söyrinki *et al.*, 1977).

Finally, the dynamics of lichen ranges in forests subjected to normal forestry regimen can not be fully understood considering dry and barren sites only. In Northern Lapland (see Mattila, 1981), about 50% of the total lichen biomass is growing on sub-dry sites (*Empetrum-Myrtillus* type), where various kind of methods in site preparation are used. Their effects are not carefully studied, but no doupt they increase grazing pressure in old forests both in sub-dry and dry and barren sites.

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Lichen ranges, animal densities and production in Finnish reindeer management

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Abstract: In the 1970s, mean lichen biomass ranged by the earmark districts (comprising of 2-9 adjacent herding associations) between 54 kg and 380 kg DM per ha correlating negatively with animal density per lichen ranges (range 1.5 - 14.3 ind. per km^2). Biomasses were far below economic carrying capacity of lichen ranges (900 kg DM per ha). The condition of lichen ranges was poorest in the southern half of the area where alternative food to reindeer lichens *(Deschampsia flexuosa*, arboreal lichens and supplementary feeding) was available. In 1980-86, recruitment (calves per 100 females) was 33% higher than in the 1970's, on an average (65 vs. 49), despite a 90% increase in animal numbers between 1970 and 1986; recruitment has not been dependent on the condition of lichen ranges. The increase in production has been some higher than expected on the basis of animal numbers. The reasons for the increasing trends in animal numbers, recruitment and production remains some unclear, but they may include favorable winter conditions, supplementary feeding, medical treatment against parasites and proper harvesting policy.

Key words: reindeer, range, carrying capacity

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Introduction

Economic carrying capacity is referred as an equilibrium where animal density is levelled so that it allows maximum primary production of the range (Caughley, 1976). Subsequently, consumption by animals is in maximum providing in turn maximum sustained yield. Both theoretical and empirical evidence shows that primary production peaks at the biomass value which is about 50% from ecological carrying capacity K (Caughley, 1976; Kärenlampi, 1973; Gaare and Skogland, 1980; Skogland 1986).

The most important winter ranges of reindeer are dominated by reindeer lichens *(Cladonia ssp.)*. Due to high preference by reindeer but slow growth rate reindeer lichens are vulnerable to over-grazing, i.e. to the reduction of biomass below the 50% limit of K. In fact, over-grazing seems to be closely associated elsewhere to intensive reindeer economy now and past (Andreev, 1971; Kärenlampi, 1973; Skogland, 1986).

In this paper we relate the existing range data (Mattila and Helle, 1978; Mattila, 1979, 1981) to animal density in northern Finland and consider how animal production and recruitment, its main determinant (see Skogland 1983, 1986), have developed in different range conditions since the beginning of the 1970's.

Material and methods

The Finnish reindeer management area is divided into 56 herding associations, which perform 14 larger units, so called earmark districts, each including 2-9 adjacent herding associations (Fig. 1). Most parts of the earmark districts of Utsjoki and Enontekiö are sub-alpine and alpine areas, whilst the others are located in coniferous forest zone (with some fells in northern Lapland).

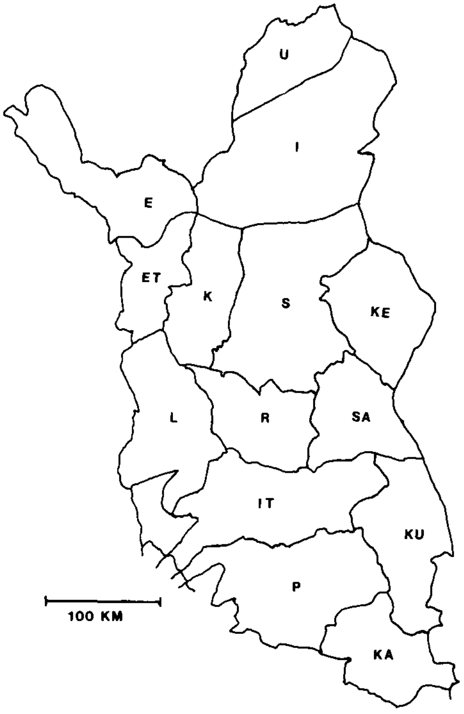

Fig. 1. The map of the reindeer management area in Finland. The earmark districts are: U = Utsjoki; I = Inari; E = Enontekiö; ET = Etelä-Lappi; K = Kittilä, S = Sodankylä; KE = Keminkylä; SA = Salla; R = Raudanjoki; L = Läntinen; IT = Itäkemijoki; KU = Kuusamo; P = Pudasjärvi; KA = Kainuu.

Range data have been obtained from a range survey carried out as a part of the Finnish National Forest Inventory (Mattila and Helle, 1978; Mattila, 1979, 1981). Biomass or relative abundance of reindeer lichens, *Deschampsia flexuosa* and arboreal lichens *(Alectoria ssp.* and *Bryoria ssp.)* was estimated from a field sample consisting of 3 282 plots.

The term "lichen range" used here includes dry and barren sites (mainly *Calluna-Cladina* -type) and sub-dry sites (mainly *Empetrum-Myrtillus* -type) in the earmark districts of Utsjoki, Inari, Enontekiö, Etelä-Lappi, Kittilä, Sodankylä and Keminkylä (where percent cover exceeds 10% at present and 50% without grazing). Ungrazed lichen biomass amounts on dry and barren sites to 3000 kg per ha and on sub-dry sites half of that.

Reindeer data are based on official statistics. Densities presented here include only $\geqslant 1$ year-old animals (both slaughtered and those left alive in round-ups kept between October and February), but they match quite well to density of winter herd, since slaughtered animals are compensated by calves.

Results

Range lands and animal density

Gross density and density per lichen range are given by the earmark districts for the periods of 1970-79 and 1980-86 in Table 1. From it appears that the proportion of lichen range from the total land area varied between 7% and 84% i increasing towards the north. During both the periods, there prevailed a significant expontential relationship between the proportion of lichen range and gross density with respective r-values of 0.563 ($p < 0.05$) and 0.771 ($p < 0.01$). In 1970-79, a 10-fold increase in the proportion of lichen range (7% → 70%) resulted in a density increase from 0.9 to 1.7, whilst in 1980-86 it allowed an increase from 1.1 to 2.7 individuals per km^2.

Table 1. Gross density (GD) and density per lichen ranges (LD) ind./km² by the earmark districts in periods of 1970-79 and 1980-86. Range data from Mattila (1981).

Earmark district	1970-79		1980-86	
	GD	LD	GD	LD
Utsjoki	2.1	2.5	3.6	4.3
Inari	1.0	1.5	2.0	3.0
Enontekiö	1.6	2.2	2.7	3.7
Etelä-Lappi	1.5	3.6	2.2	5.2
Kittilä	1.0	3.1	1.6	4.9
Sodankylä	1.2	2.4	1.8	3.5
Keminkylä	1.6	2.8	1.5	3.9
Salla	1.0	14.3	1.2	16.9
Raudanjoki	1.2	10.0	1.6	13.3
Läntinen	0.9	12.5	1.1	15.9
Itäkemijoki	1.0	12.5	1.3	16.8
Kuusamo	1.2	5.3	1.5	6.8
Pudasjärvi	1.1	12.5	1.2	13.9
Kainuu	0.4	1.7	0.7	2.8

Condition of lichen ranges

The mean height of lichens (living part) ranged between 8 and 13 mm by the earmark districts without any clear correlation to animal density per lichen range. Instead, percent cover and biomass of lichens were strongly dependent on animal density (Figs. 2 and 3). From Fig. 4 appears that lichen biomasses accounted only to 6 (Salla) - 44 (Inari) % from the most productive lichen mat being about 900 kg DM per ha. The condition of lichen ranges revealed a clear geographic pattern. Heavily grazed ranges were typical to the southern half of the area

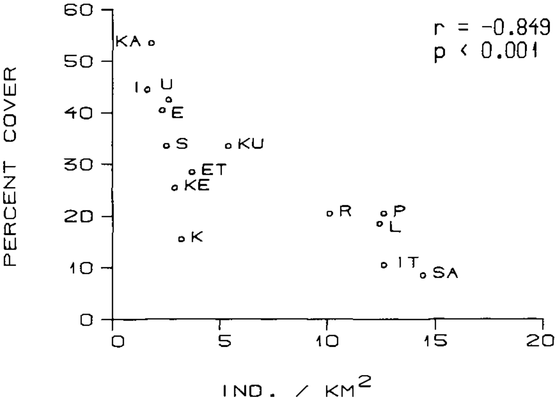

Fig. 2. The relationship between animal density per lichen range and percent cover of reindeer lichens. For abbreviations see Fig. 1. Range data from Mattila (1981).

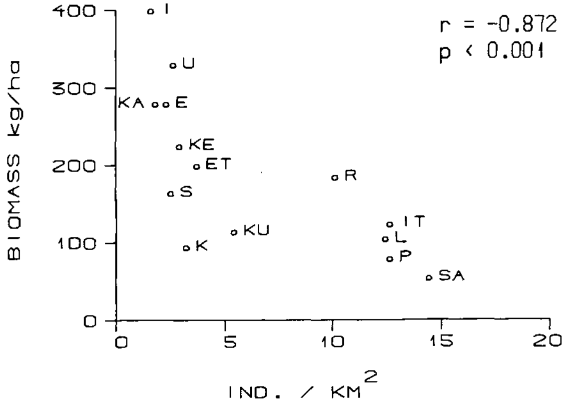

Fig. 3. The relationship between animal density per lichen range and lichen biomass. For abbreviations see Fig. 1. Range data from Mattila (1981).

(excluding Kainuu) characterized by abundant sources of *Deschampsia*, some arboreal lichens and intensive supplementary feeding (see Helle and Saastamoinen, 1979; Mattila, 1979, 1981).

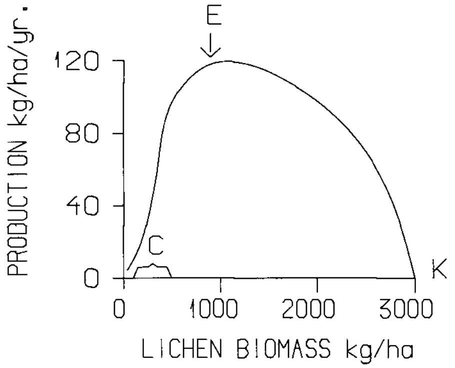

Fig. 4. The relationship between lichen biomass and annual lichen production. K = ecological carrying capacity; E = economic carrying capacity; C = the range of the mean biomasses in the 14 earmark districts in the 1970's. The production curve calculated from data of Kärenlampi (1973).

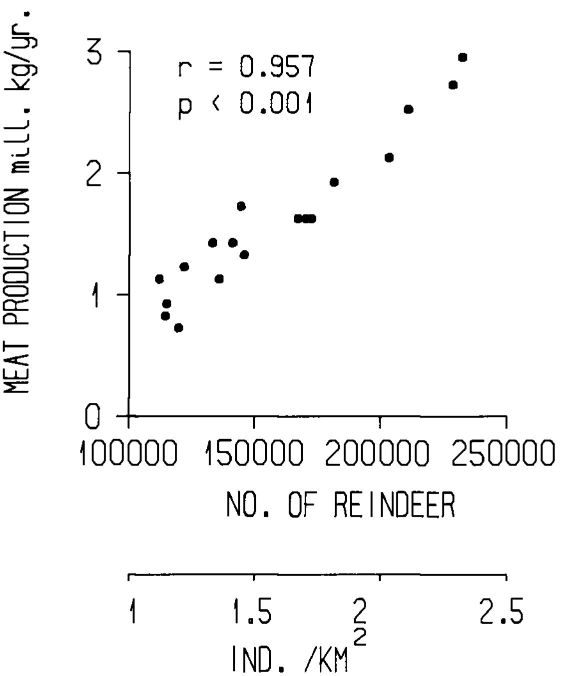

Fig. 5. The relationship between the number of reindeer (or gross density) and meat production in 1970-1987.

Production

In 1970, reindeer population totalled 121 000 animals, and by 1986 it has increased to 230 000 animals. Fig. 5 shows that meat production has increased during that period some what faster than should be expected on the basis of the number of animals. The same analysis has been made for every single herding association (n = 56) with essentially same results even in cases where gross density exceeds at present 4 individuals per km².

The mean recruitment (calculated per +1 year-old females in June-July) for the periods of 1970-79 and 1980-86 is plotted against density per lichen range in Figs. 6 and 7. It appears

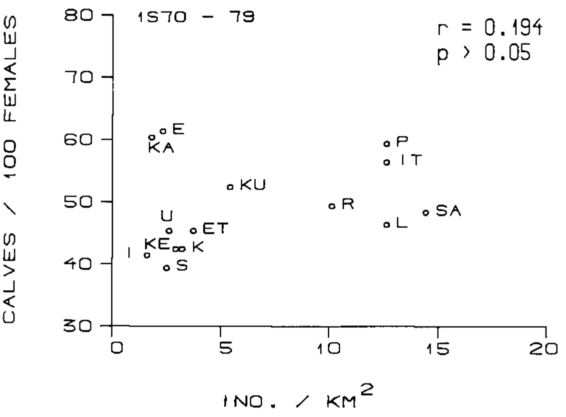

Fig. 6. The relationship between animal density per lichen range and calf crop in 1970-79. For abbreviations see Fig. 1.

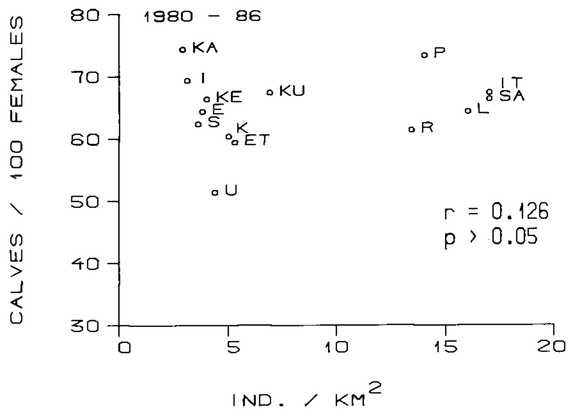

Fig. 7. The relationship between animal density per lichen range and calf crop in 1980-86. For abbreviations see Fig. 1.

that the variation in density has not had any significant effect upon recruitment. Instead, they show that recruitment has been in 1980-86 about 33% higher, on the average, than in the 1970's (65 vs 49), and that recruitment has increased especially in northern earmark districts; in 6 of them, the mean value for 1980-86 was higher than the highest value in the 1970's.

Discussion

The earliest studies suggest that 8-10 ha of lichen range (density 10-13 ind. per km^2) are required per reindeer per year (Palmer, 1926; Poijärvi, 1945; Andreev, 1954; Skuncke, 1958; Alaruikka, 1964; Helle, R. 1966). However, the present findings show that such densities over a longer period result in severe overgrazing of lichens (Figs. 2 and 3).

The low grazing value can be exemplified as follows. According to Holleman et al. (1979), the intake requirement of an adult reindeer is about 2.5 kg DM of lichen per day. The intrinsic growth rate of reindeer lichens averages in northern Finland 11% (Kärenlampi, 1973). Thus the yearly production of 10 ha of range (136 kg, Fig. 4) corresponds to only 26 days of a reindeer forage requirement; the winter season lasts about 200 days. This calculation takes into account that about 50% of the biomass removed becomes wastaged in foraging (Gaare and Skogland, 1980). So, it is evident that densities mentioned above are possible only in presence of alternative food. From the managemental point of view those estimates are not very informative because they do not take into account effects of grazing on lichen ranges and possible density-dependent influences on reindeer population.

The only empirical studies including lichen-reindeer interactions have been carried out in southern Norway (Gaare and Skogland, 1980; Skogland, 1983, 1986). Their estimates on population density at economic carrying capacity ranged between 4-20 individuals per km^2 lichen range depending how the term "lichen range" has been defined. The lowest estimate (Gaare and Skogland, 1980) included potential lichen ranges within *Loiseleurio-Arctostaphylion* or *Juncion trifidi* alliances, which corresponds quite well the definition used in this study. In northern Finland, even 4 individuals per km^2 lichen range seem to be too much to maintain lichen range in optimal condition. In the southern half of the area (excluding Kainuu), we considered as lichen range only *Calluna-Cladina* heathers. In Kuusamo, for instance, lichen biomasses are far below the optimum (Figs. 3 and 4) as a result of densities between 5 and 7 individuals per lichen range (Table 1). Earlier the density has been some lower (3-4 ind./km^2), but essential may be that such a stocking rate has continued about 100 years (Kortesalmi, 1960)

As mentioned by Skogland (1986) the Norwegian experiences are not necessarily applicable in other environments. In comparison to alpine habitats, the role of alternative food seems to be quite different in forest areas. For instance, recruitment (this study) at high density levels is in Finland clearly greater than found in southern Norway (Skogland, 1983, 1986).

Traditionally, the reindeer of forest areas have compensated scarcity or poor access of reindeer lichens by relying upon arboreal lichens in mid and late winter. The decrease of the area of old forests with abundant sources of arboreal lichens triggered effective supplementary feeding in the 1970's (Helle and Saaatamoinen, 1979). The dependence on reindeer lichens has decreased even in early winter, since abundant clear-cut areas and young forests (on fresh soils) provide to reindeer a rich resource of *Deschampsia flexuosa.* It seems to be clear that it is not profitable to adjust animal density to correspond to economic earring capacity of lichen ranges, if production of alternative high quality food is greater than that of lichen ranges in an ideal state.

The recent population increase has ruined all earlier experiences on sensible animal density and production capacity in northern Finland. The new situation has not yet been analyzed from the viewpoint of population dynamics. This paper shows a remarkable increase in recruitment determined in mid-summer. Very probably, calf mortality before mid-summer as well as between mid-summer and winter is at present smaller than in the 1970's and early 1980's (Haukioja and Salovaara, 1978; Nieminen and Eloranta, 1982), which seems to associate to the good physical condition of the reindeer.

The improvement of the net recruitment and possibly lowered adult mortality rate have forced reindeer owners to intensify harvesting in order to avoid exceeding of highest permitted number of reindeer of the herding association. In such a situation criteria for animals to be left alive are very proper. Harvesting is subjected in particular to calves and over-aged or otherwise poorly productive individuals, which improves production capacity of the herd, and contains an element of compensatory mortality.

In the southern half of the area increasing trends in animal numbers and production are based on supplementary feeding, whose economic profitability is not self-clear in all cases (Helle et al., 1985). However, just the same has happened in northernmost Lapland without supplementary feeding. The present densities are there 2-3 times higher than in the 1960's and 1970's. According to Andreev (1971), a remarkable decrease in lichen biomass was observed in northern Lapland between 1959 and 1970. The relationship between density and the condition of lichen ranges (Figs. 2 and 3) suggests that even the resent increase in animal numbers has had a negative effect upon lichen ranges forcing the animals to add to their diet increasing amount of alternative food to reindeer lichens.

One possible explanation to these seemingly contradictionary phenomena is, besides favorable snow conditions during several successive winters, the medical treatment of reindeer against warble larvae and other parasites. It began in 1976 in the central Lapland but spread rapidly over the whole area; Phention and Warbex preparates were replaced by Ivomec in 1985. The positive effects of treatments are shown in several experimental works (e.g. Nieminen et al., 1980; Persen et al., 1982; Nordkvist et al., 1983), and one might suggest that their importance has been greatest in northern Lapland, where the parasitic load has been heaviest (Helle 1980). The effects of the treatments are possible to analyse in detail comparing weights and recruitment in adjacent herding association with the different beginning year in treatments.

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Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology

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Abstract: Plant parts used as forage by caribou and reindeer *(Rangifer tarandus)* have been collected in conjunction with studies of foraging dynamics, nutrition, growth, and population ecology of this arctic ungulate over the course of several years in Alaska and other circumpolar areas. These samples were subjected to proximal analyses for percent nitrogen, phosphorus, sodium, carbohydrate, cell wall (NDF), acid detergent fiber (ADF), lignin, cellulose, and residual ash, and treated to determine *in vitro* and nylon bag dry matter digestibility (DMD). Among winter vascular plant forage only carbohydrates showed a positive correlation with digestibility, wheras in summer nitrogen, phosphorus, and in some cases sodium, also are positively correlated with digestibility. Forage from shrubs and forbs in early summer had higher nitrogen and carbohydrate levels than later in the season, wheras graminoids show an increase in these levels during the first few weeks of growth. Floral parts during anthesis showed higher nitrogen, phosphorus, and carbohydrate levels and higher digestibility than corresponding leaf material. The annual dietary cycle is the product of adjustment of the physiological cycle to seasonal fluctuation in forage quality and quantity.

Key words: *Rangifer tarandus*, forage quality, plant phenology, proximate analysis

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Introduction

It is generally accepted that forage type, phenology, and season are primary factors influencing the quality of forage available to ungulates. Forage used by reindeer and caribou is also believed to be under these influences, however, generalizations extrapolated from investigations on other species may be misleading. For example, the emphasis on nitrogen content of winter browse for North American deer as an index of quality does not have relevance to assessment of quality of the lichen-dominated winter diet of caribou and reindeer.

The foraging pattern or strategy of caribou and reindeer throughout the year is under the control of the physiological-metabolic demands of the animal and the quality and quantity of forage available. All of these factors undergo annual fluctuations that are tied to the extreme solar cycle of northern latitudes. This investigation examines variations occurring in vascular plant forage of caribou and reindeer and the correlations existing among the nutritional components of the forage.

Methods

Forage samples were collected during 1975 - 1980 in connection with studies of foraging dynamics and habitat selection of caribou, reindeer, and muskoxen, through the Alaska Cooperative Wildlife Research Unit (Thing, 1977; Wright,1979; Boertje, 1981; Robus, 1981; Kuropat,1984). All samples collected were known to be used by caribou and reindeer. These samples were subjected to proximal analyses for percent nitrogen, phosphorus, sodium, carbohydrate, cell walls (NDF), acid detergent fiber (ADF), lignin, cellulose, and residual ash at the Plant and Soil Analysis Laboratory, Palmer, Alaska. Many of the samples were also treated to determine *in vitro* and nylon bag dry matter digestibility (DMD) using a fistulated reindeer as a source of innoculum and for the nylon bag studies. This work was done at the Institute of Arctic Biology, University of Alaska Fairbanks. The following individuals assisted in the collections and analyses of forage samples reported here: Rodney Boertje, John Bryant, Karma Krelle, Peggy Kuropat, Martha Robus, Dan Roby, Hans Staaland, Henning Thing, and John Wright. Dan Roby provided assistance for data analysis.

Forage samples were grouped in the analyses of data according to the following categories (plant nomenclature is from Hultén 1974):

Winter:

Evergreen (Oct.-Apr.):	*Ledum palustre, Dryas integrifolia, Empetrum nigrum, Vaccinium vitis-idaea*
Early winter green: (Oct. & Nov.)	*Carex aquatilis/stans, Hippuris vulgaris, Stellaria longipes, Equisetum variegatum*
Early winter other: (Oct. & Nov.)	*Eriophorum vaginatum, Carex* spp., *Potentilla palustris, Salix pulchra* (leaves)
Mid-late winter green: (Dec.-Apr.)	*Pyrola grandiflora, Carex aquatilis/stans, Equisetum scirpoides*
Dead/dry (Oct.-Apr.):	*Eriophorum vaginatum, Carex.* spp., *Salix pulchra* (leaves), *Calamagrostis* sp., *Poa glauca*

Summer:

New growth-leaves (June)	Leaves of *Salix* spp., *Betula nana* and numerous forbs
New growth including flowers (June)	Leaves, terminal growing tips of twigs, and floral parts of *Salix* spp. and *Betula nana*, as well as leaves and floral parts of numerous forbs
New growth-flowers (June)	Floral parts of *Salix* spp. and forbs
Evergreen leaves: (June-July)	*Ledum palustre, Vaccinium vitis-idaea, Dryas integrifolia*
Graminoids (June-July)	*Eriophorum vaginatum, Carex aquatilis/stans, C. Bigellowii, Arctophila fulva*

Additional species represented in the grouped analysis data:

Shrubs:	*Salix pulchra, S. alaxensis, S. glauca, S. lanata, S. reticulata*
Graminoids:	*Carex aquatilis, C. Bigelowii, Eriophorum vagi-*

natum, Arctophila fulva, Poa glauca, Festuca altaica, Hierochloe alpina, Calamagrostis sp.

Forbs: *Epilobium latifolium, E. angustifolium, Artemesia arctica, A. tilesii, Pedicularis kanei, P. sudetica, P. langsdorfii, Lupinus arcticus, Oxytropis viscida, Hedysarum alpinum, Ranunculus glacialis, Anenome parviflora, Oxyria digyna, Rumex arcticus, Arctostaphylos alpina, Petasites frigidus, Boykinia richardsonii, Geum glaciale, Stellaria longipes, Sanguisorba officinalis*

Results and discussion

Considerable variation exists in the quality of natural forage available to caribou and reindeer. This variation is associated with plant species, plant part, plant phenology, and season (Table 1).

The generally accepted correlation between nitrogen (i.e. crude protein = N x 6.25) and forage quality is based on the assumption that nitrogen is usually the limiting nutrient in ruminant forage. This assumption has some validity for growing, lactating, or other animals that may be in a dynamic physiological state, which is coincident with the summer growth period of forage plants. During winter, however, when northern ruminants enter a growth plateau, protein requirements are greatly reduced over summer and metabolizable energy becomes the dominant component sought in forace consumed (White et al.,1981). Thus lichens, low in nitrogen and high in available energy and digestibility, become a major component of the winter diet of caribou and reindeer when available (Karaev, 1968, Holleman et al., 1979; Helle, 1981). Among winter vascular plant forage analyzed in this study only carbohydrates showed a positive correlation with digestibility (Table 2). This is in contrast to summer forage in which nitrogen, phosphorus, and in some cases sodium also show positive correlations with digestibility. Although nitrogen levels in winter forage are low by summer standards, vascular plants averaging in excess of 1.5 percent nitrogen may be able to provide the nitrogen required by reindeer and caribou to meet their relatively low metabolic requirements for nitrogen in winter. In addition, nitrogen available from vascular plants in winter probably also provides a necessary supplement to the lichen-dominated diet to enable optimal development of the rumen microorganism complex essential for efficient digestion of lichens. Although nitrogen levels of vascular plant forage in winter are low in contrast to summer, there are exceptions, such as *Hippuris vulgaris* and the aquatic vegetation incorporated in muskrat pushups (Table 1). Both of these are exploited as forage by caribou in early winter before snow conditions limit their availability.

In summer it is generally believed that forage plants in early stages of growth have higher nitrogen and carbohydrate levels and are therefore of higher quality than similar plants later in the growth period (Klein,1970). This generalization should be qualified, however. Whereas new growth vegetation from deciduous shrubs and forbs generally has higher nitrogen and carbohydrate levels than is the case later in the season (June vs. July), this does not appear to be true of perennial graminoids (grasses and sedges)(Fig. 1). Nitrogen and carbohydrate levels appear to increase in graminoids, in contrast to shrubs and forbs during the first month of growth, which seems counter intuitive in view of the close correlation between digestibility and these nutrients in other forage types. An inverse correlation between gross energy content and digestibility, however, also has been

Table 1. Composition and digestebility of vascular plant forage types available to *Rangifer tara*

Forage type	(n)	Proximal and detergent analyse			
		N[1]	P	Na	CHO
		$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD
WINTER					
Evergreen	9	1.35 ± 0.34	0.18 ± 0.07	0.89 ± 0.23	6.01 ± 8
Early winter green	12	1.53 ± 0.40	0.17 ± 0.05	0.71 ± 0.33	5.10 ± 5
Early winter other	10	1.11 ± 0.50	0.14 ± 0.04	0.70 ± 0.39	4.53 ± 3
Mid-late winter green	12	1.84 ± 0.58	0.20 ± 0.08	0.47 ± 0.55	11.46 ± 5
Dead/dry	15	1.17 ± 0.39	0.14 ± 0.03	0.92 ± 0.59	3.29 ± 3
Hippuris vulgaris (10/6 & 11/16)	2	2.27 ± 0.42	0.22 ± 0.03	0.74 ± 0.87	12.50 ± 14
Muskrat pushup (11/16)	1	3.18	0.38	1.19	4.53
SUMMER					
New growth - leaves	25	3.45 ± 1.02	0.38 ± 0.13	0.63 ± 0.24	5.51 ± 2
New growth inc. flowers	35	3.36 ± 1.23	0.44 ± 0.19	0.74 ± 0.36	4.34 ± 1
New growth - flowers	30	3.58 ± 1.05	053 ± 0.14	0.73 ± 0.36	7.93 ± 3
Evergreen leaves	12	1.53 ± 0.40	0.17 ± 0.05	0.71 ± 0.33	5.10 ± 5
Graminoids - June	25	2.34 ± 0.82	0.34 ± 0.15	0.67 ± 0.23	4.62 ± 2
Graminoids - July	6	4.19 ± 0.67	0.40 ± 0.12	0.76 ± 0.09	7.95 ± 1
Forbs - June	23	3.69 ± 1.31	0.51 ± 0.19	0.82 ± 0.31	8.37 ± 4
Forbs - July	5	2.98 ± 1.43	0.41 ± 0.13	0.76 ± 0.47	6.02 ± 4
Shrubs June	15	4.10 ± 0.86	0.56 ± 0.17	0.79 ± 0.47	3.12 ± 1
Shrubs July	8	3.52 ± 0.89	0.36 ± 0.12	0.73 ± 0.24	4.99 ± 1
Willow - new growth	6	4.29 ± 0.64	0.60 ± 0.13	0.97 ± 0.67	2.77 ± 0
Willow - leaves only	11	3.28 ± 0.55	0.36 ± 0.12	0.58 ± 0.30	5.41 ± 1
Sedge - new growth: leaves, culms, flowers	10	2.34 ± 0.82	0.27 ± 0.09	0.78 ± 0.18	4.13 ± 1
Sedge - new growth leaves	6	3.38 ± 1.45	0.32 ± 0.11	0.62 ± 0.18	5.97 ± 2
Pedicularis Kanei -- new growth	4	4.15 ± 0.72	0.55 ± 0.15	0.97 ± 0.42	9.55 ± 3
Betula nana - new growth	4	4.63 ± 0.55	0.49 ± 0.02	0.81 ± 0.17	3.28 ± 1.
Eriophorum vaginatum	18	2.48 ± 0.89	0.39 ± 0.16	0.63 ± 0.29	5.21 ± 3.
E. vaginatum - flowers	7	2.96 ± 0.56	0.52 ± 0.04	0.71 ± 0.18	6.59 ± 2.
Carex aquatilis/stans	6	2.46 ± 1.03	0.27 ± 0.09	0.55 ± 0.43	9.27 ± 4.
Carex Bigelowii	5	2.28 ± 0.95	0.22 ± 0.07	0.68 ± 0.13	4.44 ± 2.
Arctophila fulva	5	2.37 ± 1.60	0.29 ± 0.19	0.93 ± 0.13	11.28 ± 8.
Dryas intergrifolia	3	2.32 ± 0.38	0.28 ± 0.04	0.36 ± 0.31	6.75 ± 5.

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[1] N=nitrogen, P=phosporus, Na=sodium, CHO=carbohydrates, NDF=neutral detergent fil

hroughout their circumpolar distribution. Sample size is indicated by (n).

					Digestibility		
DF	ADF	LIG	CELL	ASH	In Vitro	Nylon Bag	(n)
± SD	x̄ ± SD	x̄ ± SD	x̄ ± SD	x̄ ± SD	x̄ ± SD	x̄ ± SD	
± 17.7	39.2 ± 9.9	13.7 ± 8.7	23.5 ± 6.4	1.94 ± 2.08	42.5 ± 14.2	57.6 ± 28.3	4
± 19.3	38.5 ± 9.4	15.0 ± 6.7	20.2 ± 7.5	3.38 ± 6.09	36.7 ± 3.1	40.4 ± 15.4	5
± 14.9	29.8 ± 14.9	7.4 ± 4.9	20.0 ± 12.4	2.43 ± 6.82	30.8 ± 8.2	53.4 ± 24.9	9
± 12.6	33.1 ± 6.6	5.8 ± 3.8	23.5 ± 6.4	3.78 ± 6.37	52.7 ± 13.5	59.6 ± 10.3	11
± 15.2	33.8 ± 14.1	7.9 ± 5.1	24.6 ± 10.9	1.25 ± 2.69	28.8 ± 8.1	51.0 ± 26.5	11
± 11.6	31.6 ± 17.6	12.0 ± 5.6	19.0 ± 12.2	0.55 ± 0.07	43.1	67.8 ± 2.8	2
	40.8	9.3	13.3	18.23	39.1	47.4	1
± 15.5	25.4 ± 6.7	6.7 ± 2.8	17.7 ± 5.6	0.97 ± 1.75	53.5 ± 16.5	56.8 ± 14.2	25
± 23.0	25.8 ± 9.7	6.7 ± 3.7	18.5 ± 7.9	0.56 ± 1.10	53.8 ± 16.1	55.2 ± 13.7	33
± 18.6	21.7 ± 5.9	5.3 ± 2.6	16.2 ± 4.3	0.38 ± 0.48	70.7 ± 14.3	65.3 ± 13.5	26
± 19.3	38.5 ± 9.4	15.0 ± 6.7	20.2 ± 7.5	3.38 ± 6.09	36.7 ± 3.1	40.4 ± 15.4	5
± 7.1	29.1 ± 8.0	5.1 ± 2.1	23.8 ± 5.9	0.42 ± 0.49	57.9 ± 20.3	59.0 ± 14.8	19
± 5.6	21.4 ± 6.9	3.4 ± 1.9	17.6 ± 6.4	0.43 ± 0.54	65.4 ± 21.2	68.6 ± 8.0	6
± 7.2	20.3 ± 6.4	5.8 ± 3.4	14.2 ± 4.6	0.33 ± 0.39	70.8 ± 14.9	66.8 ± 10.5	22
3 ± 13.2	22.6 ± 10.0	5.8 ± 2.4	14.3 ± 5.6	2.56 ± 3.59	63.7 ± 2.9	67.6 ± 10.9	4
7 ± 10.6	28.6 ± 9.5	9.3 ± 4.2	17.9 ± 5.1	1.43 ± 2.98	46.6 ± 9.7	49.4 ± 12.7	15
2 ± 6.5	22.1 ± 3.7	6.7 ± 2.2	14.7 ± 4.0	0.66 ± 0.67	48.5 ± 7.2	53.9 ± 11.6	8
5 ± 10.5	23.2 ± 8.8	7.7 ± 4.0	14.5 ± 4.4	1.10 ± 2.26	46.0 ± 6.8	53.3 ± 10.7	6
5 ± 6.8	24.5 ± 4.8	7.5 ± 2.4	16.3 ± 3.7	0.63 ± 0.61	51.0 ± 6.8	55.5 ± 11.6	11
5 ± 4.8	31.6 ± 5.0	5.3 ± 1.6	26.1 ± 3.7	0.20 ± 0.25	52.8 ± 15.0	53.2 ± 11.3	10
6 ± 8.7	28.8 ± 7.7	5.0 ± 3.0	23.3 ± 4.9	0.57 ± 0.57	46.2 ± 21.9	57.1 ± 19.6	6
9 ± 8.9	20.8 ± 5.2	6.0 ± 3.0	14.6 ± 3.8	0.15 ± 0.19	80.1 ± 3.7	60.2 ± 6.9	4
3 ± 11.9	23.5 ± 6.7	8.6 ± 3.3	14.8 ± 4.6	0.10 ± 0.14	42.8 ± 3.5	45.6 ± 5.9	4
6 ± 7.7	28.0 ± 9.7	4.9 ± 2.6	23.0 ± 7.1	0.34 ± 0.41	58.8 ± 20.6	62.5 ± 13.3	15
2 ± 8.6	19.4 ± 4.9	3.5 ± 2.4	16.4 ± 2.8	0.34 ± 0.30	80.1 ± 11.2	72.7 ± 6.2	6
9 ± 3.6	29.6 ± 2.4	3.7 ± 1.7	25.2 ± 2.9	0.67 ± 0.55	60.5 ± 17.1	60.5 ± 13.6	6
1 ± 4.3	32.1 ± 3.8	6.2 ± 1.8	25.5 ± 1.8	0.42 ± 0.45	41.7 ± 17.5	44.0 ± 15.5	5
3 ± 18.4	23.5 ± 10.8	3.7 ± 0.8	19.6 ± 10.7	0.32 ± 0.36	60.2 ± 24.8	68.1 ± 14.0	5
6 ± 6.0	35.2 ± 6.3	12.2 ± 6.7	21.4 ± 3.0	1.57 ± 1.52	42.5 ± 8.9	49.5 ± 8.4	3

F = acid detergent fiber, LIG = lignin, CELL = cellulose

Table 2. Correlation (Pearson's product-moment) between digestibility (IV = *in vitro* and NB = nylon bag) and chemical composition of forages grouped by season, phenology, and forage type. Positive and negative correlations with p values <0.05 are shown.

	N^1		P		Na		CHO		NDF		ADF		Lignin		Cellulose		Ash	
Forage Type	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB
Winter																		
Early winter green					-		+	+		-	-							
All forage minus lichens					-		+	+			-	-	-	-		-		
Summer																		
New growth - leaves		+		+			+	+		-	-	-	-	-	-	-		
New growth - flowers					+		+	+			-	-	-	-	-	-	-	-
All growing forage	+	+	+	+			+	+	-		-	-	-	-	-	-		
Graminoids	+	+	+	+	+		+	+	-	-	-	-	-	-	-	-		
Forbs	+		+		+					-	-	-	-	-				-
Shrubs							+	+					-	-			-	-
All forage	+	+	+	+			+	+	-	-	-	-	-	-	-	-		-

N = nitrogen, P = phosphorus, NA = sodium, CHO = carbohydrates, NDF = neutral detergent fiber, ADF = acid detergent fiber.

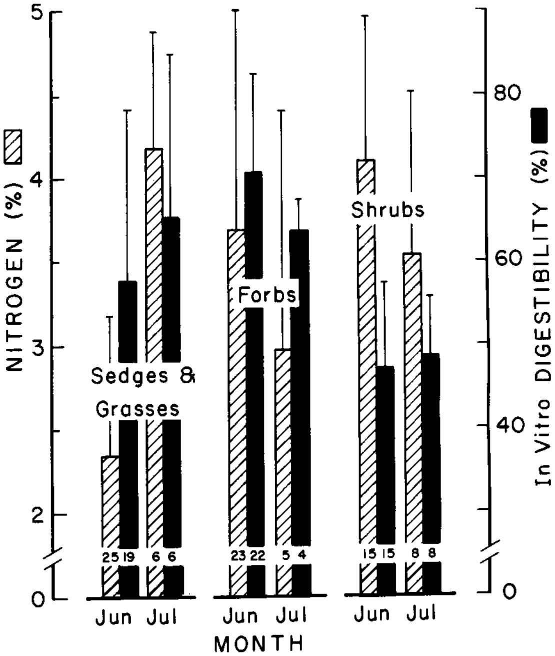
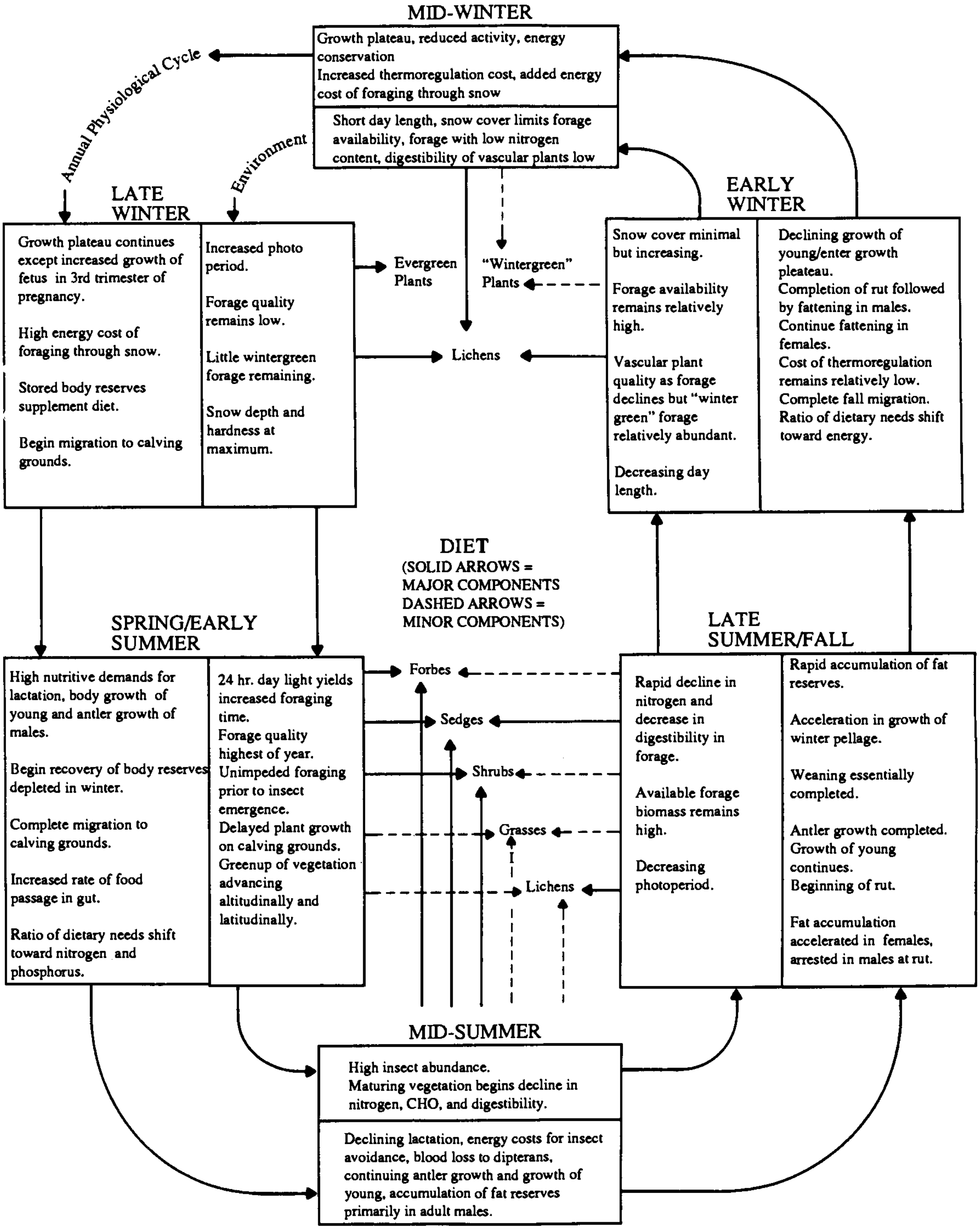


Fig. 1. Differences in quality of major forage types in the Arctic at initiation of plant growth (June) and during peak growth (July) as reflected in nitrogen content and in digestibility. Histograms represent means with inclusive sample sizes, plus one standard deviation.

observed among forage species eaten by other herbivores associated with secondary chemicals apparently employed by the plants as defense against herbivory (Bryant and Kuropat, 1980). Deciduous shrubs have been shown to have high plasticity in the production and mobilization of secondary chemicals that inhibit digestion (Bryant et al., 1983).

Floral parts during anthesis, as a general rule, have higher nitrogen, phosphorus and carbohydrate levels than corresponding leaf material and also have higher digestibility levels (Table 1). This would justify the selective foraging for floral parts that has been observed among caribou and reindeer, often at the expense of optimization of biomass ingestion.

Analyses of forage types presented herein allow refinement of generalization about optimal foraging strategies of caribou and reindeer. The annual physiological cycle of caribou and reindeer has apparently evolved to follow the annual cycle in forage quality and quantity, therefore, the annual dietary cycle reflects this relationship. Figure 2 provides a simplified mo-



MID-WINTER

Growth plateau, reduced activity, energy conservation
Increased thermoregulation cost, added energy cost of foraging through snow

Short day length, snow cover limits forage availability, forage with low nitrogen content, digestibility of vascular plants low

LATE WINTER

Growth plateau continues except increased growth of fetus in 3rd trimester of pregnancy.

High energy cost of foraging through snow.

Stored body reserves supplement diet.

Begin migration to calving grounds.

Increased photo period.

Forage quality remains low.

Little wintergreen forage remaining.

Snow depth and hardness at maximum.

EARLY WINTER

Snow cover minimal but increasing.

Forage availability remains relatively high.

Vascular plant quality as forage declines but "winter green" forage relatively abundant.

Decreasing day length.

Declining growth of young/enter growth pleateau.
Completion of rut followed by fattening in males.
Continue fattening in females.
Cost of thermoregulation remains relatively low.
Complete fall migration.
Ratio of dietary needs shift toward energy.

SPRING/EARLY SUMMER

High nutritive demands for lactation, body growth of young and antler growth of males.

Begin recovery of body reserves depleted in winter.

Complete migration to calving grounds.

Increased rate of food passage in gut.

Ratio of dietary needs shift toward nitrogen and phosphorus.

24 hr. day light yields increased foraging time.
Forage quality highest of year.
Unimpeded foraging prior to insect emergence.
Delayed plant growth on calving grounds.
Greenup of vegetation advancing altitudinally and latitudinally.

LATE SUMMER/FALL

Rapid decline in nitrogen and decrease in digestibility in forage.

Available forage biomass remains high.

Decreasing photoperiod.

Rapid accumulation of fat reserves.

Acceleration in growth of winter pellage.

Weaning essentially completed.

Antler growth completed.
Growth of young continues.
Beginning of rut.

Fat accumulation accelerated in females, arrested in males at rut.

MID-SUMMER

High insect abundance.
Maturing vegetation begins decline in nitrogen, CHO, and digestibility.

Declining lactation, energy costs for insect avoidance, blood loss to dipterans, continuing antler growth and growth of young, accumulation of fat reserves primarily in adult males.

Fig. 2. Hypothetical model of the relationship of diet in caribou and reindeer to their annual physiological cycle and seasonal changes in the environment.

del of the annual foraging cycle of caribou and reindeer in relation to the annual physiological cycle and provides a basis for examination for variations from the model as well as verification of its components.

Conclusions

Although nitrogen levels of vascular plant forage are low in winter, some ”winter green” forage has nitrogen levels in excess of 1.5% with exceptions to over 2 or even 3%. Among winter vascular plant forage, only carbohydrates showed a positive correlation with digestibility. In summer forage, nitrogen, phosphorus, and in some cases sodium, also are positively correlated with digestibility. New growth vegetation in early summer from shrubs and forbs has higher nitrogen and carbohydrate levels than later in the season, whereas graminoids show an increase in these levels during the first few weeks of growth. In shrubs, digestibility does not appear to be directly correlated with nitrogen and cabohydrate levels. Floral parts during anthesis, as a general rule, have higher nitrogen, phosphorus, and carbohydrate levels and higher digestibility than corresponding leaf material. The annual physiological cycle of caribou and reindeer has evolved to follow the annual cycle in forage quality and quantity, therefore the annual dietary cycle reflects this relationship.

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Alpine-forest selection - an alternative to clear-cutting in uneven-aged Norway spruce (*Picea abies* (L.) Karst) forests?

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Abstract: Clear-cutting of forests is considered to be a serious problem for reindeer management. For uneven-aged Norway spruce forests, the alpine-forest selection or some other selection system could be an alternative to clear-cutting, and a way to combine forestry and reindeer management on the same area. The selection system is a silvicultural system which requires and maintains uneven aged full-storied forest which are cut through periodically, whereby a part of the growing stock is removed. With alpine- forest selection the interval between cuttings is usually 25-40 years, and more than half of the growing stock may be cut each time. The lost trees are replaced by ingrowth from below, which must be present in the stand before the cutting takes place. Preliminary studies indicate that after an alpine-forest selection the annual timber volume growth is proportional to the remaning growing stock, with a relative growth rate of approximately 3-4 % per year.

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Clarification of some api characteristics in relation to caribou (*Rangifer tarandus*)

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Abstract: A total of 2 177 comparisons of api hardness vs. density in northern Saskatchewan, southeastern Manitoba and northeastern Finland revealed no consistent correlation (*r* varied from +.70 to -.17).

A total of 1 395 comparisons of horizontal hardness of the top layer of api to vertical hardness of the same layer of api in southeastern Manitoba, northeastern Finland and far eastern middle Finland revealed no consistent correlation (*r* varied from +.99 to -.20). Therefore one cannot substitute density for hardness nor horizontal hardness of the top layer for vertical hardness of the top layer in the terms of the Värriö Snow Index.

Key words: snow, snow index, *Rangifer*

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Introduction

One of the better-known attributes of api (snow on the ground) is that it affects different species of animals in different ways. For subnivean mammals (Penny and Pruitt 1984), invertebrates (Aitchison 1978, 1985) and plants it acts, primarily, as an insulating blanket. In contrast, for some supranivean animals such as large ungulates it acts to hinder movement. Moreover, its morphological variations act to influence digging for subnivean food. These latter features are those which affect caribou (*Rangifer tarandus*). In a series of studies I have shown (Pruitt, 1959; 1979; 1981; 1985) that one may quantify these features and construct a mathematical model that agrees with the observed movements and behaviour of *Rangifer*, not only in North America but in Finland as well. This model I have called the Värriö Snow Index (Pruitt 1979).

The most important characteristics of api affecting caribou are hardness, density, thickness and duration. Hardness (Klein, *et al.* 1950) is the force (in grams per cm^2) necessary to collapse or break the physical bonds between crystals of api. Density, on the other hand, is a ratio of the amount of ice in a given sample and the amount of space or air in the same volume. Density is quite easy to measure in the field; simple "kitchen hardware" devices can suffice. Hardness, in contrast, requires special, expensive instruments, is incovenient to measure and the results are difficult to reproduce consistently. Considerable practice with a spectrum of api types is necessary before achieving reliable and consistent results. Therefore, one of the questions frequently asked is why not use density instead of hardness when measuring the morphological parameters of api to determine the Värriö Snow Index?

For animals such as caribou, on which the api exerts negative effects by impeding walking as well as when digging the different types of feeding craters (Pruitt 1979), the critical parameter is hardness. The animal must exert muscular force in order to break the inter-crystal bonds so that the leg or foot can scoop through the api (Davydov 1963; Fancy and White 1985). But could one derive hardness from some mathematical manipulaton of density data?

Another question, or objection, commonly raised is why bother taking vertical hardness of the top layer of the api as well as horizontal hardness of this same layer? Would they not be the same or very similar? Horizontal hardness is much easier to measure. The rationale for using vertical hardness is that caribou excavate feeding craters by downward strokes of a front leg so that the hoof travels downward and backward. Caribou also periodically plunge the muzzle into the api and withdraw it with a horizontal and backward movement. This has been interpreted as "smelling for lichens" (Miller 1976; Helle 1984) but it could also provide a contact between the api surface and pressure sensors in the muzzle or mentum (Pruitt 1979).

Materials and methods

Previous to 1957 density and thickness were the main properties of api considered in relation to *Rangifer* (e.g. Formozov 1946; Nasimovich 1955). In the winter 1957-58 I began collecting hardness as well as density data in relation to *Rangifer tarandus groenlandicus* movements and behaviour (N=462). I also have collected records of horizontal and vertical hardness of the top layer in several studies *(Rangifer tarandus tarandus* and *R.t. fennicus)* (N=241). In addition I am indebted to R.R.P. Stardom for permission to include some of the api data from his pioneering study (Stardom 1975) of winter ecology of woodland caribou *(Rangifer tarandus caribou)* at Taiga Biological Station in Manitoba (N=472). I am also indebted to J. Schaefer for permission to include some of the api data from his study (Schaefer 1988) of the effects of forest fire on woodland caribou at Taiga Biological Station (N=597). I am indebted to the students in my university classes in Boreal Ecology who have put in long days doing repetitive api control stations at Taiga Biological Station (51° 02'40"N. Lat., 95° 20'40"W. Long.) in Feburary 1985, 1986, 1987 and 1988 (N=406). These latter data sets derive from three types of transects in two different topographic situations each year: "undisturbed", "ski trail" (two passes by 6 to 12 people on skis, left overnight to stabilize) and "snowmobile trail" (two passes by one person driving a Bombardier Élan, left overnight to stabilize), along a protected stretch of the Blind River and across the centre of You Bay exposed to southerly winds.

Results and discussion

The questions may rephrased as null hypotheses:

(1) There is no consistent correlation between vertical and horizontal hardness of the top layer of api and (2) There is no consistent correlation between hardness and density. Tables 1 and 2 show that there is, indeed, no consistent correlation. For the first statement *r* varies from -.20 to +.99 (I discarded the record for "1986 TBS You bay undisturbed" because it consisted of only 3 observations.); for the second statement *r* varies from -.17 to +7.0. Thus the null hypotheses were not disproven. In each of these cases, some types of disturbance of the api resulted in closer correlation than others, but, again, no consistent pattern emerged.

Table 1. Api horizontal hardness of top layer vs. vertical hardness of top layer (Descending values of r)

	r	N
1986 TBS You Bay undisturbed	1.00	3
1988 TBS Blind River ski trail	.99	8
1987 TBS You Bay ski trail	.98	8
1977 January-February, Varriö Subarctic Research Station, Finland	.98	161
1985 TBS You Bay undisturbed	.97	10
1985 TBS Schaefer caribou data	.93	332
1988 TBS You Bay snowmobile trail	.86	12
1988 TBS You Bay ski trail	.86	12
1986 TBS Blind River ski trail	.84	60
1988 TBS You Bay undisturbed	.78	8
1986 TBS Schaefer caribou data	.65	265
1986 TBS Blind River undisturbed	.64	37
1985 TBS You Bay snowmobile trail	.62	20
1985 TBS Blind River ski trail	.61	9
1987 TBS Blind River snowmobile trail	.56	14
1986 TBS Blind River snowmobile trail	.51	60
1987 TBS You Bay undisturbed	.49	12
1986 TBS You Bay ski trail	.39	15
1985 TBS You Bay ski trail	.38	20
1988 TBS Blind River snowmobile trail	.36	6
1984 Finland, Kainuu region (March)	.32	241
1987 TBS Blind River ski trail	.27	14
1987 TBS You Bay snowmobile trail	.24	8
1988 TBS Blind River undisturbed	.22	6
1986 TBS You Bay snowmobile trail	.17	14
1985 TBS Blind River undisturbed	-.03	18
1985 TBS Blind River snowmobile trail	-.07	8
1987 TBS Blind River undisturbed	-.20	14

Such a fortuitous agreement may have been the one described by Skogland (1978). An extreme case may be observed in spring when during diurnal heating the hardness of the api may become quite low. In contrast, at night the api may freeze, resulting in vastly increased hardness but with the density essentially unchanged.

The lack of consistent variation in correlation between horizontal hardness and vertical hardness of the top layer occurs not only in the central taiga of North America but in Finland as well. Finnish api occurs in a warmer, damper and more maritime environment than does that in the continental climate of Manitoba or northern Saskatchewan. Correlation in Finland ranged from $r = .98$ in the vicinity of Värriö Subarctic Research Station (feral *Rangifer tarandus tarandus*) (Pruitt 1979) to $r = .32$ in Kuhmo in the Kainuu region of far eastern middle Finland (*Rangifer tarandus fennicus*)(Pruitt 1985).

From these results one can conclude that one cannot substitute horizontal hardness for vertical hardness of the top layer nor density for hardness of the api when calculating the Värriö Snow Index.

Table 2. Api hardness vs. density correlation (Descending values of *r*)

	r	N
1985 TBS You Bay ski trail	.70	48
1986 TBS Blind River snowmobile trail	.69	53
1977 January-February, Värriö Subarctic Research Station (Finland)	.64	161
1988 TBS You Bay snowmobile trail	.61	26
1988 TBS You Bay undisturbed	.61	28
1957-58 Saskatchewan "Occasional caribou"	.60	85
1986 TBS You Bay snowmobile trail	.55	42
1986 TBS You Bay ski trail	.53	45
1986 TBS Blind River ski trail	.52	56
1987 TBS You Bay undisturbed	.49	46
1957-58 Saskatchewan "Caribou concentration"	.48	129
1986 TBS You Bay undisturbed	.47	11
1988 TBS Blind River ski trail	.44	20
1988 TBS You Bay ski trail	.44	20
1988 TBS Blind River undisturbed	.43	28
1987 TBS Blind River undisturbed	.42	48
1971-72 Stardom's caribou-api data	.41	472
1985 TBS You Bay undisturbed	.35	144
1985 TBS You Bay snowmobile trail	.35	42
1987 TBS Blind River ski trail	.35	43
1988 TBS Blind River snowmobile trail	.35	18
1957-58 Saskatchewan "no Caribou"	.33	248
1985 TBS Blind River ski trail	.32	29
1987 TBS Blind River snowmobile trail	.26	38
1985 TBS Blind River snowmobile trail	.19	21
1986 TBS Blind River undisturbed	.19	72
1987 TBS You Bay ski trail (2 passes)	.19	26
1987 TBS You Bay snowmobile trail (2 passes)	.14	41
1987 TBS You Bay snowmobile trail (1 pass)	.13	42
1985 TBS Blind River undisturbed	.07	65
1987 TBS You Bay ski trail (1 pass)	-.17	30

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Managing second-growth forests as caribou habitat

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Abstract: Habitat management for woodland caribou *(Rangifer tarandus caribou)* in southeastern British Columbia has generally focussed on protecting old-growth forests from logging. As that strategy becomes more difficult to maintain, biologists are beginning to explore opportunities to manage second-growth stands to provide arboreal lichens and other habitat resources important to caribou. Special harvesting and stand management practices are being developed and formulated into strategies for maintaining caribou populations in managed stands.

Key words: woodland caribou, British Columbia, habitat management, arboreal lichens, forestry

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Introduction

The woodland caribou of southeastern British Columbia typically winter in old-growth forests, where their primary forage is arboreal lichens. Habitat management for those caribou has generally been directed at trying to protect old-growth forests from logging. As the demand for timber increases, that strategy becomes more and more difficult to maintain. Researchers and managers have begun to ask whether second-growth forests can be managed so that they will function as caribou habitat before they are logged again.

That question has become urgent in some caribou ranges east of Prince George. Spruce bark beetle attacks have resulted in extensive salvage logging over the last seven years. Low- and mid-elevation ranges formerly used by caribou are now in an early seral stage. Because so much of the low-elevation timber has been removed, logging companies are beginning to harvest high-elevation stands formerly considered unprofitable. Wildlife managers are asking how this logging is affecting caribou, and what can be done to make the cut areas into future caribou habitat. To address those questions, the British Columbia Ministry of Environment, in cooperation with the Ministry of Forests and the forest industry, is initiating a research and management project centred east of Prince George. The purpose of this paper is to present some of the ideas that are to be developed and implemented in that project.

Caribou studies in southeastern British Columbia (Antifeau 1987; Rominger and Oldemeyer 1989; Scott and Servheen 1985; Simpson 1985; Simpson et al. 1985) have suggested a number of attributes that are important to caribou on winter ranges: standing crop of lichens on accessible portions of trees, arboreal lichens available through litterfall and blowdown, canopy modification of snow depth and snowpack characteristics, availability of vascular forage, and remoteness from vehicle access. In this paper, I will focus on management practices for stands in which the principal objective is to encourage the development of arboreal lichen forage (mainly *Bryoria* spp. and *Alectoria sarmentosa*) while producing merchantable timber.

The habitat management strategies proposed here must be integrated with an overall plan for population management, which includes consideration of direct mortality factors. Providing an extensive habitat base by managing second growth is expected to allow caribou to disperse sparsely over large areas, reducing the risk of mortality from predation and poaching.

Factors limiting arboreal lichen forage in young stands

The development of management strategies for enhancing arboreal lichens should be based on an understanding of the factors that limit their abundance in young stands.

Source of propagules

The early establishment of lichens in some young stands is limited by the presence of lichen propagules. Lichen dispersal can be accomplished by spores, soredia, or thallus fragments, but thallus fragments account for nearly all the early colonization of second growth (Stevenson, 1988).

Studies conducted on Vancouver Island, British Columbia have shown that beyond about 400 m from the edge of the mature timber, young twigs in second-growth stands support almost no lichens (Fig. 1; Stevenson, 1988). Lichen abundance in second-growth stands also depends on lichen abundance in the adjacent mature timber. The maximum values shown in Figure 1 are from stands adjacent to mature timber with high lichen abundance. The low values are mostly from stands adjacent to mature timber with moderate or low lichen abundance. The data suggest that managers should only count on natural dispersal for early lichen colonization within about 350 m of a mature timber stand with high lichen abundance.

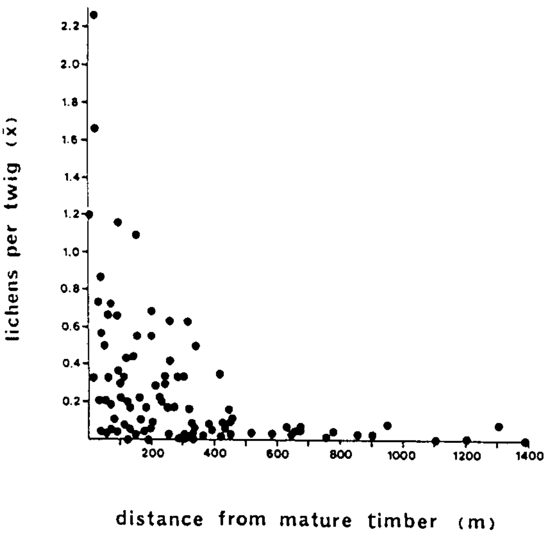

Fig. 1. Lichen fragment on two-year-old twigs in second-growth and distance from mature timber in several Vancouver Island studies (Stevenson 1988).

Substrate

Lichen fragments that land on suitable substrate become attached by entanglement with twigs, needles, or bark scales, and by the formation of hapters (fungal holdfasts). Of the many substrate characteristics potentially affecting lichen colonization, texture seems to be particularly important. In Douglas fir, lichen fragments are retained poorly on the longest twigs (the ones that have grown the fastest), despite their greater surface area (Stevenson and Palmer 1988). That probably occurs because twigs that have grown rapidly tend to have smooth slippery bark, which offers few attachment sites, and widely separated needles, which limit opportunities for entanglement of fragments. In Douglas fir, young trees that are growing at an average or below-average rate seem to offer better substrate for lichen colonization than rapidly-growing trees. The applicability of those observations to tree species growing on caribou ranges has not yet been evaluated.

Microclimate

Changes in stand structure that occur during succession result in changes in stand microclimate, and those changes affect the suitability of a stand as lichen habitat (Fig. 2; Stevenson and Palmer 1988).

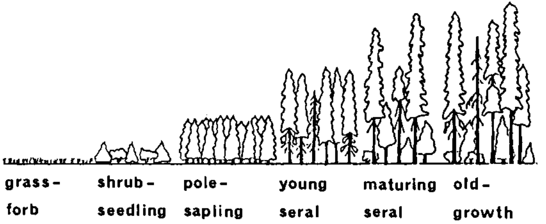

Fig. 2. Hypothetical development of an unmanaged, fully-stocked stand.

In the *grass-forb stage*, the tree seedlings are surrounded by a layer of grasses, herbs and shrubs, which affect the microclimate of the site. The microclimate is more severe than it is within a forest, but less severe than it is over bare grond. Arboreal lichens are generally absent.

In the *shrub-seedling stage*, the trees have grown above the ground vegetation, but the canopy has not yet closed. The crowns of the young trees are exposed to light, and they have an open-grown form. If a dispersal source is present, lichen fragments colonize the branches and trunks on suitable sites. However, the microclimate is still relatively severe, and on some sites, conditions may be too dry or warm for lichen development at the shrub-seedling stage, even though lichens may do well in adjacent mature timber stands.

At the beginning of the *pole-sapling stage*, canopy closure occurs. Solar radiation below the level of canopy closure is much reduced. The lower branches begin to die back. Although lichen development at the pole-sapling stage has not been studied, it seems likely that in many cases the microclimate in the lower part of the canopy is not suitable for *Bryoria* and *Alectoria* unless the stand is opened. Lichen establishment continues in the lighted portion of the crown, but the branches are quickly overtopped and shaded.

At the *young seral stage*, a branchless trunk zone is present, and the process of natural thinning begins. Many snags are produced, but they are small and usually bear little lichen. The microclimatic zones characteristic of a mature forest are present, although the shaded crown zone is likely to be even more shaded than it is later in succession. Lichen biomass is typically very low, although it may be moderate if for some reason (such as topography, rootrot disease, or thinning) the stand is exposed to light.

At the *maturing seral stage*, the rate of natural thinning declines and stabilizes. Fewer snags are produced, but they are larger, and may bear some lichen. Natural thinning increases light levels in the main canopy. The whipping action of windblown branches also contribute to the development of spaces among the crowns ot the trees. A regeneration layer may become established and affect the microclimate in the lower part of the stand. The lichens respond to the increased light in the canopy, and may become abundant.

At the *old-growth stage*, tree growth slows and most stand characteristics are stable. The horizontal zones offer a gradient of potential habitats for arboreal lichens, but the characteristics of those habitats depend on the regional climate. In a wet regional climate, *Bryoria* and *Alectoria* are well-adapted to the upper part of the canopy, which receives high levels of light and precipitation, but is subject to high water loss and to extremes of temperature. In a dry regional climate, *Alectoria* is likely to be sparse or absent, and *Bryoria* distributed lower in the canopy, where the extreme regional climate is moderated. Most caribou ranges in southeastern and central British Columbia fall between those two extremes, and intermediate distribution patterns are seen.

In summary, the canopy in fully-stocked stands in dense through the pole-sampling and young seral stages, usually resulting in conditions that are not exposed enough for good lichen development. On dry sites, however, lichens may not benefit from increased exposure.

Accessibility to caribou

Managers need to consider not only the standing crop of arboreal lichens, but also their accessibility to caribou. In high-elevation winter ranges, lichens are typically present in the lower part of the canopy, and caribou gain access to them when the snowpack is deep and settled. Thus, the accessibility of the lichens is limited mainly by snow conditions.

When the snowpack is soft, many caribou use low- and mid- elevation forests. The standing crop of lichens within reach of caribou is relatively low, and the lichens are available mainly as litterfall or on windthrown trees. Thus, in low- and mid- elevation winter ranges, the accessibility of the lichens is limited by stand characteristics.

Managers have wondered whether rates of litterfall and blowdown in second-growth stands might restrict the availability of arboreal lichens to ungulates, even if they could develop methods to enhance the standing crop of lichens. An analysis of the available data for Douglas fir stands suggests that, given equal biomass, lichen litterfall rates might be about 2/3 lower in second-growth stands than they are in old-growth stands, because overall litterfall rates are lower (Stevenson 1986a). However, the methods that are available for enhancing lichen development may themselves result in reduced rates of litterfall and blowdown. That problem is discussed further below.

Opportunities to enhance lichen production in young stands

Limitations of lichen forage due to propagule source, stand microclimate, and rates of litterfall and blowdown can be addressed through special management practices.

Maintaining natural dispersal.

There are several approaches to providing mature, lichen-bearing trees as a source of propagules. Diameter-limit logging and the harvesting of very small patches can maintain opportunities for lichen dispersal onto young trees; the tradeoffs associated with those harvesting practices have been discussed elsewhere (Stevenson 1986b). Alternatively, the size and configuration of cutblocks can be planned with consideration to the dispersal limitations of lichens. In a three-pass system (a logging system in which all the merchantable timber within a planning unitis removed in three successive cuts, equally spaced throughout the rotation), it is theoretically possible to maintain a large proportion of the area within 350 m of mature timber during the first half of its rotation. Patches of unmerchantable timber, such as swamp fringes and inaccesssible areas, contribute to the area that functions as a dispersal source. If the advanced regeneration in the cut areas can be retained during harvesting, lichen recovery will occur more rapidly. Harvesting alternatives such as these require special planning and cooperation between wildlife biologists and foresters.

Inoculating young stands with lichen propagules

The modified harvesting methods disussed above may be feasible where there is still flexibility in harvesting plans, but they cannot be used in places where extensive harvesting has already occurred. To meet the need for lichen propagules in second-growth stands that are distant from mature timber, an inoculation technology is being developed (Palmer 1988). The method involves first spraying the trees with an adhesive agent, then with mechanically chopped lichens. Handheld equipment has been used to spray trees up to 7.5 m, and aerial application may be practicable.

Modifying stand microclimate to enhance lichen development

An important microclimatic limitation to lichen developments believed to occur in fully-stocked stands on moist sites after the time of canopy closure. On those sites, a carefully planned thinning program could be applied to maintain better conditions for lichen development (Stevenson and Palmer 1988). A thinned stand has fewer trees, longer and wider crowns, and maximum foliage biomass located closer to the ground than an unthinned stand. Those differences in stand structure affect stand microclimate. Light intensity and throughfall precipitation in the lower canopy are increased. Temperatures are expected to be intermediate between those of open areas and uncut forests. Summer humidity is expected to be lower in thinned than in unthinned stands.

On sites where lichen abundance in the canopy is limited by light, increased stand openness should result in a larger portion of the canopy providing suitable habitat for arboreal lichens. On drier or warmer sites, however, thinning may result in summer temperatures that are too high or humidity levels that are too low for optimum lichen development. Observations of the vertical distribution of lichens in existing stands can be used to predict how lichens will respond to thinning, but those predictions must be refined and tested.

Managing for litterfall and blowdown

Litterfall and blowdown are the major sources of arboreal lichen forage for caribou on low- and mid- elevation winter ranges. Thinning dramatically reduces the rates both of litterfall and of tree mortality, which is related to blowdown (Bray and Gorham 1964; Gessel and Turner 1976). Thus, the methods that are used to increase the standing crop of lichens in the canopy could prevent them from becoming accessible.

That problem could be addressed in either of two ways. A harvesting system that leaves a residual stand of older trees will ensure not only a source of lichen propagules, but also a source of litterfall and blowdown over many years.

Partial cutting is unacceptable to foresters on some sites for economic or silvicultural reasons. An alternative approach to ensuring litterfall production is to use thinning techniques that result in standing dead trees, rather than felled trees. Early in stand history thinning is carried out in the usual way with chainsaws, but when the trees are larger and support more abundant lichens, alternate thinning techniques are used. One potential method, which is increasingly used in British Columbia, is thinning by chemical injection (e.g. monosodium methanearsenate or glyphosate). That technique should not be used operationally for lichen enhancement until its effects on the arboreal lichens have been determined; it is possible that the herbicides would either kill the lichens or cause them to accumulate substances that are toxic to wildlife. Another option that does not carry those risks is the use of girdling tools. In either case, the objective is to produce standing dead trees which provide a substrate for lichen growth and a source of litterfall and blowdown.

Conclusions

The special management practices that have been suggested here are ideas that are being tested for use in an overall management strategy. That strategy will encompass a number of variations. Sites differ in the importance to caribou of various habitat attributes, in climatic limitaions on the potential of the site to produce those habitat attributes, and in the constraints of silviculture and forest economics. The strategy must take into consideration the relationships between management of caribou habitat and populations; for example, practices intended to enhance lichen production may lead to increased disturbance and poaching unless access control is practiced. Potentially, it could provide alternatives to the preservation of old growth as the primary mode of managing habitat for caribou in southeastern British Columbia.

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Adaptations of barren-ground caribou to forest fires and snow

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Abstract: The movement patterns of the Beverly herd of barren-ground caribou (*Rangifer tarandus groenlandicus)* were monitored on its forested winter range from 1982 through 1988. Caribou distribution was noted in relation to forest age, the general pattern of burns, individual burns of various sizes and ages, and snow characteristics. Caribou did not remain long in forest stands younger than 50 years and they seemed to prefer to feed in forests older than 70 years to those 50-70 years since fire. The main concentrations of wintering caribou were in areas very lightly to moderately burned and were almost exclusive of areas highly burned in the last 50 years. Caribou showed no avoidance of burns of any size. When travelling from one area to another, they passed through burns on a few trails aligned about parallel to one another. The caribou did not remain in areas with snow deeper than 65-70 cm. Their winter movements appeared to be based in part on traditional responses to snow variations across their range.

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Home ranges in Svalbard reindeer

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Introduction

Reindeer and caribou *(Rangifer tarandus)* are typically migratory and seasonally nomadic. Many continental populations, for example, travel between distinct summer and winter ranges which may lie hundreds of km apart. Others, whose summer and winter ranges are contiguous, also range extensively, moving not only seasonally but also within seasons in response to local changes in the quality and abundance of forage, wind, predators and insects. Much less is known about the movements of animals belonging to island populations. This abstract describes seasonal and annual movements of Svalbard reindeer *(R. t. platyrhynchus)* on the island of Spitsbergen.

Methods

Nine Svalbard reindeer were captured and individually marked in Adventdalen, Spitsbergen, between 1977 and 1982 (Tyler and Øritsland, 1989). Four ear-tagged animals (one male and three females) were followed extensively for between 4 and 7 years. Five radio-collared females were followed intensively by snowmobile and on foot for seven months (Feb.-Aug.) in 1982.

Results

Ear-tagged animals were consistently found within the same small parts of the study area in corresponding seasons in different years. Radio-collared females were sedentary within seasons, travelling, on average, less than 0.7 km per day in both summer and winter. Interestingly, they confined their movements within small areas for several weeks or even months at a time in both summer and winter. One female, for example, remained within 1 500 m of the spot where she was caught and marked for three months during winter.

Conclusions

Svalbard reindeer do not undertake long seasonal migrations like mainland reindeer and caribou, nor are they nomadic within seasons. Instead, individual animals appear normally to confine their daily routine activities within small, seasonal home ranges. Some animals display long-term fidelity to particular areas, returning to these season by season over periods of several years. Taken together, these observations suggest that individual reindeer adopt particular seasonal home ranges more than once, returning to them season by season, year by year, perhaps even for life. The size and duration of occupancy of particular home ranges is individually highly variable (Tyler and Øritsland, 1989).

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Population Dynamics

Key note address:

Population dynamics of reindeer

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Abstract: Five types of reindeer populations are distinguished in terms of population dynamics, population density, social structure and migration distance. Differences in the biological rhythms of the populations result in calving occuring 20 days before snow melting in all populations as well as maximal utilization by the deer of young green vegetation in summer. The growth of antlers may serve as a regulatior of biological rhytms. Populations differ in the level of social motivation. Formation of groups of not less than 30-35 animals ensures cooperative protection from insects and management of the group by man. The fidelity to the calving sites, summer ranges and constant migration routes is based on the common orientation reactions of the animals and social attraction. The direction and migration routes are detemined by obligate learning. The dynamics of populations depends on the fertility of 2 and 3 year old females which is determined by feeding conditions in summer and the activity of males during the rut. Migration plays an important role in the population dynamics.

Key words: populations, rhythms, spatial

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The large amount of information collected from different populations of reindeer from various parts of this species vast range has helped to provide new insight concerning the dynamics of *Rangifer* as well as to improve our evaluation of the adaptive potential of individual populations.

Populations are named after their localities, a practice which emphasises the significance of adaptation to local conditions. It is important to understand that a population which settles down in a particular locality has adapted itself to the complex of conditions actually existing here. Such as view helps both in estimating the potential of not yet occupied ecological niches and in understanding co-existence of different populations in the same winter ranges. Their differences may concern migration traditions, the phenology of deer from another population is a limiting factor for forage reserves, which distracts predators. A characteristic example is furnished by a co-existence in the same locality for wild and domestic deer. It should be emphasized that some ecological and behavioural properties of populations require a minimum of at least a single generation before they can change. For instance when tundra deer are transported to the forest zone, only their taiga-born calves become fully adapted to local conditions (Druri, 1952). It took about 10 years for migration routes to change in Taimyr (Pavlov et al, 1985), and about 20-25 years passed before lichen-eating reindeer changed their foraging habits to become essentially herbivorous as lichen pastures became depleted in Chukotka (Arefyev and Chechukov, 1981)

Biological rhythms

In numerous populations of reindeer the relative proportion of protein carbohydrate and vitamins in the diet is seasonally highly variable. Feeding conditions during the summer season determine the rates of calf growth and the rates of antler growth, moulting and the restoration of body tissue after winter. The principal objective of entire annual foraging in adult deer is to follow the "wave" of new growth of vegatation for as long as possible and thereby to maximize their intake of green vegetation, which is richest in proteins, vitamins and salts.

The welfare of calves and their ability to survive their first winter is enhanced by a matching of the time of appearence of the first vegetation with the calves' ability to consume it. The date of the birth of the first calves is constant on any locality and is a function of the dates of snow melting. Most births occur 10-30 days before snow melting. The timing of the rut is regulated accordingly (Baskin, 1970). According to Klein (1985) the purpose of migration in spring is to ensure that the peak of lactation occurs when the animals have acces to high- quality feeds. In addition, Klein related migration to the search for ranges where the numbers of the wolf and blood-sucking insects are low.

Antlers apparently play an important role in the humoral regulation of seasonal biological rhythms in reindeer. Their growth is regulated by the level of consumption of young vegetation and the time of shedding of the velvet determines the time of the onset ot the rut and, hence, also calving. Reindeer are seasonally polyoestrus. Their oestral cycle and ovulation occur only in autumn and is induced by the males. Thus, the activity of males may regulate the timing of conception. (Mashdovtsev, 1940; Wislocki, 1943; Baskin, 1970).

Pronounced differences in seasonal cycle of growth and fattening exist between males and females but these have so far attracted little attention. Sex differences in fattening may be the reason for differences in the dates and distances of migration in males and females. Big males can dig deep snow more easily and males of tundra populations are therefore able to move further south and to penetrate the taiga more deeply in winter.

Social structure

Reindeer populations display considerably variability in their social structure. Differences are thought to be related to reproduction (rutting and calving) and to represent adaptations to environmental conditions. Reindeer are gregarious but although this behaviour is innate, most other social behaviours are formed through obligate learning. Social behaviour is intimately related to defense behaviour and defense behaviour is likewise a characteristic of particular populations. The level of defense behaviour can be judged by the flight distance, while social behaviour can be estimated by the frequency of visual contacts between neighbours, by the coordination of alarm behaviour and by group size. The level of social motivation depends not only on the conditions of obligate learning but also on environmental conditions (Baskin, 1989).

Sociality may depend directly on environmental conditions. For instance, if reindeer are driven out of the forest and into the alpine zone, their behaviour becomes more coordinated and the animals follow the leader more obediently. Such an effect must be associated with sharp changes in communication conditions. Sociality is highly seasonal in tundra reindeer. Analysis of the sociality of reindeer in Taimyr (Yakuskin, 1976) demonstrated that the group size is the largest in July (mean group size = 83.7) due to the abundance of blood sucking insects, and in October (mean group size = 308.2). Large accumulations of animals occur at obstacles during autumn migrations. Group size is smallest during the calving season (mean group size = 12.5 - 18.6) and in late June - early August after the fly-season (mean group size = 18.7). In the latter case 26.5% of the animals occur singly or in pairs.

Forest reindeer live in small groups. In a population which lives on the left bank of the middle reaches of the Yenisei river the mean group size is 13 in marshes and 4.3 in pine and leaved forests. In the montane taiga in the upper reaches of the Lena river the mean group size is 3.2 (Zyryanov, 1976). Quite a number of males in these populations are solitary. The group size of reindeer, which are generally thought to be highly social, is close to that of the moose, which lives singly or in small groups. But group size is a poor measurement of sociality. Reindeer are highly sociable even when found in small groups as indicated by their highly synchronized pattern of grazing, and the way in which the group follows the leader rather than dispersing as moose or roe deer.

It is believed that females' tendency to congregate on relatively small calving grounds is an adaptive strategy against predators (Geist, 1971, Bergerud 1974). Geist (1971) designates reindeer as "swampers", animals in which females congregate in dense aggregations at calving, thereby heavily outnumbering their predators. This view can be endorsed, with reservation, only with respect to tundra populations. Forest reindeer calve alone and Geist (1971) correctly designates these as "mountant followers" (i.e. the mother and the calf remain at one site for 2-3 days before social bonds are established, whereupon she leads her calf away). Tundra reindeer do not form such dense aggregations as many other typical "swampers". Species and such aggregations are not always successful in defence. For instance, brown bears occasionally inflict much damage, killing many reindeer calves.

Blood-sucking insects penetrate no more than five rows of reindeer and consequently the animals form large aggregations in summer when insects are active. The full protective effect of group formation is attained with a minimum of 31 animals in group. (Baskin 1970).

In 1931-1938, when numbers of reindeer in the Kola Peninsula were low, an the mean size of groups in summer was approximately 3 individuals (Semenov-Tien-Shansky, 1977). The deer protected themselves from insects by running about slowly in the forest for most of the day. When numbers increased (1958-1972) the animals began to aggregate and the mean size of groups in summer rose to 55. The size of groups during rut increased from 15-25 to 18-35 animals over the same period.

Spatial dynamics

The females of each population retain fidelity to particular calving sites (Dau and Cameron, 1986; Gunn and Miller, 1986) In addition, it has been established that populations are characterized by fidelity to particular summer ranges (Cameron et al., 1986). When several populations use the same wintering grounds they migrate in spring, each in its own direction (Azarov, 1976; Carruthers and Jakimchuk, 1986). Presumably, populations use traditional migration routes. Despite this "spatial fidelity" the animals evidently display a certain degree of lability in their movements. When reindeer first confront artificial barriers on their migration routes (a gas pipline, a road, ice broken by ice breakers) they hesitate but eventually find a detour to new ranges. Another step towards the understanding of population management will be elucidation of the significance of spatial fidelity in adaptation to changing conditions in the environment.

Reindeer females show fidelity to calving sites. They return there even from a distance of

200-500 km (Brown et al. 1986, Valkenberg and Davis, 1986). According to Brown et al. (1986), cows calve no farther than 10 km from the calving site ofi the preceding years and sometimes even use the same site twice. Similar fidenlity is found on other ungulates, e.g. camels and moose.

The question arises how traditional calving sites are formed. One could agree with Bergerud (1974) that there exist some laws of orientation which guide the deer. Rindeer move towards the sea in spring and inland in autumn following familiar routes.

Young females tend to calve with other females. This social effect described by Allee (1939) is well known for reindeer (Pruitt, 1960; Baskin, 1970). This is may be a peculiar form ofi transmitting tradition (Gunn and Miller 1986).

Presumably obligate learning accounts for the traditional use of particular migration routes. The direction of migration is determined by lichen conditions as stated by Sokolov, (1983), who monitored migrations in the mountains of Southern Siberia. In winter, reindeer travel from upland tundras to the upper edge of the taiga. In April and May they move to south-facing slopes and in summer they move to the mountains where there are no blood-sucking insects.

Population dynamics

The possible limits of change in demographic parameters of reindeer populations are well-known now. Parameters from some of the best reindeer breeding farms of the USSR are as follows: barreness of females of all ages = 6% number of calves per 100 females = 88%; survival of adult animals = 96%; maximum annual harvest = 40%.

Analysis of the dynamics of some individual populations provides examples of both sharp falls and increases in numbers as well as the existence of some stable populations. The latter included five isolated populations in the montain massifs of southern Siberia: 1000 - 1400 reindeer in Altai, 3000 in Tuva, 1200 - 300 in the western Sayans and approximately 6000 - 7000 in the eastern Saynas (Sokolov, 1983). Is it only the balance between reproduction and death that determines the stability of these populations? Or are there some internal mechanisms of population homeostasis?

Changes in female fertility and survival of calves account for the large changes in rates of increase of a population. In caribou over 50% of yearling females (12-23 mo. old) may be infertile (Parker, 1981): Fertility depends ofi their physical development: at 53 kg the probability of pregnancy is 8%, at 57 kg it is 75% and all females weighing over 67 kg will normally be pregnant (Thomas, 1982). Pavlov *et al.*, (1985) found 53.7% barren individuals among 3 year old females. Among the females of 4 years and older infertility was low and changed little between years, varying form 12.3 to 17.4%. These authors believe that many female calve at intervals so that on the average a female gives birth to 4 - 11 calves during her lifetime.

There is no doubt that the number of males born is larger than that of females, but males are less likely to survive. Young and old males do not participate in the rut and the male: female ratio in mating groups in 1:5.3 (range = 1:2 to 1:8) (Fil, 1976). In domestic tundra reindeer the male: female ratio in rutting groups is 1:18 and the majority of females are covered, since the animals keep in compact groups. The average percentage of barren females in reindeer populations is 8.45 (Baskin, 1983).

It is often thought that nomadism can, in some critical situations, be a major component in population regulation. Reindeer move when food is in short supply. The greater the lack of food the more they are likely to move. The question of whether the frequency of contacts with conspecifics may, in accordance with Wynne-Edwards' (1962) hypothesis, be one cause of migration still remains controversal. We can now distinguish at least 5 types of reindeer populations: (1) Forest montaine - the size of populations is small, their numbers are constant, migrations are both vertical and horizontal, sociality is low and variable; (2) Forest sedentary populations - population density is low, migrations are short and associated with seasonal change of habitats, sociality is minimal; (3) Forest migratory - population fluctuations are minimal, population density is relatively high, migrations are consederable, sociality is moderate; (4) Forest-tudra migratory - large populations (up to several hundred thousand animals), density is moderate, population fluctuations are small, ingrations are small, sociality is considerable. Populations on Arctic islands can be considered as a variant of this type (Kuprijanov *et al.*, 1985): numbers usually remain low on account their poor habitat but may occasionally increase at which time a tendency to migrate appears.

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Fluctuation in plant growth and in reindeer populations in Svalbard

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Expanded abstract:

Introduction

The rate of incerase of populations of reindeer in Svalbard fluctuates greatly between years. Snow and ice conditions in winter are widely belived to be the principal proximal factors responsible for declines. Recent analysis of climate records and mortality data, however, shows that rates of death from starvation in late winter are correlated with climate in the preceding summer. We suggest that plant production in summer has an important influence in the abundance of winter forage and, consequently, on reindeers' survival. This prompts two questions: first, does plant growth vary significantly between years in Svalbard? and second, what factors affect growth?

Methods

Between year variation in plant productivity was measured in *Cassiope tetragona* collected from Adventdalen, Spitsbergen in July 1987. This species, which is not eaten by reindeer, can be used as phytometer, in a way similar to dendrochronology, because annual increments of growth can be identified on the shoots. Annual growth was assessed by measuring the number and length of leaves in strict sequence along individual shoots. An historical record of growth over the last 20 yeares was established by this means.

Results

Plant growth in Adventdalen varied considerably between years. Two sorts of variation were apparent in *C. tetragona:* first, variation in the number of leaves per year (range = 4 - 20 leaves) and second, variation in the size of those leaves (range = 1 - 8 mm). Annual leaf performance was positively correlated with both mean July temperature and precipitaion in May. Interestingly, however, the total length of a given year's complement of expanded leaves, corrected to remove developmental trends, also correlated with the number of leaves produced in the preceding year. Furthermore, correlations between leaf performance in a given year and weather conditions in the preceding year were also often significant.

Discussion

Positive correlation between growth of *C. tetragona* and precipitaion in May, which normally falls as snow in Svalbard, suggests that snow cover is important in protecting sensitive shoot apices from late frosts.

Correlation between leaf performance in successive pairs of years indicates that leaves are pre-formed in the year before they expand. It may reflect an important mechanism to buffer production against vagaries of weather during the short growing season in the high arctic (Callaghan, Carlsson and Tyler, 1989). This may also occur in some forage species.

Conclusions

Retrospective analysis of the past growth of long-lived plants is a good tool for investigating relationships between plant preformance and enviromental factors such as weather. It is likely to be particularly useful in areas where, therefore, traditional techniques (e.g. clipping quadrats) are impractical over long periods.

In many parts of Svalbard, reindeer eat mainly vascular plants and mosses, not lichens, in winter. Substantial variation in plant production between years, as demonstrated here, together with variation in the availability of forage, is therefore potentially likely to have an important influence on the potential abundance of forage in winter and, hence, survival in reindeer. This aspect of the ecology of Svalbard reindeer has hitherto been largely ignored.

Correlation analysis of plant growth and climate is in progress and trends of plant productivity will be related to patterns of reindeer mortality.

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Callaghan, T.V., Carlson, B. and Tyler, N.J.C. 1989. Historical records of climate-related growth in *Cassiope tetragona* from the high arctic. - *Journal of Ecology* 77:823-837

Climatic changes and caribou abundance in northern Québec over the last century.

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Abstract: The temperature increase observed in the Northern hemisphere during the first half of this century was also detectable in Québec; it affected both summer and winter. In northern Québec, warmer summers stimulated growth and favored range expansion of trees and shurbs. Based on black spruce krummholz height and water level in lakes, the warmer period was also characterized by greater snowfall and deeper snow cover. This period of deep snow coincided with apparent caribou scarcity. Three hypotheses were explored to relate increased temperature with caribou decline: 1) destruction of winter habitat due to high frequency of forest fires, 2) increased energy cost to obtain forage in deep snow and 3) delayed melting of snow on calving grounds that shortened the time to raise calves. The combined effect of the 3 mechanism could explain caribou scarcity, particularly for the Rivière George herd whose calving ground becomes snow free in late June. Ways to test the third hypothesis are proposed.

Keywords: caribou, climate, Québec, *Rangifer*

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Introduction

Various factors have caused continuous changes of earth's climate over geological time (Harrington 1987). The temperature increase obeserved in the Northern Hemisphere during the first half of the 20th century was associated with reduced volcanic activities (Harrington 1987). Vegetation of northern Québec reacted to warm summers during this period: growth of black spruce *(Picea mariana)* was better than during the preceding 5 centuries (Payette et al. 1985), and green alder *(Alnus crispa)*, tamarack *(Larix laricina)* and white spruce *(Picea glauca)* exhibited range expansion at the tree line (Gilbert and Payette 1982; Morin and Payette 1984; Payette and Filion 1985). Such vegetation response must mainly have depended on longer and warmer growing seasons, but temperatute records in southern Québec since 1876 indicate that the warming trend also occured in winter. Warm winters during the first half of the century in Greenland were apparently caused by a displacement of the polar front; they were characterized by greater snowfall and rainfall (Meldgaard 1986). In northern Québec, mean snow depth may have increased by 20 cm during this period (Payette et al. 1985).

Even if quantitative information remains unavailable for most of the period, caribou numbers have fluctuated drastically over the last 100 years. They were seemingly plentiful at the turn of the century but became suddenly scarce until 1950-1960 (Audet 1979). During the following decades, the Rivière George herd increased at an annual rate exceeding 10 percent (Messier et al. 1988), to reach 682 000 (S.E. = 145000; n = 81) individuals in 1988 (Crête et al. 1989). Calf production has diminished by 20 percent since 1984 (Messier et al. 1988) and the herd may be leveling off or decreasing (Crête et al. 1989; Hearn et al. in press.). The Rivière aux Feuilles herd, the other herd calving on the Québec tundra, was made up of more than 100 000 individuals in 1986 (Crête et al. 1987); animals are in excellent condition (unpubl.), but the population dynamics of this herd remain unknown. Comparable fluctuations in caribou numbers with peak density by 1900 and in recent decades were also reported for Greenland (Meldgaard 1986). We examined climatic changes over the last 100 years in relation to fluctuation of caribou abundance. We tried to find relationships between temperature warming and caribou scarcity. We investigated the following hypotheses: 1) the incidence of forest fire was higher during the first half of the century, particularly in the north of the boreal forest so that caribou prime winter habitat became limited; 2) snow cover was deeper during this period and incidence of winter rain was higher so that forage was more difficult to obtain; 3) deeper snow cover delayed snow melt in spring so that emergence of green vegetation came later on calving grounds.

Study area and methods

The calving ground of the Rivère George herd is located east of Kuujjuaq on a tundra plateau which ranges in altitude between 500-750 m. (Fig. 1.). Before the mid-seventies, the herd used to spend the snow-free period in the vicinity of the calving area and migrate south and west in the forest-tundra and the boreal forest during the winter, east of longitude 70°. More recently, the herd has initiated fall migration earlier and has expanded its range west to Hudson Bay, occupying on an annual basis around 600 000 km^2 (Messier et al. 1988). The Rivière aux Feuilles herd calves in the middle of the Ungava peninsula, northwest of Kuujjuaq on a gently rolling plateau averaging 225 m in elevation (Fig. 1). Apparently, it spends the summer north of the tree-line and part of the herd migrates south in winter generally west of longitude 68° - 70°. Recently, winter range of both herds has partly overlapped while common use of the same range has been limited during the calving season and the snow-free period (unpubl.).

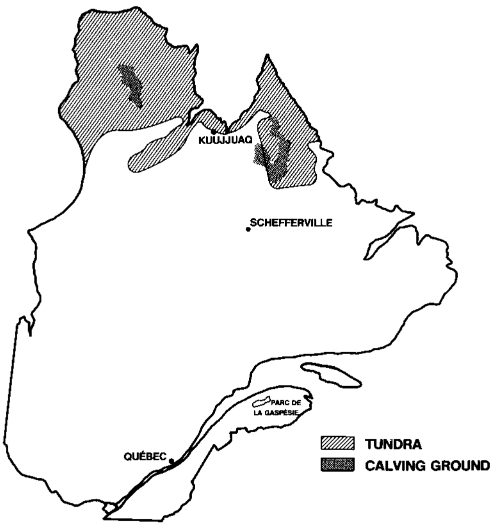

Fig. 1. Location of the 3 weather stations from which meteorogical data were analysed, distribution of the tundra in northern Québec and calving grounds used in 1986 by the Rivière aux Feuilles caribou herd (west) and the Rivière George herd (east).

Weather records were provided by the Ministère de l'Énergie et des Ressources du Québec for Québec City (1876-1986), Schefferville (1948-1986) and Kuujjuaq (1947-1986) (Fig. 1). Monthly temperature averages and total snowfall and rainfall served as input data. The year was divided into periods, November - April and

Table 1. Pearson correlation coefficient matrix computed with annual winter and summer average temperatures between 3 weather station in Québec, 1946-1948 to 1986. All coefficients significant (P<0.02).

	November - April		May - October	
	Shefferville	Kuujjuaq	Shefferville	Kuujjuaq
Québec	0,525 (38[a])	0,402 (38)	0,624 (38)	0,535 (38)
Schefferville	—	0,858 (37)	—	0,879 (36)
Kuujjuaq	0,858 (37)	—	0,879 (38)	—

[a] number of years compared

May - October. In addition NOAA/AVHRR satellite images were used to examine snow cover disappearance between 1980 and 1986 over northern Québec (St-Pierre et al. 1987). In 1984 and 1986, vertical aerial photographs were used to determine percent snow cover during calving (Crête et al. 1987); in 1987, visual estimation was made from an aircraft flying 200-300 m above the ground (Vandal and Couturier 1988).

Results and discussion

Temperature and precipitation trend: 1876-1986

Continuous weather records began in the late forties in northern Québec so that data were not available for most of the warmer period that started at the turn of the century. For Québec City however, observation began in 1876, which covers the complete cycle of warming and cooling trend. For the 1946-1986 period, there was a significant (P<0.02) relationship for the average annual winter and summer temperature between Québec City, Schefferville and Kuujjuaq (Table 1). The strength of the relationship was greater for Kuujjuaq and Schefferville that are relatively close, than for Québec City and 2 other areas; the relationship between the 3 weather stations was slightly closer for summer than winter temperature. On the other hand, no significant (P>0.1) relationship was found for winter snowfall or rainfall between Québec City and Schefferville or Kuujjuaq. We concluded that the temperature trend in northern Québec during the last century could be extrapolated from Québec City, but not precipitation trends.

A clear tendency for increasing winter temperature between 1880-1950 was apparent

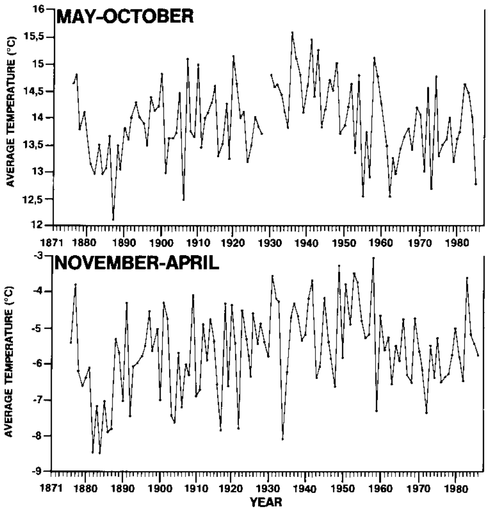

Fig. 2. Average winter (November-April) and summer (May-October) temperature between 1876 and 1986 in Québec City.

in Québec City, while summer temperature may have peaked a decade earlier (Fig. 2). Since 1950, temperature averages decreased by 1-2°C. Summer temperature trends observed in Québec City match well with vegetation growth and range expansion documented in northern Québec between 1900-1950 (Gilbert and Payette 1982; Morin and Payette 1984; Payette and Filion 1985; Payette et al. 1985).

It is difficult to reach any conclusions concerning the impact of warmer winter on snow cover in northern Québec because no historical data in snow preciptitation or depth are available. Based in black spruce krummholz (stunted trees) height close to the tree line, snow depth could have been 20 cm greater during the warming period than before (Payette et al. 1985). The same conclusion can be reached when considering water level in a lake of the same area that raised to a maximum height in the 20th century (Begin and Payette 1988). Water level in lakes is mostly determined by snow cover at the tree line in northern Québec. Increased snow depth during the first halfı of the century concurs with what probably occured in Greenland where the polar front may have moved north at that time (Meldgaard 1986). The trajectory of major snow storms that currently often follows the Atlantic coast in northeastern North-America may have moved north during the first half of the century if the polar front slightly retreated; that would explain the increased snowfall.

Incidence of fire in the boreal forest during the last century

Age and size of detectable fires were recently mapped in a 54 000 km^2 strip of land of northwestern Québec between latitude 55°and 59° (Payette et al. 1989); it incompasses part of the boreal forest, the forest tundra and the tundra (Payette 1983). Fire rotation was estimated at 7 300 years, 200-1 200 years and 100 years for the tundra, forest tundra and boreal forest respectively. In the prime winter caribou habitat - the fringe of the boreal forest - approximately 50 percent to the study area burnt over between 1920 and 1940. Moreover a similar proportion of land was affected by fire during decades 20s, 30s and 50s in the south of the forest tundra. It is difficult to determine if the incidence of fires increased during the warmer summers of the first half of the century because it is often impossible to know the history a site previous to a fire. However stands containing enough fuel to allow large fires to develop were present at the beginning of the twenties. Warmer summers obviously had a limited impact on fires in the tundra and the north of the forest tundra; however fires reduced by more than 50 percent prime winter habitat of caribou. In the worst situation, assuming no forage production for a few decades after fire, the carrying capacity of the boreal forest would hav decreased by more than 50 percent between 1920 and 1960. No precise data on fire history are available for the boreal forest and the forest tundra around Schefferville, which served as the winter range of the Rivière George herd in the sixties and the seventies. Fire rotation may have been longer there than further west due to greater precipitations and numerous fire breaks (Foster 1983).

Increased difficulty of obtaining winter forage

Cost of locomotion increases exponentially with snow depth in cervids (Mattfeld 1973; Fancy 1986) as is the energy spent by caribou digging in the snow to reach forage (Fancy 1986). In particular, the presence of ice crust may be very detrimental. Increased snow depth during the first half of the century certainly inflated the annual energy budget ofıcaribou. No massive caribou die-off was reported during winter in northern Québec for this period, but it could have gone unnoticed in this vast and unaccessible area. Caribou of the Rivière George herd, particularly lactating females, actually enter the winter with limited fat reserve (Huot 1989) due to poor summer range (unpubl.);

however they do not exhaust their fat store in winter because of a good winter range (Huot 1989). Increased energy demand for winter foraging would be actually detrimental to the herd productivity.

Effect of delayed snow melting on calving grounds

Actually, caribou from northern Québec appear to find enough energy in their forage during winter, wich however is deficient in protein (Huot 1989). Forage rich in protein is necessary to complete gestation and to nurse calves in cervids (Smith et al. 1975; Sadleir 1980). New graminoid shoots represent the first green vegetation found in rumens during spring and are consumed in early June by females on both calving grounds (Gauthier et al. 1989). Their emergence depends certainly on snow melt. Increased snowfall in winter, if not compensated by warmer weather and greater rainfall in spring, might reduce forage availability on calving ground. The Rivière George calving area is particularly vulnerable to such a phenomenon. By June 15, percent snow cover was 45, 44 and < 20 in 1984, 1986 and 1987 respectively (Crête et al. 1987; Vandal and Couturier 1988). At the Rivière aux Feuilles calving ground, snow covered 34 percent of the ground on June 3, 1986 (Crête et al. 1987). In general, snow melts more rapidly on the Ungava peninsula than along the Rivière George as illustrated satellite images taken in late June 1985 and 1986 (Fig. 3). Greater snowfall in the past could have resulted in complete snow cover on the Rivière George calving area until late June and early July, which would leave too short a period for females to successfully complete an annual cycle there.

Conclusion

Overgrazing, habitat destruction, overhunting, predation, disease, and climatic changes all constitute possible explantions for the decline of caribou observed in northern Québec during the first half of this century. Of all, climatic changes possess the greatest potential of affecting equally all animals over vast areas. As pointed by Meldgaard (1986), their effect may be subtle and slow, making them difficult to measure. Moreover, climate could have a carry over effect in cervids throughout their life (Peterson et al. 1988), which further complicates the study of its consequences.

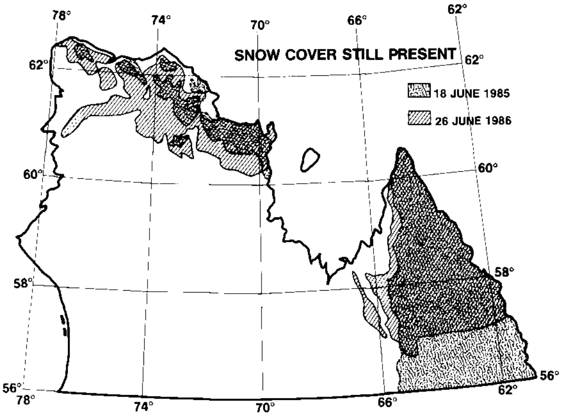

Fig. 3. Distribution of the remaining snow cover in northern Québec on June 18, 1985 and June 26, 1986 according to visual interpretation of NOAA/AVHRR satellite image (St-Pierre et al. 1987).

Warmer winters during the first half of the century were associated with greater snowfall and deeper snow cover. This period coincided with great scarcity of caribou. It will never be possible to determine if climatic changes caused caribou rarity. However it is possible to partly test the hypothesis that delayed access to green vegatation in spring, coupled with greater energy expenses during period of snowy winters, would have prevented caribou from completing their annual cycle in some parts of their actual range. Parturition should occur earlier where snow melt is earlier. This can be observed currently in northern Québec, where, for comparable latitude, calving has occured 7-10 days earlier in recent years on the Rivière-aux-Feuilles calving ground than in the Rivière George area (Crête et al. 1987). In southern

Québec, most calves are born by the beginning of June for the Gaspésie Park herd (Fig. 1; unpubl.). Manipulation of forage protein content in spring for captive caribou would be the best way to test the hypothesis.

Our analysis could not explain caribou fluctuations over the last century. However it may point out important aspects of the environment that have been overlooked in Québec, i.e pattern and timing of snow melt in spring, snow depth in winter and frequency of forest fires. As human activity on the earth risks provoking increased temperature during the coming decades (Harrington 1987), conditions observed during the first half of the century may reappear. Caribou managers should monitor closely climate changes.

Acknowledgements

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Seasonal movements of caribou in arctic Alaska as determined by satellite

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Abstract: Between 1985 and 1987, 49, 283 locations and 79, 101 sets of activity data were obtained for 34 adult female caribou of the Porcupine and Central Arctic caribou herds using satellite telemetry. Daily movement rates of female caribou from the two herds, which differ greatly in size and separation of seasonal ranges, were similar except during the spring and fall migrations. Movement rates in July exceeded those during migration in both herds. The minimum annual distance travelled by caribou cows, ranging to 5055 km, were the longest movements documented for any terrestrial mammal.

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The intrinsic rate of increase of reindeer and caribou populations in arctic environments

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Abstract: The intrinsic rate of increase of an animal population, r_m, is specific to the environment in which it is measured. Previous estimates of maximum growth rates for reindeer and caribou *Rangifer tarandus* populations were based on introductions to islands with cool oceanic climates. The mean intrinsic rate of increase of 6 populations was 0.26 ranging from 0.21 on St Paul Island in the Bering Sea to 0.29 in the Barff herd on South Georgia. I calculated r_m for two *Rangifer* populations introduced to arctic environments to determine the effect of environmental severity on the intrinsic rate of increase. Reindeer on the Belcher islands increased at $r_m = 0.28$ and caribou on Southampton Island increased at $r_m = 0.23$ (mean $= 0.26$). The lower primary productivity and longer duration of snow cover in arctic environments did not affect the intrinsic rate of increase.

Key words: increase of populations

Rangifer, Special Issue No. 3, 1990: 169-173

Introduction

The intrinsic rate of increase of an animal population, r_m, is worth knowing for a variety of practical and fundamental purposes e.g., to compare the favourability of different environments (Begon et al. 1986), to estimate sustained yield hunting limits (Caughley and Birch 1971), and to indicate potential population regulation mechanisms (Bergerud 1980, 1983, Caughley and Krebs 1983, Tanner 1975). r_m is best estimated by measuring the growth of a newly established population increasing from minimal density with unlimited resources (Caughley and Birch 1971).

Because birth rates and survival rates are unlikely to be the same everywhere an organism lives, r_m relates only to the environment whithin which it was measured (Birch 1948). Published estimates of maximum population growth rates in *Rangifer* have all been from island environments with cool oceanic climates (ie., 4-5 months with snow cover). In this paper I present data on the growth rates of two *Rangifer* populations introduced to islands with arctic climates (ie., 8-9 months with snow cover) and compare the intrinsic rates of increase in the two environments.

Study areas

Southampton Island covers 43 000 km^2 and lies at the north end of Hudson Bay, Northwest Territories, Canada. The vegetation consists of

Dryas barrens, sedge meadows and lichen heaths (Parker 1975). The mean annual temperature is - 11°C with mean daily temperatures above freezing only in July and August. Snow cover persists from mid-September until mid-June. The Belcher island archipelago, 900 km to the southeast, covers 2800 km^2. Mosses, dwarf shrubs, lichens and sedges predominate (J. Edmonds unpublished). Snow cover persists for about 8 months of the year. Both Southhampton and the Belcher islands are usually surrounded by open water even in winter.

Caribou *(Rangifer tarandus groenlandicus)* and wolves *(Canis lupus)* coexisted on Southampton Island until the early 1900's (Parker 1975). After the establishment of a Hudson's Bay Company trading post in 1924 and the unlimited availability of ammunition, caribou numbers quickly declined from overhunting. Caribou were rare by 1935 and extirpated between 1950 and 1955. Wolves also declined to extinction, presumably from lack of prey. No natural recolonization of caribou occurred. In 1967, 48 caribou *(R. t. groenlandicus,* 19 cows, 7 yearling females, 2 female calves, 6 bulls, 6 yearling males and 8 male calves) were captured from neighbouring Coats Island and released on Southampton (Manning unpublished). One wolf was shot on Southampton in 1979 but no other sightings have been reported. Hunting was prohibited until 1978 when a quota of 25 males/yr was permitted. The quota was increased to 50 males/yr in 1980 and to 50 males plus 20 females/yr in 1984.

Native caribou disappeared from the Belcher islands in the late 1800's (Ferguson 1985). Again, no recolonization of caribou occurred and in March 1978, 60 semi-domestic reindeer *(R. t. tarandus,* 50 adult cows and 10 adult bulls) were taken from Tuktoyaktuk, NWT and released on Flaherty I, the largest island in the archipelago. Those animals were allowed to range freely. There are no wolves on the Belcher island and no animals were shot.

Methods

The intrinsic rate of increase can be calculated only when a population has a stable age and sex distribution (Caughley and Birch 1971). However, the age and sex composition of a cohort of ungulates introduced to unoccupied areas in the hope of establishing a new population is usually biassed toward adult females. In those situations the actual rate of increase (r) of an introduced population is always greater than the intrinsic rate calculated from those data.

I took distorted age and sex ratios into account by simulating the population dynamics of each herd with a simple bookkeeping model. Initial conditions were determined by the number of the animals introduced by age and sex. Calf survival (from birth to age one) was varied as required, to achieve the final population size. The model was based on the following assumptions; 1) there was an equal sex ratio at birth, 2) calf survival was equal in both sexes, 3) adult survival was 100% in both sexes, 4) all adult (yearling and older) females produced one calf each year, and 5) all rates were constant through time. Data from Southampton Island were consistent with those assumptions. All 44 females (including 10 yearlings) in 1988 and 1989 collections were pregnant. Equal survival of the Sexes can be inferred from the even sex ratio found in 1987 (104 adult males: 100 adult females; Heard unpublished); Simulation was continued until the age distribution stabilized at which time lambda, the finite rate of population change, was determined as N_t/N_{t-1}. The $\log_e$ lambda for each population was considered an estimate of the intrinsic rate of increase for *Rangifer.*

When more than two population estimates were available, I calculated the final population size and the actual growth rate from a linear regression of $\log_e$ population size on time where the line was constrained to pass through the known number introduced.

I considered the period of increase on St

Paul and St George islands from the time of introduction until hunting began.

Results

The number of caribou on Southampton Island was estimated at 1200 ± 340, 11 years after they were introduced and at 5400 ± 1130 nine years later (Heard unpublished). The actual rate of growth (r) was 0.25 and the intrinsic rate of increase was 0.23.

In March 1982, four years after the introduction, the number of reindeer on the Belchers was estimated at 287 (Ferguson 1985), an observed growth rate of $r = 0.39$ and r_m was 0.28.

Discussion

The mean intrinsic rate of increase of the two *Rangifer* populations introduced into arctic environments was 0.26; the same as the mean intrinsic rate of increase of 6 populations introduced to islands with cool oceanic climates (Table 1). Therefore lower primary productivity and the longer duration of snow cover in the arctic environments did not affect the intrinsic rate of increase, suggesting that reindeer and caribou can do well as long as the energetic costs of obtaining food (e.g., cratering) are compensated for by the energy derived from their forage.

Table 1. Maximum rates of increase for reindeer and caribou populations where r is the actual rate of increase and r_m is the intrinsic rate of increase; the rate at which the population would have increased if it had had a stable sex and age distribution.

Population	Years of increase	Number of counts	r	r_m	Climate	Source of data
Theoretical				.31		
Barff (R)	10	4	.34	.29	M	1
Brunette I (C)	5	6	.37	.27	M	2
Belcher I (R)	4	2	.39	.28	A	3
St George I (R)	6	7	.35	.26	M	4
Adak I (C)	8	2	.26	.25	M	5,6
St Mathew I (R)	13	2	.30	.25	M	7
Southampton I (C)	20	3	.25	.23	A	8
St Paul I (R)	7	8	.30	.21	M	4

R=reindeer, C=caribou
M=maritime/cool oceanic, A=arctic
1 Leader-Williams 1988
2 Bergerud 1971
3 Ferguson 1985
4 Scheffer 1951
5 Jones 1966
6 Hemming 1970
7 Klein 1968
8 Heard unpublished

The theoretical maximum rate that caribou can increase is 0.31 given a litter size that is always one, a 1:1 sex ratio at birth, caribou never become pregnant as calves (4 month old animals), no mortality until 20 years old when they all die, and 100% pregnancy among yearling and older cows. The theoretical maximum for reindeer is somewhat higher because occasionally they give birth to twins (Godkin 1986) and calves can become pregnant (Reimers 1972). The theoretical maximum rate of increase of reindeer and caribou could be higher than 0.31 if pre-natal sex ratios are biassed toward females as Skogland (1986) found for favourable environments. Neither the pre-natal nor adult sex ratios were greatly distorted on Southampton Island where pre-natal sex ratios were 9 males: 12 females and 10 males: 12 females in 1988 and 1989 collections respectively (Heard unpublished). Intrinsic rates of increase for reindeer and caribou approach the theoretical maximum of 0.31 (Table 1).

The actual rate of increase of reindeer on St Mathew, St Paul and St George islands had often been incorrectly cited as r_m (eg., Caughley and Krebs 1983, Leader-Williams 1988). When introduced cohorts are biased toward adult females, r is always greater than r_m and the difference is usually substantial (Table 1). On St Mathew I for example, 24 yearling females and 5 yearling males were introduced in 1944. By 1957 they had increased to 1350 (Klein 1968), an actual rate of increase of 0.30. Correcting for the distorted sex ratio indicates that the herd grew from 24 females to 685 females, a rate of increase of 0.26, assuming an even sex ratio of recruits (1350-29 = 1321 recrutis; 1321 x 0.5 = 661 female recruits; 661 + 24 = 685 females). After correcting for the unstable age distribution using the simulation model, the estimate of r_m was further refined to 0.25 (Table 1).

Bergerud (1971) adjusted for the distorted sex ratio of caribou introduced to Brunette Island by assuming that population composition would approach the mean sex ratio for the species at equilibrium which is only 56 males: 100 females (Bergerud 1971). My model of the Brunette population indicated that mortality was only 5%/yr for all ages and both sexes combined, providing little room for substantial differential mortality between the sexes. Therefore I believe Bergerud should have assumed an even sex ratio.

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Group dynamics of the Porcupine Caribou Herd during insect season

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Abstract: In early summer, caribou (*Rangifer tarandus granti*) form large dense groups in response to insect harassment. In early July 1984 and 1985 the maximum group size was 30 000 for the Porcupine Caribou Herd. Later in July, when insect activity subsided, maximum group size was less than 10 000. This behavior, as well as overt annoyance responses may reduce the contact between individual caribou and parasitic or blood sucking dipterans such as bot flies *(Oestridae: Cephenomyia trompe)*, warble flies *(Oestridae: Hypoderma tarandi)* and mosquitoes *(Culicidae)*. Based on the frequency of annoyance responses elicited by caribou, the windward side or the center of the group was more advantageous to caribou in terms of insect avoidance. This concurs with the findings from Helle & Aspi's experiment with animal traps to determine if herd formation reduced insect harassment among reindeer.

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A life table for female barren-ground caribou in north-central Canada

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Abstract: A survivorship curve and cohort-specific life table were developed for female barren-ground caribou *(Rangifer tarandus groenlandicus)* sampled from the Beverly herd from 1980 through 1987. Significant ($P < 0.05$)differences among yearly samples in the age distributions of females$>$2.5 years old were attributed to sampling error and real cohort size fluctuations caused by variations in productivity. Pooled data overcame much of that variation and the resultant quadratic-fit curve and life table are believed to yield about average survival/mortality statistics over the 8-year sampling period. Mortality rates increased progressively from 10.6% between age 2 and 3 years to 22.4% between age 10 and 11 years and accelerated thereafter.

Key words: mortality rate, *Rangifer*, survivorship

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Introduction

We obtained from 1980 through 1987 a sample of 1284 caribou as part of studies concerned with caribou diet, forage digestibilities, and the effect of forest fires on the winter range of Beverly herd. That herd winters in the southern Northwest Territories (NWT) and adjacent Saskatchewan.

Average mortality rates for specific ages are needed in studies where radio collars are applied and mortality rates are recorded (Edmonds and Bloomfield, 1984; D. Heard, pers. comm., NWT Department of Renewable Resources): is the observed mortality rate about average and, if not, why not? If the ages of collared caribou are known, the expected mortality can be calculated using data in the life table. Life tables when combined with fecundity tables, and particularly sex-specific fecundity, can yield estimates of rate of increase (Caughley, 1977). Survival curves can be used to assess variations in productivity in past years and relate it to variations in environmental factors.

The purpose of this paper is to provide average survivorship and mortality statistics for a migratory herd of barren-ground caribou subject to hunting and wolf predation.

Methods

From field camps established specifically to sample the herd in early and late winter, local shooters operating snowmobiles collected most of our caribou samples. We estimated ages up to 2 years by tooth eruption criteria; older caribou from stained sections of the first incisor and first molar. Data for calves and yearlings were excluded from this analysis as our shooters sometimes selected against them (less meat and fat). By weighting the data according to the relative sample sizes of females $>$2 years old in December (n=197) and March (n= 519), we pooled the mean collection dates of December 8 and March 21 and used February 21 (0.71 of a caribou year beginning June 8) as the mean date of the samples.

We pooled data for all years to reduce the variation (tested with G statistic, Sokal and Rohlf, 1981) caused by small sample sizes, heterogeneity of caribou groups, and changes in productivity. Using a quadratic form, we regressed the observed age class frequencies against age using least squares. We then used the quadratic equation to calculate smoothed frequencies in each cohort 2.71, 3.71, ... 14.71 years old in the pooled winter samples. We also calculated age class frequencies at the appropriate birth pulse (Caughley, 1977) of June 8 by substituting in the quadratic equation for ages 2.0 through 15.0 years. Estimates of survival to 1 year and from 1 to 2 years allowed us to complete the life table for all ages.

We then tested by Chi-square the expected numbers at ages 2.71 through 14.71 and observed numbers in each winter sample of 1981-82 through 1986-87. The expected numbers were calculated as the products of sample sizes and the relative frequencies of each cohort $\geqslant$ 2.71 years obtained from the quadratic equation. Relative frequency is the number in a cohort divided by numbers in all cohorts $\geqslant$ 2.71 years.

Results

Our fitted (R^2=0.96) survival curve was: $y = 0.330x^2 - 15.558x + 161.113$, where y was the pooled frequencies at February 21 and x was age 2.71, 3.71, ... 14.71 (Fig. 1A). We calculated birth pulse values (ages 2, 3, ... 15) using the regression equation and constructed a partial life table (Table 1), which revealed the average mortality pattern of the breeding component over the period of the sampling. Extrapolation to age 2 assumes no change in survival trends (Fig 1A) from age 2 to 2.71 years.

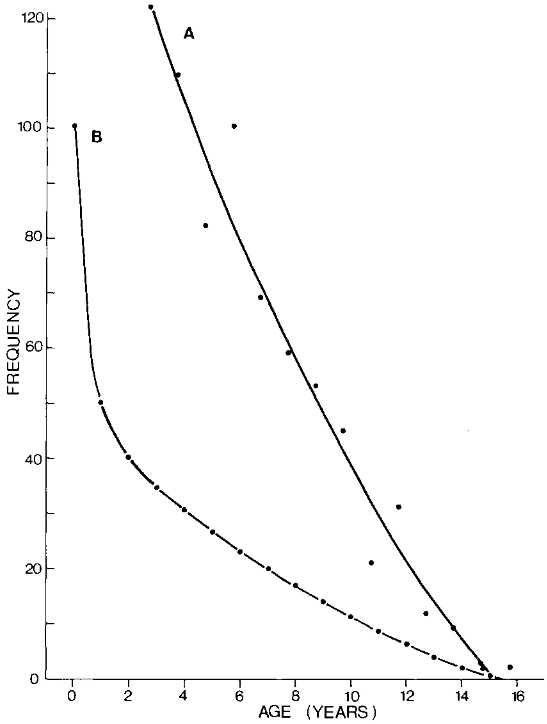

Figure 1. Survivorship curves for female barren-ground caribou 3 years old (A), based on pooled age distributions in samples from the Beverly herd, obtained from 1980 through 1987, and for all ages (B) where assumptions are made concerning survival from birth to 3 years (see Text).

The estimated survival curve for all ages (Fig. 1B) was developed by assuming 50% survival to 1 year and 20% mortality from age 1 to 2 years. The long-term average recruitment of the Beverly herd (Kelsall, 1968; Beverly and Kaminuriak Caribou Management Board, 1987; Thomas and Kiliaan, 1990) equates to about 50% survival of calves to age 1 year (Thomas, unpubl. data.) Survival and mortality values

Table 1. Contracted life table for female caribou >1.5 years old that were collected from the Beverly herd from 1980 through 1987.

Age[a] (yr) x	Observed frequency Feb 21 of_x	Frequency from Quadratic[b] Feb 21 f_x	June 8 f_x	Survival[c] l_x	Mortality[d] d_x	Mortality rate[e] q_x	Survival rate[f] p_x
2		135.5	131.3[e]	100.0	10.6	10.6	89.4
3	120	121.4	117.4	89.4	10.0	11.3	88.7
4	109	107.9	104.2	79.4	9.6	12.1	87.9
5	83	95.2	91.6	69.8	9.2	13.0	87.0
6	101	83.0	79.6	60.6	8.5	14.1	85.9
7	70	71.6	68.4	52.1	8.1	15.5	84.5
8	59	60.8	57.8	44.0	7.6	17.2	82.8
9	52	50.6	47.8	36.4	7.1	19.4	80.6
10	45	41.2	38.5	29.3	6.5	22.4	77.6
11	21	32.3	29.9	22.8	6.1	26.6	73.4
12	31	24.2	21.9	16.7	5.6	33.3	66.7
13	12	16.7	14.6	11.1	5.0	45.4	54.6
14	9	9.8	8.0	6.1	4.6	75.0	25.0
15	2	3.7	2.0	1.5	1.5	100.0	0.0
16	2						
Totals	716	853.9	813.0		100.0		

[a] Ages at June 8. Ages at February 21 are *Age — 0.29*. E.g., 1.71/2 yr.

[b] From quadratic equation: $y = 0.330x^2 - 15.558x + 161.113$ where y is frequency and x is age.

[c] Each frequency divided by 131.3 and converted to percent (X 100).

[d] Difference between survival at successive age classes.

[e] $100\ d_x/l_x$. These values were rounded from three decimal places.

[f] $100 - q_x$.

changed (Table 2) but their rates did not. Weighted mean mortality rates ($\Sigma d_x/\Sigma l_x$) calculated for various age groups: >0, >1, >2, ... >10 years were 25.2, 16.8, 16.2, 17.2, 18.5, 19.9, 21.6, 23.7, 26.2, 29.5, 33.5%, respectively.

Extrapolation of the quadratic to age 1 year yields 145.9 caribou as a starting number and a mortality rate of 10.0% at age 1 to 2 years. These values are provided as recent results from radio-collared caribou in Alaska indicated that mortality rates were similar in age classes 8 - 12, 12 - 24, and >24 months (Davis *et al*., 1988). Readers can construct a new life table where mortality rates are given (Caughley, 1977).

There was significant variation (G test, $P < 0.05$) among years 1981-82 through 1986-87 and in 1981-82 through 1985-86 when sample sizes were largest. Two sources of variation are apparent upon close examination of the age distributions (Table 3): sampling error and cohort variation. Relatively large or small cohorts that are consistent in successive years indicate variation in numbers entering the 2.5 - 3 year class. Other variation is caused by non-random distribution of age and sex classes within herds. Large sample sizes are needed to overcome heterogeneous distributions.

Strong and weak cohorts were examined statistically (Table 3) by comparing observed fre-

Table 2. A life table for female caribou in the Beverly herd, 1980 through 1987.

Age x	Frequency at June 8 f_x	Survival l_x	Mortality d_x	Mortality rate q_x	Survival rate p_x
0	100.0	100.0	50.0	50.0	50.0
1	50.0[a]	50.0	10.0	20.0	80.0
2	40.0[b]	40.0	4.2	10.6	89.4
3	35.8[c]	35.8	4.0	11.3	88.7
4	31.8	31.8	3.9	12.1	87.9
5	27.9	27.9	3.7	13.0	87.0
6	24.2	24.2	3.4	14.1	85.9
7	20.8	20.8	3.2	15.5	84.5
8	17.6	17.6	3.0	17.2	82.8
9	14.6	14.6	2.9	19.4	80.6
10	11.7	11.7	2.6	22.4	77.6
11	9.1	9.1	2.4	26.6	73.4
12	6.7	6.7	2.3	33.3	66.7
13	4.4	4.4	2.0	45.4	54.6
14	2.4	2.4	1.8	75.0	25.0
15	0.6	0.6	0.6	100.0	0.0
Totals	337.6	337.6	100.0		

[a] Approximate frequency based on data in the literature (see Text).

[b] Assumes mortality rate of 20% between ages 1 and 2.

[c] Values for $\geqslant 3$ years calculated using mortality rates in Table 1.

quencies in each cohort of each winter, 1981 - 82 through 1986 - 87, with frequencies expected from the survivorship curve for February 21. A significant difference between observed and expected frequencies in the 1979 cohort was sampling error because it only occurred in one of six samples from that cohort. Similar cases appeared in the 1977 and 1975 cohorts. Real difference in cohort sizes occured in 1978 (underrepresented) and 1973 (overrepresented). Strong trends towards over- and underrepresentation were present in 1982 and 1980 cohorts, respectively.

Discussion

Strictures on data that can be used to develop mortality tables are sufficiently rigid that most life tables are faulty to some degree (Caughley, 1966, 1977; Miller and Zammuto, 1983). The key requirement is that the age structure must be derived from a stationary age distribution. This requirement is not necessarily satisfied if the population size remains about constant. It is satisfied if the numbers in each class do not change significantly. If the rate of population change is known, data can be adjusted accordingly, provided that the age distribution is stable (Caughley and Birch, 1971). But how can the age distribution remain stable under conditions of population change? The possibilities are remote in nature, e.g., changes in mortality proportional to age-class frequencies. Stationary age distributions are rare in natural populations. There was a perception that the Beverly herd was increasing in the 1980s (Williams and Heard, 1986) but a review of the survey

Table 3. Analysis of cohort relative strengths in samples obtained from the Beverly herd of caribou from 1981-82 through 1986-87.

Cohort	1981–82		1982–83		1983–84		1984–85		1985–86		1986–87		Totals	
	O[a]	E[b]	O	E	O	E	O	E	O	E	O	E	O	E
1984											15	13	15	13
1983									20	23[c]	11	11	31	34
1982							29	26	28	21	16	10	73	57
1981					19	21	31	23	14	18	13	9	77	71
1980			15	20	13	19	15	20	14	16	8	8	65	83
1979	11	11	17	18	17	16	28	18*	15	14	6	6	94	83
1978	4	10	10	16	19	14	10	16	5	12*	4	5	52	73*
1977	10	9	19	14	20	12*	10	13	11	10	1	4	71	62
1976	5	8	7	12	7	11	12	11	13	8	0	3	44	53
1975	5	7	19	10**	6	9	3	9*	3	6	2	3	38	44
1974	10	6	8	8	7	7	1	7*	5	5	0	2	31	35
1973	6	5	9	7	9	6	10	5*	5	3	0	1	39	27**
1972	6	4	5	5	3	4	1	4	4	2	0	0	19	19
1971	3	3	7	4	2	3	2	2	0	1	0	0	14	13
1970	4	2	2	3	2	2	2	1	0	0	0	0	10	8
1969	2	2	1	2	0	1	1	0	0	0	0	0	4	5
1968	0	1	0	1	0	0	0	0	0	0	0	0	0	2
1967	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Totals	66	68[c]	120	120	124	125	155	155	137	139	76	75	678	682

[a] The observed (0) numbers are females $\geq$ 2.5 years old in pooled December and March samples.

[b] Expected (E) numbers are the relative frequencies of the age classes at February 21 (weighted mean date of samples) based on the smoothed distribution (quadratic) for females$\geq$2.71 years. E.g., 1984 cohort, 1986-87 sample, E = 76 × 121.4/718.4, where 76 is the total number of females$\geq$2.71 years in the 1986-87 sample, 121.4 is the derived number in the 2.71 year (1984) cohort and 718.4 is the derived total sample size for all ages >2.71 years (853.9 - 135.5, Table 1).

[c] Differs from observed because of rounding.

* $P<0.05$.

** $P<0.02$ (Chi square).

data suggests little change has occurred since 1967. The most recent analysis of survey data suggests that the herd has remained about stable in numbers since 1982 (D. Heard, pers. comm.).

A second stricture that is seldom met with large mammals is the need to distinguish between natural mortality and hunting mortality. Total mortality is the most important statistic for many research and management purposes. Natural mortality is the residual if hunting mortality can be measured accurately. The annual kill of caribou in the Beverly herd by hunters, mostly natives seeking meat only, is in the order of 5000 to 10 000, however, reliable estimates are not available. This annual kill is believed to constitute about 2 - 5% of the herd.

A third requirement, which is seldom satisfied, is an adequate sample size. Caughley (1977) suggested that 150 was the minimum number, though many factors (e.g., homogeneity and longevity) are involved. At one extreme, sample sizes as small as 16-40 males (ages 1 - 3 years) and 24 - 51 females (ages 1 - 5 years) were adequate to produce reliable time-specific life tables for short-lived Belding's ground squirrels *(Spermopbilus beldingi)*, even when fecundity and mortality changed markedly because of changes in environmental conditions (Zammuto and Sherman, 1986).

An unbiased sample is a fourth requirement in life table analysis. A sample of female caribou older than 2 years should have no human biases because hunters are unable to distinguish among female cohorts after age 2. Sampling at the front or rear of a movement could create a biased sample and investigation is needed in this area. Most of our samples were obtained from central portions of the distribution or from a cross section as the herd moved past a campsite. Obtaining an unbiased sample of male caribou would be exceedingly difficult because of the habits of older males to segregate from other groups except during late summer and in the rut and in their propensity to segregate by age.

An assumption implicit in this type of analysis is that the mortality rate changes uniformly from cohort to cohort and also within years. In the Beverly herd, the majority of hunting mortality occurs from November through March. Annual rates of natural mortality are unknown and rates at which natural mortality occurs during a caribou year are even more elusive. Accurate data on hunting mortality specific to sex and broad age classes would have yielded good estimates of natural mortality in this study. It should be afforded high priority in the future.

Previous life tables for barren-ground caribou have suffered from a number of problems. Banfield (1955) grouped males and females, obtained samples from hunters (l_x data) and skulls (d_x data) found on the summer range, estimated ages from eruption schedules and degree of wear, and didn't account for biased sampling by hunters and biases caused by differential survival and detection of skulls and mandibles. Miller's (1974) sample was afflicted with high (1958-60) and low (1961-63) waves of productivity; with low recruitment during the study (1966-68) and perhaps after 1961; with samples obtained throughout the annual cycle; and with atypical samples which he excluded. His survival value for calf caribou is much higher than indicated by the recruitment data. Martell and Russell (1983) had a large sample (535) of unsexed caribou (that should not be grouped) but only 76 males and 62 females over 2 years old. In spite of those problems, average weighted mortality values differ marginally for females >3 years: Miller (1974) 17%; Martell and Russell (1983) 20%; this study 17.2%. These equate with 19% for radio-collared caribou >2 years old in the Delta herd in Alaska (Davis *et al.*, 1988).

Messier *et al.* (1988) obtained a standing age structure from 875 females among about 10 000 woodland caribou (*R. t. caribou*) that drowned on 28 and 29 September 1984 in Quebec. They adjusted observed age cohort values by 11%, the calculated growth rate ofthe population after 1970. Their calculated mortality rates of 1 and 2% in 1 - 2 and 2 - 3 year age classes obviously are low in view of an estimate 5 - 7% harvest in the mid 1980s (Messier *et al.*, 1988). The George River herd may have peaked in 1984 (Couturier *et al.*, 1988) or earlier. We arbitrarily decided to consider the herd's growth inclusive of age cohorts representing 75% of females in our table, i. e., to 6 years. We only accepted the survey results of 1980 and 1982 after 1978. The 1984 estimate was photographic, which usually exceed visual estimates by factors of 1.6 to 2.5 and once by 4.5 (D. Heard, pers. comm.) to 52:100 in late October growth from 1978 through 1984, developed the quadratic equation: $y = 0.567x^2 - 20.237x + 176.731$ ($R^2 = 0.92$) at ages x.31 (June 8 to September 28 is 0.31 of a caribou year) and then calculated values at the birth pulse. Mortality rates for 1 - 2, 2 - 3, ... 15 - 16 years were calculated as: 11.8, 12.6, 13.4, 14.4, 15.6, 17.0, 18.7, 20.7, 23.4, 26.8, 31.7, 39.0, 52.0, 83.5, and 100.0%. The mortality rate from 0 to 4.5 months was calculated as 28% based on a calf:cow ratio change of 72:100 at calving (Parker, 1972; Thomas and Barry, this issue; D. Heard, pers. comm.) to 52:100 in late October (Messier *et al* ., 1988). Assuming that mortality after 4.5 months equals that of yearlings (11.8%), (Davis *et al* ., 1988), the calculated mortality rate in the first year was 37%, which completes the life table. We acknowledge that the herd was growing before 1978 but did not adjust 1978 and earlier cohorts. Smoothed cohort frequencies could be adjusted by a sliding rate of growth if accurate herd numbers could be obtained. The mortality rates probably lie somewhere between those calculated by us and by Messier *et al.*, 1988.

Weak and strong cohorts relate to fluctuations in fecundity and early mortality. Where these can be related to environmental fluctuations we can begin to gain insights into caribou ecology. The relatively strong cohort in 1982 may be related to large fat reserves and high fecundity in breeding-age females in March 1982; the weak 1980 cohort to moderate pregnancy rates and low fat reserves in March 1980 (Thomas and Kiliaan, 1990). D. Heard (pers. comm.) observed an unusually large number of dead calves on the calving ground ofithe Beverly herd in June 1978. Causes of death were not determined.

The weakest link in the life table for all ages of caribou is the mortality rate for caribou 1 to 2 years old. We initially selected 20% because by late winter of most years some yearlings are thin and marginally heavier than large calves (Thomas and Kiliaan, 1990). They likely are more susceptible to predation than older caribou. The mortality rate of yearlings will vary considerably among and within herds depending on their nutritional state and the prevalence of predators. Fortunately, manipulating mortality rates in the first two age classes does not affect the rates in older classes in the life table.

The strongest support for this cohort specific analysis comes from the work of Zammuto and Sherman (1986) on ground squirrels. A cohort-specific life table using combined data from 8 years was statistically indistinguishable from time- specific tables generated from six

Conclusions

1. A pooling and smoothing of age distributions of female caribou $\geqslant 2.5$ years old obtained each winter from 1979-80 through 1986-87 yielded a cohort-specific life table containing average long-term mortality and survival rates for those age classes.
2. The frequency of females (y) in cohorts 2.71, 3.71, ... 14.71 years old at February 21 was described by the quadratic equation: $y = 0.330x^2 - 15.558x + 161.113$ where x was age.
3. We used the regression equation to calculate birth pulse life tables: mortality rates gradually and progressively increased from 11.3% from 3 to 4 years of age to 22.4% from 10 to 11 years and accelerated therafter to 100% from 15 to 16 years.
4. The long-term average mortality rate of females 2 to 3 years old was calculated at 10.6% after extrapolating the survival curve to age 2 using the regression equation for older caribou.
5. Variation among years in age class structures was caused by differences in productivity and by sampling errors, attributed to sample size (chance) and non-randomness of age classes in samples.
6. The statistics produced by this analysis are believed to be the best obtained for a population of barren-ground caribou in Canada; previous attempts suffered from various problems.
7. The results are useful in studies on populations with similar habits, habitats, and mortality factors (predators, hunting etc.). Such comparative data are useful where the mor-

tality rate is measured by use of radio collars, particularly where the environment (e.g. wolves) is manipulated.

8. Life table analysis combined with good data on hunting mortality will yield the rate of natural mortality, which is needed to effectively manage caribou and to understand their ecology.

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Nutrition, Rumen Physiology and Metabolism

Key note address:

Microbiology of digestion in the Svalbard reindeer *(Rangifer tarandus platyrhynchus)*

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Introduction

The Svalbard reindeer *(Rangifer tarandus platyrhyncbus)* lives on the high arctic archipelago of Svalbard (77 to 81° N). It is the only indigenous herbivorous mammal found there, and with the exception of possible contact with introduced Musk-ox *(Ovibos moschatus)* in Spitsbergen, has been isolated from other ruminants for possibly 40,000 y (Hakala, Staaland, Pulliainen & Røed, 1985).

Both climatic and nutritional conditions for the Svalbard reindeer are extreme. During winter for a period of about three months there is continuous darkness, and snow covers much of the ground from October to late May. Although snow cover rarely exceeds 30 cm (Tyler, 1987), maritime climatic influences cause the ambient temperature in winter to occasionally rise above zero for short periods. This results in cycles of thawing and refreeezing of the snow which turns into a hard ice layer over much of the vegetation on the tundra. Before the vegetation is locked in the ice, the animals can dig in the snow to find forage, but after the ice forms they are forced to abandon these areas and seek food on the more windswept areas of the valley sides and mountains which are devoid of ice (Tyler, 1987). In these regions the standing plants may provide only a few grams of forage per square metre (Tyler, 1987). In some years when the animals are forced into these nutritionally inadequate areas, over 25% mortality due to starvation occurs before the onset of plant growth in the spring (Tyler, 1987).

Unlike many reindeer or caribou populations, the Svalbard reindeer does not have the option of migrating to better feeding areas in winter because of its geographically isolated habitat. In Svalbard plant growth is restricted to about eight weeks in the summer when mean ambient temperatures are in the range of 1-6°C. From mid-June to September, when the snow returns, food is abundant and of high nutrient value (White & Staaland, 1983,; Staaland *et al.* 1983). During this period the animals have to restore depleted body reserves of fat and protein used up during the winter period, in addition to providing energy for maintenance and for lactation in the females. The deposition of up to 30% of their body weight as fat in the autumn, however, is not sufficient to guarantee their survival over winter (Mathiesen *et al*, 1987, Tyler 1987).

In the summer the animals have access to a wide range of plant species. By September, many of these plants, particularly grasses and sedges, have formed seed heads which comprise a major part of the diet which is consequently rich in non-structural carbohydrates and protein (Staaland *et al*, 1983). In winter, mostly mosses and other fibrous plants such as the woody *Dryas octopetala* are available as food; thus, the annual food cycle ranges from young forage in spring, to a concentrated diet including seed heads in September, to a highly fibrous diet including mosses in winter (Person *et al*, 1983; Punsvik *et al*, 1980). In order to survive under these nutritional conditions the animals must make maximum use of the high quality summer forage, in addition to being able to digest the poor quality forage which is often the only food available during the eight month winter period.

Since the Svalbard reindeer occupies such an unusual ecological position, it was of considerable interest that the microbiology of digestion be examined. It was considered that the possession of a rumen and/or caecal microflora particularly adapted to a high-fibre diet could be critical to the survival of these animals (Orpin *et al*, 1985), since the caecum in Svalbard reindeer is relatively large, comprising 11% of the alimentary tract in summer and 7% in winter (Staaland *et al*, 1979) and in domestic ruminants, caecal fermentation may provide up to 30% of the volatile fatty acids entering the blood stream (Williams, 1965; Faicheny, 1986).

This paper summarises research into the digestive microbiology of the Svalbard reindeer, done in this area, and compares the results with what is known of the microbiology of digestion in other reindeer and caribou, and in domestic ruminants. The work was undertaken in April (late in the high-arctic winter) and September (late in the high-arctic summer). Full details are

Table 1. Population densities of rumen large bacteria from the Svalbard reindeer, estimated by direct microscopy of diluted rumen fluid, in September (high-arctic summer) and April (high-arctic winter) (Orpin & Mathiesen, 1985).

Counting method, bacteria	Mean population density + SD (x 10^8) in:		April populations as % of September populations
	September	April	
Total large bacteria	5.97 ± 1.53	0.54 ± 0.13	9.0
Oxcillospira guilliermondii	0.07 ± 0.03	0.008 ± 0.032	11.4
Magnoovum eadii	0.25 ± 0.08	0.064 ± 0.018	25.6
Quin's Oval	0.94 ± 0.21	0.082 ± 0.021	8.7
Large *Selenomonas* sp.	3.75 ± 0.72	0.280 ± 0.047	7.4
Other large bacteria	0.96 ± 0.14	0.109 ± 0.033	11.4

given by Orpin *et al* (1985) and Mathiesen *et al* (1987).

Ruminal and caecal pH and volatile fatty acid levels

The low pH values recorded in the rumen of the free-ranging Svalbard reindeer (Table 1) and the relatively high total concentration of volatile fatty acids when compared with grazing domestic ruminants suggested that active fermentation of dietary materials occurred in both seasons. The rumen pH in cattle fed a high concentrate diet is usually in the range of 5.5-6.7 (Hungate, 1966), thus, the pH of the reindeer rumen in summer, grazing a diet rich in seedheads, is within this range. The rumen pH in winter was high and may be caused by reduced volatile fatty acid production in winter. The winter volatile fatty acid concentration of 98.7 mM was surprisingly high considering the high pH and paucity of food available; it was comparable with that found in both sheep and cattle fed good pasture, and better than found in domestic ruminants fed high roughage diets where the volatile fatty acid concentrations may fall to as low as 55 mM (Hungate, 1966). The acetate to propionate ratio, higher in winter than in summer, might reflect the increased fibre content of the diet in winter compared with that in summer.

In the caecum the pH was above 7.0 in winter, suggesting that little acid production occurred in this organ in that season. A drop in caecal pH to 6.81 in summer, when food availability was high indicated that more fermentable material was reaching the caecum compared to that in the winter. The caecal pH in the Svalbard reindeer was thus similar to that of domestic ruminants, which is close to neutrality, ranging from 6.6 to 7.8 in sheep fed lucerne, and from 5.7 to 7.2 in sheep fed grain diets (Hungate, 1966).

Rumen digesta and epithelial populations

Electron microscopic examination of digesta fragments (K-J. Cheng *et al*, unpublished results) undergoing digestion in the rumen revealed that the major cellulolytic bacteria adherent to plant fragments were *Fibrobacter succinogenes* and *Ruminococus albus,* identified by their characteristic glycocalyces. Some adherent *Butyrivibrio fibrisolvens* cells were observed, and these may be representative of cellulolytic strains. These cells were relatively few, particularly in relation to the high proportion of cellulolytic butyrivibrios cultured from the rumen liquor.

Direct examination by SEM of sites on the rumen walls of the summer animals showed that only about 30% of their epithelial surfaces were covered by adherent bacteria, compared to 75% in well-fed cattle (K-J Cheng, personal communications). Many epithelial cells were partially sloughed. The adherent bacterial populations consisted largely of curved rod-shaped cells, and cocci which resembled *Ruminococcus* spp. by their possession of a condensed glycocalyx on the cell surface. Other small cocci (<0.3 μm) were observed amongst the larger bacteria (<8 μm) in the adherent populations. In contrast, less than 10% of the epithelial surfaces were covered by adherent bacteria in samples of rumen epithelium taken from animals shot in April. This value is low and corresponds to that found in starved cattle (K-J Cheng, personal communications). No individual epithelial cells were extensively colonized, and fewer cells were in the process of sloughing than observed on the rumen epithelium from summer- shot animals. Colonized regions were principally occupied by cocci possessing less glycocalyx than observed in summer- harvested epithelium, and the majority of cells were smaller in size (<0.3 μm). Bacteria of this type were not, however, identified amongst strains isolated during the viable culturing techniques employed to characterize the bacterial population of the rumen liquor. No comparative data is available for other reindeer subspecies.

While the removal of rumen contents, the washing of the rumen wall and complete starvation of domestic cattle, reduced their rumen wall-associated bacterial populations to <3% of their original values (K-J Cheng, personal communication), the natural seasonal changes in food quality and food intake of Svalbard reindeer reduced both the number and cell size of the rumen wall-associated bacterial population from summer to winter and eliminated the glycogen-rich bacterial population associated with celulose fibres undergoing bacterial digestion in winter. Starvation-induced reductions have been documented in rodents and in marine verebrates and invertebrates.

However, the Svalbard reindeer retain residual bacterial populations on their rumen surfaces, aided perhaps by reductions in the rates of epithelial cell sloughing. Cellulosic material in the rumen contents is effectively colonized and digested by adherent bacterial consortia of which cellulolytic *B. fibrisolvens* do not appear to be major members, despite their occurrence at high populations densities in the rumen liquor.

Protozoal and fungal populations of the rumen

Microscopic examination of the rumen contents of the Svalbard reindeer revealed that as in domestic ruminants, bacteria, protozoa and anaerobic fungi were present. Direct microscopic counts of protozoa in diluted rumen fluid stained with iodine (Coleman, 1987) showed that protozoal population varied from 10^5 in summer to 10^4 in winter, and that it consisted of only entodiniomorphid ciliates. No holotrich ciliates were observed. The major species of entodiniomorphs identified were *Entodinium simplex*, *E. triacum triacum*, *E. longinucleatum*, *Polyplastron multivesiculatum*, *Eremoplastron bovis* and *Eudiplodinium maggii*. The population density of the ciliates in summer was similar to that found in domestic ruminants fed a good quality diet (Hungate, 1966) falling to about 10% of the summer value in winter, The species of protozoa detected are also found in domestic ruminants althoug *E. triacum triacum* is rare and has not been recorded previously from reindeer. There is little evidence to suggest that the *Entodinium* spp. are important in fibre digestion in ruminants utilizing principally starches and bacteria as carbon source (Williams & Coleman, 1988), but *E. maggii, Polyplastron multivesiculatum* and *Eremoplastron bovis* are all known to ingest plant particles, and contain cellulase (Coleman, 1985). Among the other subspecies of the reindeer/caribou complex, *E, maggii* has only been found in reindeer in Russia and *P. multivesiculatum* in Russia and Alaska (Dehority, 1986).

Holotrich ciliates, whilst common in domestic sheep and cattle, have been found in reindeer in Russia, Finland and Alaska, and in Alaskan caribou but not in Canadian or wild Alaskan reindeer (Dehority, 1986, Westerling 1970). Thus, their absence from the Svalbard reindeer is not exceptional and, since they metabolize only soluble carbohydrates and starch (Williams & Coleman, 1988), play little direct role in fibre digestion. There absence may reflect the repeated starvation cycles to which the animals are exposed.

Anaerobic fungi are now known to be common inhabitants of the rumen and alimentary tracts of large herbivores (Orpin & Joblin, 1988). Several different species and unnamed morphological types are known to exist, but only one type was found in the rumen of the Svalbard reindeer. This was a monocentric species with polyflagellated zoospores, endogenous development and a branching rhizoidal system characteristic of *Neocallimastix* spp. The population density of rumen fungi as determined by enumeration of thallus-forming units (Joblin, 1981) was in the range of 10^3-10^4 in summer and 10^2-10^3 in winter. Using the same methods the population density of fungal thallus forming units in forage- fed cattle and sheep is 10^3-10^5 (Orpin & Joblin, 1988) depending on the diet; thus, the winter population density is low compared with cattle and sheep.

Table 2. Culturable bacteria from the rumen liquor of Svalbard reindeer (Orpin *et al* 1985) and from the caecum (Mathiesen *et al* 1986). Results are the means from six animals in each season.

Rumen	Summer	Winter
Total viable bacteria	$2.1 \pm 1.3 \times 10^{10}$	$3.6 \pm 2.8 \times 10^{9}$
Lactate utilizers	$2.6 \pm 3.0 \times 10^{9}$	$3.9 \pm 1.9 \times 10^{7}$
Spirochetes	$1.9 \pm 2.6 \times 10^{8}$	$2.5 \pm 3.0 \times 10^{7}$
Cellulolytic species	$3.0 \pm 5.4 \times 10^{9}$	$1.3 \pm 8.7 \times 10^{9}$
Methanogenic species	10^{4}	10^{7}

Caecum	Summer	Winter
Total viable bacteria	$8.9 \pm 5.3 \times 10^{8}$	$1.5 \pm 0.7 \times 10^{8}$
Lactate utilizers	ND	$1.1 \pm 0.3 \times 10^{6}$
Cellulolytic species	$8.7 \pm 3.2 \times 10^{-7}$	$9.9 \pm 3.8 \times 10^{7}$

ND = not determined

Ciliated protozoa were not observed in the caecum of these reindeer, and attempts to isolate anaerobic fungi from caecal contents were not made. Flagellated protozoa, however, occurred at 10^{2}-10^{3} cells ml^{-1} in the caecum and 10^{3}-10^{4} cells ml^{-1} in the rumen. This is similar to levels found in domestic ruminants (Hungate, 1966).

Bacterial populations of the rumen and caecum

All of the recognised species of rumen large bacteria, i.e. *Oscillospira guilliermondii*, *Magnoovum eadii* (Orpin, 1976), Quin's Oval, and large strains of *Selenomonas* sp. were present in the rumen during both seasons (Table 2). The population density in winter showed a greater decrease when compared with the summer value than did the small bacteria., with Quin's Oval and large selenomonads showing a greater decrease in population density than the other species. An unidentified large bacterium (classified as 'other large bacteria' in Table 1) similar in size to Quin's Oval, but differing in its motility pattern was observed in both seasons. The rumen large bacteria are known to ferment only soluble carbohydrates (Orpin, 1972, 1973) and their lower population density in the winter is most likely due to a reduction in dietary soluble carbohydrates and starch in the diet in winter compared with summer.

Conventional normal bacterial populations

The population density of the conventional bacteria of the rumen decreased in winter to about 17% of the summer population density (Table 3) probably reflecting the reduced availability and quality of diet in winter. A similar decrease in the population density of caecal bacteria was recorded in winter compared with the summer values.

Table 4 presents the species distribution of bacteria other than large bacteria, present in rumen and caecum fluid of the Svalbard reindeer in both summer and winter; their main fermentation niches are presented in Table 5. Population densities in general showed a large decrease in winter compared with the summer values, with most species declining to 10-50% of the summer values. Exceptionally, increases in population density of individual species occurred in winter, for example, *Fibrobacter succinogenes* in the rumen showed a 107% increase and *Lactobacillus* sp. in the caecum showed a 143% increase compared with summer values. It is difficult to compare the species distribution

Table 3. Culturable ruminal and ceacal bacterial populations expressed as a percentage of total culturable bacteria in winter and summer.

	Rumen			Caecum		
	summer	winter	winter as % of summer	summer	winter	winter as % of summer
B. fibrisolvens	22*	30	24	23	18	14
B. fibrisolvens[a]	10	18	33	7	1	3
Selenomonas ruminantium	12	14	21	10	8	14
Selenomonas ruminantium subsp. *lactilytica*	4	2	7	ND	ND	—
Lachnospira multiparus	2	ND	—	1	ND	—
Lactobacillus sp.	8	3	7	1	7	143
Megasphera elsdenii	1	1	29	2	3	22
Bacteroides ruminicola	4	10	49	10	26	45
Bacteroides amylophilus	10	3	6	7	5	13
Fibrobacter succinogenes	1	8	107	ND	ND	—
Ruminococcus albus	3	7	39	3	5	28
Ruminococcus flavefaciens	1	2	57	ND	ND	—
Ruminococcus bromii	ND	ND	—	3	1	7
Succinivibrio dextrinosolvens	3	1	5	2	ND	—
Streptococcus bovis	17	4	5	17	5	5
Streptococcus faecium	ND	ND	—	5	7	22
Eubacterium ruminantium	2	1	7	ND	ND	—

a = cellulolytic strains ND = not detected

Table 4. Ecological niches of the major bacterial species isolated from the rumen and caecum of Svalbard reindeer.

	Major substrates
Butyrivibrio fibrisolvens	Pectin, hemicelluloses, some strains cellulose and starch
Selenomonas ruminantium	Soluble carbohydrates, most strains utilize starch
S. ruminantium lactilytica	Soluble carbohydrates, lactate, glycerol, and many strains starch
Lachnospira multiparus	Soluble carbohydrates, pectin
Lactobacillus sp.	Soluble carbohydrates, some strains starch
Megasphera elsdenii	Starch, lactate, soluble carbohydrates
Bacteroides ruminicola	Hemicelluloses, xylan, pectin, some strains starch
Bactroides amylophilus	Starch, soluble carbohydrates
Fibrobacter succinogenes	Cellulose
Ruminoccus albus	Cellulose, xylan
R. flavefaciens	Cellulose, xylan
R.bromii	Starch, amylopectin
Streptococcus bovis	Starch, amylopectin, soluble carbohydrates
Succinivibrio dextrinosolvens	Pectin, soluble carbohydrates
Eubacterium ruminantium	Soluble carbohydrates, xylan

Table 5. Population densities of some cellulolytic bacteria in the rumen of Svalbard reindeer in September (summer) and April (winter).

Bacteria	Population densities[a]	
	in September	April
Ruminococcus albus	3.0 ± 1.1	6.7 ± 3.3
Ruminococcus flavefaciens	0.7 ± 0.5	2.2 ± 1.0
Fibrobacter succinogenes	1.3 ± 1.5	8.0 ± 5.2
Butyrivibrio fibrisolvens	9.5 ± 7.1	18.2 ± 7.7
Total viable cellulolytic species as % of total visible population	14.6 ± 5.4	35.0 ± 8.7
Cellulolytic *B. fibriosolvens* as % of total *B. fibrisolvens*	44.6	60.1

[a] values are expressed as % viable bacterial populations

found with that occurring in other animals since we know of no comparable detailed work giving full quantitative data.

The viable bacterial population of the rumen in summer was dominated by *Butyrivibrio fibrisolvens* and *Streptococcus bovis*, together representing 39% of the total isolates. In winter, ruminal *S. bovis* declined considerably, but *B. fibrisolvens* increased from 22% to 30% of the population. Amongst the other species, an increase in the differential population of the celluloytic species was recorded in winter, as was the case with *Bacteriodes ruminicola*, a hemicellulose digester. Similar seasonal fluctuations were also found amongst the caecal bacterial population, which reflected the rumen population in species composition with the exception that more *Streptococcus* spp., including *S.faecium* and *S.faecalis* were present, and *Ruminococcus bromii*, a starch digester, which was not identified amongst the ruminal isolates (Table 4).

Methanogenic bacteria in rumen contents were estimated to be present at 10^4 cells ml^{-1} in the summer and 10^7 cells ml^{-1}in the winter; in the caecum their population densities during the same seasons were 10^7 and 10^5 cells ml^{-1}respectively. These levels are similar to those found in domestic ruminants with the exception of the summer value which is very low and may have been caused by cultivation problems.

When the bacteria isolated from the viable count medium were individually assessed for their ability to ferment the major plant components in the diet, a large proportion were found to be fibrolytic, able to use cellulose, xylan or both as carbon sources. In the rumen, 31% and 74% of isolates were fibre fermenters in summer and winter respectively, and in the caecum the corresponding values were 36% and 48% respectively. Indeed, in the rumen, cellulolytic bacteria alone accounted for about 15% of the total population density in summer and 35% in winter, (Table 6). The dominant cellulolytic bacteria in the rumen were *B. fibrisolvens* with *Ruminococcus albus*, *R. flavefaciens* and *Fibrobacter succinogenes* present at lower population densites. The latter three species are commonly the most abundant cellulolytic bacteria in the rumens of domestic animals (Hungate, 1966), with cellulolytic *B. fibrisolvens* being rare, having been isolated routinely only from sheep in South Africa (van Gylswyk & Roche, 1970). Cellulolytic *B. fibrisolvens*, however, have been found abundantly in the rumen of African Antelopes (Margherita & Hungate, 1963) and was found by Dehority (1986) in lucerne-fed

Table 6. Distribution of cellulase (CMCase) activity in cultures of *Butyrivibrio* A46

Carbon source	Glucose		Cellobiose		Cellulose[a]	
Age of culture (h)			Activity against CMC[b]			
	cells	supt.	cells	supt.	cells	supt.
6	—	1.9	0.6	5.1	4.8	1.2
16	0.2	6.5	0.5	11.8	11.7	2.4
64	0.4	9.7	0.4	8.7	12.3	14.1
88	0.3	9.2	0.4	13.2	9.1	18.6

[a] acid-swollen Sigmacell

[b] units mg cell protein^{-1}or ml supt^{-1} (1 unit = 1 μ mole glucose equivalent h^{-1})

reindeer in Alaska. In the caecum, the only cellulolytic species identified other than *B. fibrisolvens* was *Ruminococcus albus*, representing 3 and 5% of the total population in summer and winter respectively compared with cellulolytic *B. fibrisolvens* which comprised 7 and 3% of the summer and winter populations respectively.

Degradation of plant cell walls is a function of both celluloytic and hemicellulolytic organisms. All of the celluloytic species except *F. succinogenes* also degraded xylan, a major hemicellulose of grasses, but in addition a number of xylan- utilizing strains of *Bacteriodes ruminicola* and *Eubacterium ruminantium* were found.

Starch digestion

There was little difference in the proportion of the bacterial population able to utilize starch in the two seasons, but the population density of starch digesting bacteria in winter was only 16.6% of the summer value. The dominant starch-digesting bacterium in summer was *Streptococus bovis*, whilst in winter it was *Butyrivibrio fibrisolvens*. In winter the *S. bovis* population decreased to only 5% of its summer value, with starch-utilizing *Bacteroides ruminicola* increasing from 4% in summer to 10% in winter. In winter only 85% of *B. ruminicola* strains utilized starch, compared with 100% in summer. Similar decreases in starch-digesting ability of *Selenomonas ruminantium*, *Sr lactilytica* and *B. fibrisolvens* was evident. Of the total viable population, 68% could utilize strach in the summer, compared to 64% in winter. Many of the *B. fibrisolvens* could also utilize xylan, cellulose or both as substrates (Orpin *et al*, 1985). In the ceacum, the proportion of the bacterial starch digesters was *Butyrivibrio fibrisolvens* in summer, and *Bacteroides ruminicola* in winter. Other starch utilizers present were *Streptococcus bovis*, *Selenomonas ruminatium*, *Bacteroides amylophilus* and *Ruminococcus bromii*, each showing a decrease in numbers in winter compared with the summer populations (Mathiesen *et al*, 1987).

Proteolytic and ureolytic bacteria

Isolates with proteolytic activity or ureolytic activity were common in both seasons. In summer, 51% of the population and in winter, 28% showed proteolytic activity. All of the *Streptococus bovis* isolates were proteolytic with azocasein as substrate, with over 80% of these able to use plant fraction 1 protein as sole nitrogen source. Other species found to be commonly proteolytic were *Bacteroides amylophilus* (100% in sumer, 67% in winter) all of which could also use fraction 1 protein as sole nitrogen source, and hydrolysed up to 1 mg/ml of protein in laboratory culture in 24 h. Of the *Selenomonas ruminantium* isolates, 80% of the summer and 43% of the winter isolates were proteolytic when tested with azocasein, but none hydrolysed plant fraction 1 protein *in vitro*, which suggests they many not be important in proteolysis in the rumen.

The summer population density of proteolytic bacteria was higher than previously recorded for any ruminant. Fulghum & Moore (1963) recorded up to 46% of proteolytic bacteria in cattle, but the proteolytic population of domestic ruminants is normally smaller (Wallace & Cotta, 1988). The lower proteolytic population in winter compared to summer coincides with a lower protein content in the winter diet.

Ureolytic bacteria were also common in the rumen of Svalbard reindeer, with about 40% of strains in winter and 54% in summer possessing weak urease activity. All the *Bacteroides ruminicola* and *Succinivibrio dextrinosolvens* isolated in both seasons were ureolytic together with large numbers of *Selenomonas ruminantium* and *Butyrivibrio fibrisolvens*. However, the urease activity of all these isolates was low compared with *Streptococcus faecium* (Cook, 1976) and other rumen epithelium-associated bacteria (Cheng *et al*, 1979).

Nitrogen recycling via urea could be of significance in these animals in maintaining their nitrogen balance in winter where food quality and availability is low. The large ureolytic bacterial population supports this suggestion, and agrees with the finding of large weakly ureolytic bacteria populations in cattle fed a diet containing urea (Jones *et al*, 1964).

Ammonia can be used by many rumen bacteria as a source of nitrogen. Some species require peptides or amino acids for growth (Wallace & Cotta, 1988). During periods of starvation, ammonia produced by hydrolysis of urea (by urease), which enters the rumen via the saliva and crosses the rumen epithelium from the blood, would satisfy the nitrogen requirements of the ammonia-utilizing species. A large proteolytic population of bacteria in the rumen may be necessary to supply peptides by hydrolysis of proteins, from the diet, dead rumen microbes, or sloughed eptihelial cells during the winter. Protein hydrolysis would also result in the generation of branched-chain amino acids which would aid in the maintenance of the bacterial population under conditions of semi-starvation (Bryant, 1974).

Studies on the cellulolytic Butyrivibrio

We have examined the cellulase activity of *Butyrivibrio fibrisolvens* A46, isolated from one of the Svalbard reindeer shot in September, and have cloned a fragment of DNA coding for endo-ß-1,4-ß-glucanase (carboxymethyl cellulase) activity in *Escherichia coli* (Hazlewood, Clarke, Davidson, Romeniec & Orpin, *et al*, 1990).

Table 7. Activity of *Butyrivibrio fibrisolvens* A46 cellulase on polysaccharides

Polysaccharide	Activity[a]
Carboxymethyl cellulose	0.54
Lichenan	0.00
Laminarin	0.31
Avicel[b]	0.00
ß-1,3-glucan	2.17
Arabinogalactan	0.96
Galactomannan	0.24

[a] Activity expressed as μ mols of reducing sugar mg protein^{-1} h^{-1}.

[b] Avicel is a highly crystalline cellulose

Cellulase activity was produced constitutively by A46 when grown on glucose or cellobiose, but at lower concentrations than when grown on cellulose. The activity was present in both the cells and the cell-free supernatant, with the proportion of cell-bound enzyme greatest when grown on cellulose (Table 7). Since cellulase was produced when A46 was grown on soluble carbohydrates, it is likely that it is produced continuosly in the rumen and not subject to major catabolite repression as occurs with other cellulolytic rumen bacteria (Chesson & Forsberg, 1988; Taylor *et al*, 1987). Cellulase (carboxymethyl cellulase; CMCase) was purified from *Butyrivibrio* A46 cells to a specific activity of 700 U mg protein^{-1} or from cell-free culture supernatant that had an apparent molecular mass of 57 kDa. Purified enzyme was most active against CMC and aryl-cellobiosides but also hydrolysed acid-swollen Sigmacell to a lesser extent. Activity was optimal at pH 5.6 and was thermolabile, being rapidly inactivated at 55°C. Hydrolysis of CMC resulted in the production of reducing sugar and a rapid fall in viscosity, characteristics of endo-ß-1,4-glucanase activity. A gene coding for CMCase activity was contained on a 2.4 kbp *EcoRI* fragment cloned from *Butyrivibrio* A46 in lambda phage gt11, and was subcloned in *Escherichia coli* using the plasmid vector pUC12. CMCase encoded by the cloned fragment of DNA was purified to a specific activity of 142 Umg protein^{-1}. In general, the properties of the cloned CMCase were similar to those described for the enzyme purified from cultures of *Butyrivibrio* A46.

The cloned enzyme showed activity against laminarin (a ß-1.6-glucan), ß-1,3-glucan, arabinogalactan and galactomannan (S.P. Mann, personal communications; Table 8) as well as carboxymethyl cellulose, but not avicel, a highly crystalline form of cellulose. Thus, the probability exists that the enzyme produced *in vivo* is a multi-functional enzyme with cellulase activity, produced with limited regulation; its activity at any particular time being controlled by substrate availability in its immediate environment. Such an enzyme, would be of great benefit in the rumen of an animal that needed to digest food rapidly and which fed on diets ranging greatly in quality, such as the Svalbard reindeer.

As yet there is not proof that the cellulolytic *Butyrivibrio fibrisolvens* adheres to the plant tissue like the other major rumen cellulolytic bacteria, *Ruminococcus albus, R. flavefaciens* and *F.succinogenes.* In these species adherence is a prerequisite to cellulolysis, and the production of cellulase tightly regulated. In the *B. fibrisolvens*, the continuous production of cellulase may stimulate cellulolysis by the other cellulolytic species by removal of oligosaccharides from the immediate vicinity of the digesta fragments being degraded. This would minimise the chance of the oligosaccharides being hydrolysed to glucose and cellobiose, catabolite repressors of cellulase, and thus help maintain cellulolysis by the adherent cellulolytic population. However, adherence by cellulolytic *B. fibrisolvens* has been demonstrated *in vitro* (Cheng, Mathiesen & Orpin, unpublished).

In vitro digestibility experiments

In vitro digestibility trials of food plants, including mosses, were conducted using plants, collected from the range in both seasons. The methods used were based on those of Tilley & Terry (1963) scaled to 100 mg of plant material, and using centrifugation to separate residual plant tissues from bacteria after incubation. Since mosses form a large part of the diet of these reindeer in winter, and large fragments of moss were observed in the caecal contents (Mathiesen *et al*, 1987), particular attention was paid to the digestion of mosses in the caecum. Comparable data for the digestibility of these species in domestic ruminants are not available, but in the Svalbard reindeer rumen moss digestion was in the range of 11-36%, and caecal moss digestion 11-27%. The *in vitro*

DMD of standard samples of Timothy *(Phleum pratense)* of high (74.7% *in vivo)* DMD and low (57.6% DMD *in vivo* DMD) in sheep, gave similar DMD values *in vitro* using reindeer rumen fluid in summer, but in winter the DMD of the poorer quality Timothy grass in caecum fluid was marginally greater than in sheep.

Thomas & Kroeger (1980) investigated the *in vitro* ruminal range plant in Peary caribou *(Rangifer tarandus pearyi)*. Whilst the apparent digestibility of vascular plants in summer was in the range of 50-80%, that of mosses was 11-35%, in close agreement with the results found for the Svalbard reindeer. However, the Svalbard reindeer rumen fluid digested mosses condsiderably more extensively in winter (16-31% over 48 h of incubation) than fluid from Peary caribou (3-11% over 60 h).

These results suggest that moss digestion in both the rumen and the ceacum may be of value in the nutrition of the animal, especially with *Callergon sarmentosum,* but its quantitative significance is still not known.

In vitro digestibility values for mosses collected in the summer and incubated with summer caecum fluid were 11-28%, suggesting that some moss digestion in the caecum would occur if mosses reach the caecum in that season. In winter, when the diet is relatively rich in moss, ceacal digestiblity was lower, in the range of approximatley 14% in the two species tested.

In winter the rumen and caecal contents smelt strongly of earth, and sand grains were found in the rumen. The occurrence in one animal of 10^8 cells ml^{-1} of *Serratia marcescens,* a soil bacterium, is indicative of soil ingestion, which could happen when the animal uproots the whole plant including some soil, when eating.

Conclusion

The rumen bacterial population of the Svalbard reindeer is very specialised in relation to fibre digestion and nitrogen recycling with large numbers of fibrolytic, proteolytic, and ureolytic strains present in both summer and winter. The high population density of species such as *Butyriribrio fibrisolvens* that are capable of fibre and starch digestion enables the animals to make best use of the very variable diet that the animals eat. The ability of these organisms to ferment starch in the summer as well as fibre may allow the maintenance of high population densities of cellulolytic bacteria in the presence of the concentrated diet. The high ruminal bacterial population density in the winter despite apparent starvation of the animals, may in part be supported by urea recycling ensuring a sufficient nitrogen supply to enable the bacterial population to maintain high activity despite the low protein diet.

The low population density of methanogenic bacteria in the summer compared with winter would ensure that additional energy is conserved from the diet in summer. In addition, the high concentrate diet would produce additional propionate in summer and lead to increased gluconeogenesis in the animal.

Winter survival of the Svalbard reindeer is aided by some moss digestion in the rumen and possibly the caecum.

Our results indicate that the caecal bacteria may contribute substantially to forage utilization in the Svalbard reindeer, but their precise role cannot be determined until particle flow rate and compositon measurements have been made.

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Voluntary intake of feed concentrates and changes in the body weight of reindeer in different seasons

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Abstract: Voluntary intake of feed concentrates of reindeer was studied during 1987-88. Six hinds and their calves were fed with feed concentrates (20.7 % CP in DM) during the summer and fall until the end of the rutting period. After that the hinds and calves were separated and two hinds and calves were added to the groups. The reindeer were fed with less nutritious feed concentrates (10.5 % CP in DM) during the winter until next calving period. The reindeer were fed twice daily up to appetite. The voluntary intake of feed concentrates varied between 1.8 kg and 5.4 kg/hind and its calf/day and increased from July until September. The voluntary intake of feed was 3.2 kg/hind/day and 2.6 kg/calf/day in November and decreased during the winter to 2.0 kg/hind/day and 2.1 kg/calf/day in March. After calving the body weight of the hinds (mean 64.2 kg) increased 14.8 kg until end of November. The growth rate of the calves was rapid during the summer and fall and the body weight was on average 52.7 kg at the end of October. From November to March the calves gained still body weight on average 6.2 kg.

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Ice and mineral licks used by caribou in winter

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Abstract: In winter, barren-ground caribou obtain minerals from ice and soil licks. Between December and April we have seen caribou cratering on the surface of frozen lakes and licking the ice. Ice samples from eight licks on four lakes contained concentrations of calcium, magnesium, sodium, potassium, phosphorus, chloride and sulphate many times higher than in the surrounding unlicked ice or than would be expected in lake water. Soil licks being used in March and June had high concentrations of calcium, magnesium, sodium phosphorus and potassium. In winter caribou may be seeking supplements of all of the major mineral elements (calcium, magnesium, sodium and potassium) at ice and soil licks because lichens, their staple winter diet, are low in minerals and may also reduce the absorption of some minerals.

Key words: barren-ground caribou, Northwest Territories

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Introduction

The use of mineral licks by wild ungulates is generally confined to summer (Cowan and Brink 1949, Skoog 1968, Calef and Lortie 1975, Jones and Hanson 1985). In winter (December-April) we have observed barren-ground caribou *(Rangifer tarandus groenlandicus)* cratering on frozen lakes and licking the ice. This paper describes the chemical composition of lake ice and soil that caribou used as mineral licks in winter.

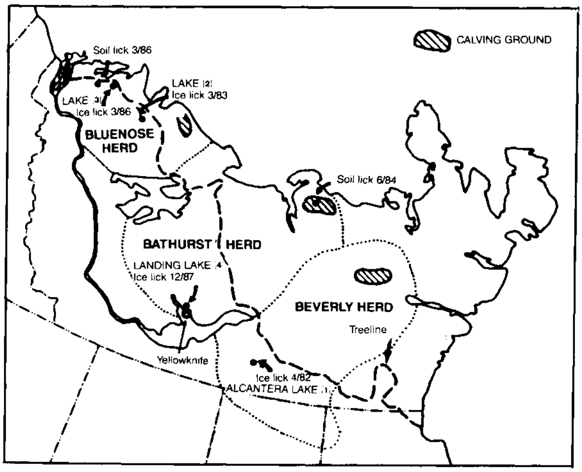

Figure 1. The location of ice and soil mineral licks sampled on barren ground caribou winter range.

Table 1. Mineral concentrations in ice licks, unlicked ice, caribou urine and representative water samples.

Sample type	Ice licks							Unlicked ice[1]		Caribou urine	Representative water[2]		
Sample number	1[3]	2	3	4	5	6	7+8[4]	9	10		W1	W2[5]	W3[6]
Lake number	1	2	2	3	4	4	4	4	4	4			
Measurement													
Sampling date	4/82	3/83	3/83	3/86	————12/87————						7/82	5	6
pH		7.7	8.4	8.0	9.6	9.7	9.8	6.6	6.3	5.0		7.5	6.6
Conductivity#		990	1 400	622	600	2 000	2 000	4.5	27	2 100		51	35
Turbidity@		1.4	0.5									2.3	
Colour		15	20									5	
Suspended solids		< 5	< 5		24	104	64	6.8	8.0	87		1.7	3
Disolved solids*		610	860	370	610	2 500	2 400	44	25	11 000		23.5	
Calcium*	62	34	34	17	20	28	33	4.5	2.7	180	3.8	4.6	4.4
Magnesium*	15	40	62	26	46	200	200	1.6	0.8	29	0.9	1.7	1.1
Hardness*	220	251	340		240	880	890	18	9.9	570	13	18.6	14.5
Alkalinity*		110	120		148	438	462	13	7.1	3.2		15.1	11.7
Sodium*	18	96	158	84	33	144	145	1.5	1.3	4.6	1.5	1.7	1.2
Potassium*	12	5.6	8.8	3.6	18	81	75	0.9	1.0	79	0.7	0.9	0.7
Chloride*		170	260	60	49	207	200	1.5	1.3	48	1.3	1.6	1.2
Sulphate*		110	170	170	92	400	350	4.2	2.9	105	3.0	3.1	3.0
Ammonia Nitrogen*		.08	.20		0.17	0.28	0.22	0.19	0.11	197		0	
Nitrate + Nitrite*		<.04	<.04									0.03	
Total Kjeldahl N*		1.4	1.7										
Phosphorus O-P*		<.05	<.05		0.063	0.25	0.19	.005	0.011	0.75		0.006	
Phosphorus Tot*		<.05	<.05		0.079	0.70	0.62	0.022	0.029	2.7		0.004	

μmho/cm @ Jackson turbidity units * mg/L

[1] Samples 9 and 10 were taken approximately 100 m from samples 5 and 6 respectively

[2] W1 is Porter Lake (60° 02'N × 109° 13'W); W2 is Yellowknife River (62° 30'N × 114° 18'W); W3 is Thoa River (60° 31'N × 109° 47'W)

[3] Sample volume too small to analyze for nitrogen and phosphorus.

[4] Samples 7 and 8 were combined to provide sufficient volume for analysis.

[5] Arithmetic mean of 6 samples taken between January and October 1987.

[6] Arithmetic mean of 7 samples taken between February 1986 and November 1987.

Methods

We collected ice samples from the bottom of eight craters on four different lakes where we saw caribou licking the ice (Figure 1). For comparison, samples were collected from below undisturbed snow about 100 m from two ice licks. Ice samples were melted and analyzed by the Water Resources Laboratory, Department of Indian Affairs and Northern Development, Yellowknife.

We collected two lumps of caribou urine frozen in the snow from Landing Lake near sample six to determine if caribou urine was a component of the ice licks. The urine samples were

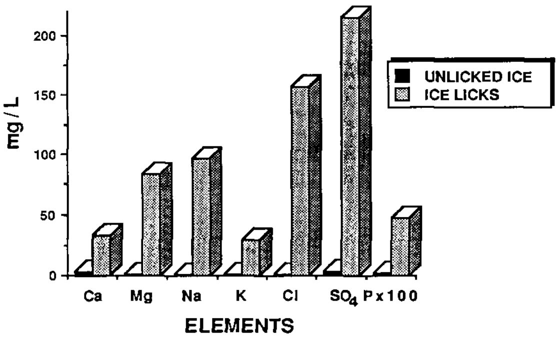

Figure 2. A comparision of the mineral composition of unlicked ice with ice at ice licks.

combined to obtain sufficient volume for analysis.

We collected soil samples from three locations (Figure 1). Four soil samples were taken from one of the five known mineral licks on the Bathurst herd's calving ground. For comparison, a single soil sample was collected at our camp 25 km to the east. We collected one soil sample near the Kugalik River on the Bluenose caribou herd's winter range where caribou were seen licking the exposed ground. Soil analysis was carried out by the Manitoba Provincial Soil Testing Laboratory in Winnipeg.

Results and discussion

Caribou demonstrated strong attraction to the lick sites by permitting us to approach within 30-100 m before moving away, by returning to the lick immediately after we left and by aggressively displacing other caribou from the lick craters.

Ice that was being licked at the bottom of craters was either clear or was tinged with yellow, orange or brown in contrast to lake ice which is normally clear. The discoloured ice on Landing Lake (samples 5-8) formed a relatively soft 1 to 5 cm thick layer on the surface of clear ice.

Ice from licks contained concentrations of calcium, sodium, phosphorus, chloride and sulphate many times higher than in the surrounding unlicked ice or than would be expected in lake water (Table 1, Figure 2).

We do not know how those elements became incorporated into the ice surface but the low concentrations of ammonia nitrogen in the lick indicated that it was not contaminated by caribou urine (Table 1 and Fraser et al. 1980). Water had not flowed onto the ice from streams or from the adjacent land. There were no streams nearby and the discoloured ice did not extend from the lick to shore. Possibly gaseous upwelling from anaerobic decomposition of vegetation on the lake bottom had brought organic material to the water-ice interface. This may later have risen to the ice surface as overflow (water that seeped to the surface through cracks in the ice). Because ice licks were about 100m from shore and the nearest emergent vegetation, we deduced that the water was probably too deep to freeze all the way to the bottom, so that decomposition could proceed throughout the winter. We have no data with which to judge the plausibility of this suggestion.

The soil lick being used in March 1986 had higher concentrations of calcium, magnesium, sodium, phosphorus and potassium than licks used in the summer (Table 2). Minerals from the calving ground lick were probably sought for the same reasons as in March because caribou were still on their winter diet during calving. Although soil at the calving ground lick had lower mineral concentrations than at the Kugalik River, concentrations were generally 2 to 3 meters higher than in the unlicked soil sample (Table 2).

Ice licks are apparently also used by caribou in other areas. Edwards and Ritcey (1960) in British Columbia and Skoog (1968) in Alaska assumed caribou were eating snow from the ice-covered surface of lakes but the behaviour they describe was similar to our observations at ice licks.

In winter caribou may be seeking supplements of all of the major mineral elements (calcium, magnesium, sodium and potassium) at ice and soil licks because lichens, their staple

Table 2. Mineral composition of the soil lick being used in March 1986 near the Kugalik River and on the Bathurst herd's calving ground compared to unlicked soil and to summer caribou licks.

Measurement	Kugalik River lick	Bathurst Herd calving ground lick[1]	Bathurst Herd calving ground control	Summer licks
Sampling date	3/86	19/6/84	19/6/84	
Calcium (me/100 g)	61	4.9	2.5	20.4*
Magnesium (me/100 g)	35	3.8	1.4	7.2*
Sodium (me/100 g)	90	0.7	0.3	1.3*
Potassium (me 100 g)	1.8	0.89	0.27	0.38*
Phosphorus (ppm)	43.6	24.8	4.0	1.0#
Nitrate (ppm)	19.2	7.4	6.0	226#
Copper (ppm)	0.5	4.3	1.7	
Iron (ppm)	21	464	385	
Manganese (ppm)	7.0	3.3	1.0	
Zinc (ppm)	0.86	0.67	0.24	
Sulphate (ppm)		20	2.4	880#

[1] Geometric mean of 4 samples from one lick

* Geometric mean of 1090 samples from 5 licks (Jones and Hanson 1985)

\# Data from Calef and Lortie (1975); sample number 5 at one lick.

winter diet (Thomas and Hervieux 1986) are low in minerals and may also lower the absorption of some minerals (Staaland et al. 1986).

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Glucose and fatty acid oxidation in reindeer

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Abstract: Although winter energy expenditure (EE) in reindeer is lower than in summer and is thought to be highly regulated, there are no data on nutrient substrate oxidation. This study was conducted on adult reindeer given either a high quality pelleted ration (QT, 18% CP) or mixed lichens (ML, 3% CP) and the oxidation rate of fatty acid and glucose was determined using ^{14} C labeling (1-^{14}C stearic acid, U-^{14}C glucose). Stearic acid made up 21 to 31% of the total NEFA (0.07-0.18 mM/ml) and supplied 1 to 6% of the EE for both diets; 36 to 45% of stearate was oxidized. Glucose levels on the QT diet (5.96 mM/l) exceeds those for lichens (3.59 mM/l) and likewise glucose oxidation provided 6.0% QTX vs. 4.5% ML of EE. Total fatty acid contribution to EE was 25%, glucose 6 and rumen volatile fatty acid 60%.

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Environmental and General Physiology

Key note address:

Survival strategies in arctic ungulates

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Abstract: Arctic ungulates usually neither freeze nor starve to death despite the rigours of winter. Physiological adaptations enable them to survive and reproduce despite long periods of intense cold and potential undernutrition. Heat conservation is achieved by excellent insulation combined with nasal heat exchange. Seasonal variation in fasting metabolic rate has been reported in several temperate and sub-arctic species of ungulates and seems to occur in muskoxen. Surprisingly, there is no evidence for this in reindeer. Both reindeer and caribou normally maintain low levels of locomotor activity in winter. Light foot loads are important for reducing energy expenditure while walking over snow. The significance and control of selective cooling of the brain during hard exercise (e.g. escape from predators) is discussed. Like other cervids, reindeer and caribou display a pronounced seasonal cycle of appetite and growth which seems to have an intrinsic basis. This has two consequences. First, the animals evidently survive perfectly well despite enduring negative energy balance for long periods. Second, loss of weight in winter is not necessarily evidence of undernutrition. The main role of fat reserves, especially in males, may be to enhance reproductive success. The principal role of fat reserves in winter appears to be to provide a supplement to, rather than a substitute for, poor quality winter forage. Fat also provides an insurance against death during periods of acute starvation.

Key words: appetite, brain cooling, caribou, energetics, fat, growth, heat balance, metabolism, muskox, *Ovibos*, *Rangifer*, reindeer.

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Introduction

The arctic is a hostile place in winter, yet the cold, dark polar 'wastes' sustain life. The environment is truly marginal and for this reason it is tempting to conclude that endothermic animals which spend the winter there must endure a truly marginal existence. Paradoxically, however, most arctic animals usually neither freeze nor starve to death. They are evidently well adapted to the several challenges of the environment. This paper reviews some of the physiological adaptations which enable ungulates to survive and reproduce in the arctic.

Several species of monogastric mammals circumvent the problem of cold and the scarcity of food in winter by hibernating. These typically store large quantities of fat in summer and autumn and, by reducing their metabolic rate, they may literally 'live off' their fat for weeks or even months at a time during winter. But, as a result of their reduced metabolism, they become hypothermic with body temperature falling as low as 0-4°C in some cases (Hensel, Brück and Raths, 1973).

Reindeer and caribou, however, are ruminants. Unlike monogastric species they have to remain active to feed continuously throughout winter. Moreover, they are truly homeothermic, requiring maintenance of a constant internal body temperature which is considerably above environmental temperature. For these, like other true homeotherms, the problem of survival becomes one of keeping warm. To do this they need both to reduce heat dissipation and to ensure an adequate supply of fuel, in the from of metabolites from food, for heat production. Adaptations for survival can, therefore, be divided between those which help the animals to reduce their energy expenditure (and, hence, also to reduce their food requirements), which are the subject of this paper, and those which help them to make best use of what food they find (see Orpin, *et al.* 1985; Mathiesen, *et al.* 1987; Orpin and Mathiesen, 1990).

Reduction in energy losses

In reindeer and caribou, like other arctic homeotherms which maintain a high internal body temperature, the temperature difference between the body core and the environment may be as much as 100°C. Despite this they can maintain a very low lower critical temperature. Nilssen, Sundsfjord and Blix (1984a), for example, calculated that the lower critical temperature of Svalbard reindeer was approximately -40°C in winter (Fig. 1). Reindeer and caribou have two principal defenses against cold. First, they are very well insulated by fur and second, they restrict respiratory heat loss.

The insulative properties of fur depend on the inherent thermal conductivity of the individual hairs themselves and their collective ability to trap and hold a layer of air next to the skin. This is important because the conductivity of still air is less than half of that of most furs (Mount, 1979:92). Reindeer fur includes two types of fibers: long guard hairs and a fine underfur (Bohl and Nikolajewsky, 1931; Timisjärvi *et al.*, 1984). The insulative properites of the fur are enhanced both by the high density of fibres on the skin and by their special structure. Each guard hair is hollow, containing thousands of air-filled cavities separated by thin septa (Timisjärvi *et al.*, 1984).

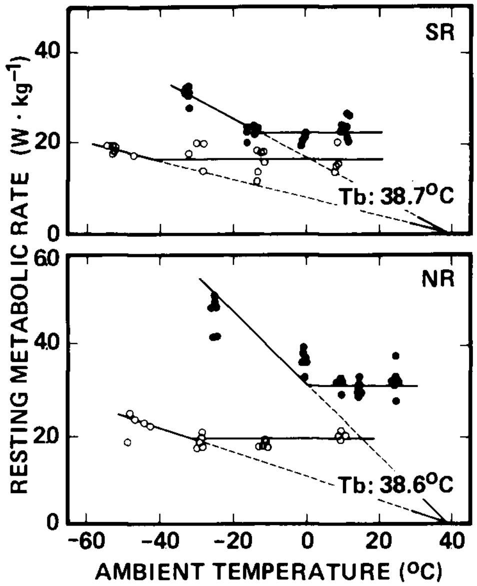

Fig. 1. Resting metabolic rate at different ambient temperatures during summer (●) and winter (o) in adult Svalbard (SR) and Norwegian (NR) reindeer fed *ad libitum*. Lines are fitted by eye to extrapolate through ambient temperature equal to deep body temperature (T_b). The animals' lower critical temperature in winter is approximately -40°C (SR) and -30°(NR). Note the pronounced reduction in the animals' resting metabolic rate in winter (from Nilssen, Sundsfjord and Blix, 1984a).

In addition to excellent insulation by fur, reindeer and caribou defend themselves against cold by restricting heat and water loss from the respiratory tract. Respiratory heat loss can potentially account for a large proportion of total heat loss (Folkow and Mercer, 1986). In humans exposed to low ambient temperature but

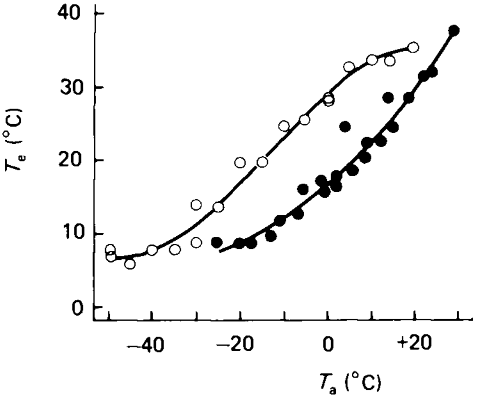

Fig. 2. Exhaled air temperature (T_e) in Norwegian reindeer over a range of ambient temperatures (T_a) in summer (●) and winter (o) (from Blix and Johnsen, 1983).

warmly dressed and at rest, the lowest mean expired air temperature measured is approximately 26°C (Webb, 1951) and the heat lost in exhaled air may account for more than 20% of metabolic heat production (see Blix and Johnsen, 1983). In resting reindeer exposed to cold, by contrast, expired air temperature may be as low as 6°C, which is approximately 33°C below core temperature (Fig. 2). Hence, respiratory heat loss in these animals is much reduced. In fact, about 70% of the heat and 80% of the water added to the inspired air in the nose and lungs is regained upon expiration (Blix and Johnsen, 1983).

Such heat and water conservation in the nose is based on counter-current heat exchange in the nasal cavity (Jackson and Schmidt-Nielsen, 1964; Schmidt-Nilsen, 1981). The respiratory chamber of the nasal cavities of reindeer are filled with an elaborate system of scrolled structures (*conchae*, Fig. 3) which are coated with a richly vascularised mucosal layer (Parsons, 1971). Cold air which the animals breathe in passes over the warm mucosa and, as a result, is heated to body temperature and saturated with water vapour before it reaches the lungs. The nasal mucosa is cooled as a result and, moreover, it stays cool while the air remains in the lungs. When the animals breathe out, the warm, humid air passes down a temperature gradient as it flows over the cold mucosa and is therefore both cooled and dried.

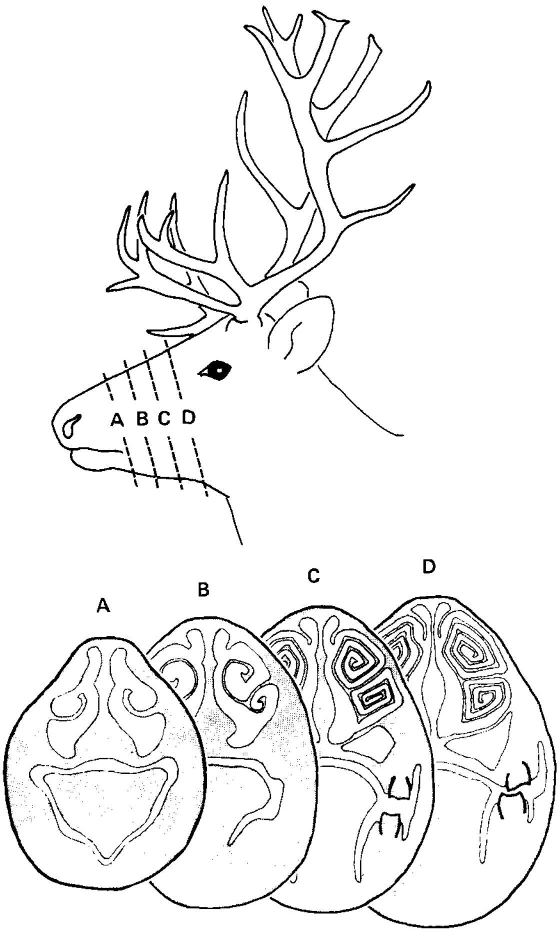

Fig. 3. Cross sections of the reindeer nose obtained at four different levels (A, B, C, and D). Sections were made at approximately 1 cm intervals and illustrate the elaborate organization of the maxilloturbinates which project into each nasal cavity from the lateral wall (from Johnsen, 1988).

The *conchae* of the nasal cavity both increase the surface area over which heat exchange can occur and divide the air flow into thin layers. Consequently, the distance between the centre of the air stream and the mucosal surface is reduced to a minimum. Both factors, large surface area and short distance between adjacent lamellae, promote rapid transfer of energy between the mucosal layer and the air stream. Nasal heat exchange is, nevertheless, not a passive process in reindeer. On the contrary, it is carefully regulated, enabling the animals to maintain thermal balance at widely varying ambient temperatures and work loads despite substantial seasonal changes in their fur insulation.

The first evidence for this is shown in Fig. 2. These data, from a study by Blix and Johnsen (1983), show that at any given ambient temperature (T_a) reindeers' expired air temperature is consistently lower in summer than in winter. The animals were evidently capable of adjusting the level of thermal exchange to conserve more heat at one and the same T_a in summer when they were relatively poorly insulated compared to in winter when their total body insulation was greatest. Johnsen, Blix *et al.* (1985) subsequently showed that nasal heat exchange is regulated by vasomotor adjustments in the nasal mucosa and that those changes are under central (hypothalamic) control (Mercer *et al.* 1985).

Reduction in energy expenditure

Metabolism

Good insulation and nasal heat exchange help reindeer and caribou to conserve energy by minimising dissipation of heat. Another potential way of reducing energy expenditure is to reduce the basal level of heat production itself. In winter, basal metabolism (BMR) accounts for between 50 and 70% of the normal daily energy expenditure of adult females (caribou: Boertje, 1985; Fancy, 1986; reindeer: Tyler, 1987a) and, consequently, even small reductions in metabolic rate would potentially contribute relatively large overall savings to the animals' energy budget.

Mammals' basal rate of metabolism is often assumed to be constant. This is not necessarily true although in many situations the approximation may be adequate. There are a variety of circumstances in which BMR may fall below the predicted value. In several species, for example, BMR fluctuates with a pronounced diurnal cycle (Aschoff and Pohl, 1971). It may also fall in early pregnancy (Prentice and Whitehead, 1987), with increasing age (Kleiber *et al.* 1956) and during starvation (Keys *et al.*, 1950; Grande *et al.* 1958; Kleiber, 1975: 247; Markussen and Øritsland, 1986; Nordøy and Blix, 1985). Reduction in BMR during starvation, however, is fundamentally different from the reductions which occur during early pregnancy or with increasing age. The metabolic response to starvation is driven by a change in the individual's nutritional status. Reduction of BMR during pregnancy or with increasing age, by contrast, appears to occur independent of any such change.

The basal metabolic rate of several temperate and sub-arctic species of ungulates appears to fluctuate in anticipation of predictable changes in the quality and abundance of their food. Seasonal variation in animals' minimum energy expenditure has been recorded in domestic sheep (Blaxter and Boyne, 1982) and white-tailed deer *Odocoileus virginianus* (Silver *et al.*, 1969). Argo and Smith (1983) found that the interpolated metabolizable energy requirement for maintenance in Soay rams fell 25% from 6.1 W/kg $M^{0.75}$ in summer to 4.6 W/kg $M^{0.75}$ in winter (M = total body weight). A similar cycle, perhaps even more marked, might certainly be expected in arctic species such as Svalbard reindeer owing to the extreme seasonality of the food supply at high latitudes.

Rather surprisingly, however, and despite an earlier suggestion based on changes in blood levels of thyroxine which themselves appeared to indicate that the minimum metabolic rate of Svalbard reindeer might fall in winter (Ringberg, 1979), no experimental evidence has been found for such a drop, at least in captive animals (Nilssen, Sundsfjord and Blix, 1984a). The resting metabolic rate of reindeer fed *ad libitum* shows a marked reduction from summer to winter (Fig. 1). This, however, is not in itself evidence of any seasonal change in the animals' minimum energy expenditure.

Reindeer, like many other species of ungulates (e.g. Kay, 1979), show pronounced seasonal changes in appetite (McEwan and Whitehead 1970; Fig. 4). Obviously, if an animal consumes more feed in summer than in winter, then its total heat production can be expected

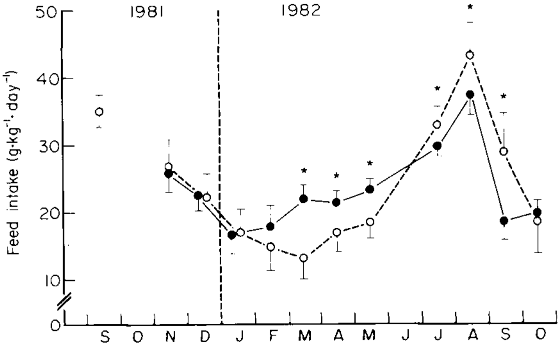

Fig. 4. Seasonal changes in voluntary food intake (g·kg body weight^{-1}day $^{-1}$) of captive Norwegian reindeer (●) and Svalbard reindeer (o) fed a concentrate ration *ad libitum*. The symbols represent mean values obtained during the middle ten days of each month and the bars represent standard deviation of the daily individual food intake. Asterisks denote significant differences (from Larsen, Nilsson and Blix, 1985).

to increase simply because there is a greater increment of heat associated with ingestion of the larger amount of feed. The significance of the seasonal changes in the metabolic rate of sheep and white-tailed deer is that they occurred independent of levels of food intake. These species, in other words, eat less in winter because their metabolic rate is reduced, not the other way around. This is the converse of the metabolic response to starvation (above): metabolism, in that case, falls as a consequence of reduced food intake. Nilssen, Sundsfjord and Blix (1984a) demonstrated a close relationship between metabolic rate and food intake in both Svalbard and Norwegian reindeer (Fig. 5).

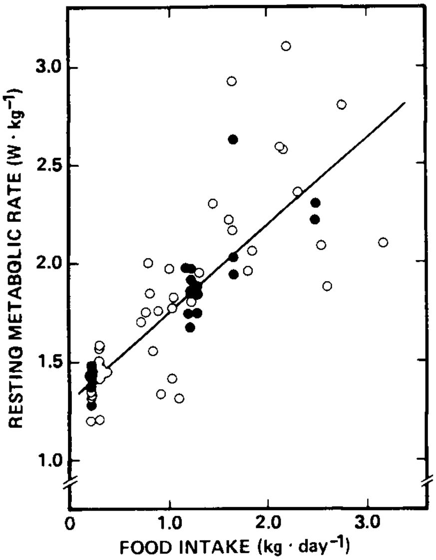

Fig. 5. Resting metabolic rate as related to daily food intake in adult Svalbard (o) and Norwegian (●) reindeer (from Nilssen, Sundsfjord and Blix, 1984a).

Furthermore, they found close agreement between the metabolic rate in reindeer based on linear extrapolation to zero food intake (1.3 W·kg $^{-1.0}$) and measured values (1.4 W·kg$^{-1.0}$). They concluded that seasonal variation in resting metabolic rate in *ad libitum* fed reindeer (Fig. 1) was due to changes in the animals' voluntary food intake and did not represent a physiological adaptation to energy conservation in winter mediated by a reduction in fasting metabolic rate (FMR).

Their conclusion was supported by observations made in a subsequent series of experiments on Norwegian and Svalbard reindeer in which Nilssen and his colleagues measured metabolism every second day for two weeks during which time the animals were given only 15% of their *ad libitum* food intake. As expected the animals' metabolism initially fell rapidly, reaching a stable minimum after 5 to 10 days. There were no differences between summer and winter minima in either sub-species (Nilssen, Sundsfjord and Blix, 1984b). Thus, it appears that there is no seasonal variation in FMR in reindeer.

Another arctic ruminant, the muskox *Ovibos moschatus*, provides an interesting contrast in this respect. These animals belong to a different taxonomic group *(Bovidae, Caprinae)* from deer *(Cervidae)*. Muskox, unlike Svalbard reindeer, appear to have developed two metabolic adaptations to winter. First, their metabolic rate shows pronounced seasonal variation. FMR in adult female muskoxen fell approximately 20% from 3.0 W·kg $M^{-0.75}$ in summer to 2.4 W·kg $M^{-0.75}$ in winter (Nilssen, Mathiesen and Blix, unpublished). Second, their FMR (lying) in winter appears to be almost 40% lower than the FMR (lying) of Svalbard reindeer (Table 1). The difference between these two high arctic species, as well as the difference between reindeer and sheep, is intriguing and deserves further attention.

Heart rate telemetry

All the measurements of metabolism discussed above were made by indirect calorimetry. An alternative technique involves monitoring animals' heart rate by radio telemetry. There exists a fairly linear relationship between oxygen uptake and heart rate under aerobic (steady-state) conditions, at least in tame, trained reindeer (Nilssen, Johnsen *et al.*, 1984) and it is therefore in principle possible to calculate energy expenditure in unrestrained animals from heart rate alone. Hitherto only one detailed study of the application of this technique has been carried out on *Rangifer* but the authors concluded that it is potentially useful, at least in winter (Fancy and White, 1986).

The technique has two drawbacks, however. First, as Fancy and White pointed out, the relationship between heart rate and oxygen consumption varies not only seasonally (see also Nilssen, Johnsen *et al*, 1984) but is also individually variable in caribou, especially in summer. In reality, therefore, each animal tested must be calibrated separately. Second, and rather more fundamentally, there are circumstances in which the normal linear relationship between heart rate and oxygen consumption

Table 1. Fasting metabolic rate of different wild and domestic ungulates (all adults).

	Fasting metabolic rate (x $M_b^{0.75}$ kcal·day^{-1})			Source
Domestic sheep	48.6	W	F & C	(1)
Muskox	49.1	W	F	(2)
Cattle	76			(3)
Red deer	79	Sp	F	(4, 5)
Svalbard reindeer	80.3	W, S	F	(6)
Caribou	91	Sp	F	(7)
Roe deer	94.6	W		(8)
White-tailed deer	97.1	W	M & F	(9)
Interspecies mean	70			(10)

M_b: live body weight (kg).
M: males; C: castrates; F: females.
W: winter; Sp: spring; S: summer.
Sources: (1) Blaxter and Boyne (1982); (2) Nilssen, Mathiesen and Blix, unpublished; (3) ARC (1980); (4) Brockway and Maloiy (1968); (5) Maloiy *et al.* (1970); (6) Nilssen, Sundsfjord and Blix (1984a); (7) McEwan (1970); (8) Drozdz *et al.* (1973); (9) Silver *et al.* (1969); (10) Kleiber (1975).

breaks down and during which heart rate may, in fact, considerably exceed the value predicted from the observed consumption of oxygen. This is called 'additional heart rate' (AHR) (Blix *et al.*, 1974; Strømme *et al.*, 1978). The physiological basis of this phenomenon is not known but it may be linked to some kind of psychological activation. This may explain why better results seem to be obtained with large, confident animals compared to small, nervous ones (Hudson and Christopherson, 1985). We know nothing about AHR in reindeer or caribou. Clearly, however, if AHR also occurs in these, then interpretation of data collected by telemetry from free-ranging animals would become considerably more difficult. Hudson and Christopherson concluded, somewhat pessimistically, that "there appears to be little hope of deriving suitable general regressions that could be applied to wild populations but the technique may be quite useful in studies with individually calibrated research animals" (ibid.).

Doubly-labelled water

One of the most interesting developments since the fourth Reindeer/Caribou Symposium has been the application in reindeer and caribou of the doubly-labelled water method for measuring energy expenditure (see Fancy, Blanchard, *et al.*, 1986). The method is based on the relative rates of decrease in the concentrations of two isotopes, $H_2{}^{18}O$ and either deuterated water (^2H_2O) or tritiated water (^3H_2O), in the total body water pool. A single dose of 'doubly-labelled water' is injected into an animal and the subsequent disappearance of each isotope is measured by taking serial blood samples normally over periods of up to ten days. ^{18}O in the body equilibrates between water and bicarbonate through the carbonic anhydrase reaction and the disappearance of the isotope therefore measures the sum of CO_2 and water fluxes. The water flux can be predicted independently from the rate of disappearance of the hydrogen isotope so that, in principle, the rate of CO_2 production can be calculated by difference. Energy expenditure is calculated from CO_2 production rates using standard calorimetric calculations (Lifson and McClintock, 1966; Nagy, 1980).

The advantage of the doubly-labelled water method over conventional techinques is that it can be used to measure the total energy expenditure of animals in their natural environments (e.g. Bryant and Westerterp, 1983; Gabrielsen, Mehlum and Nagy, 1987; Costa and Croxall, 1988) as well as to verify estimates based on additive models (e.g. Utter and Lefebvre, 1973; Weathers and Nagy, 1980; Williams and Nagy, 1984).

Application of the techinque in ruminants is complicated in several ways owing to their specialised digestion. Unlike in monogastric species, for example, CO_2 produced by gut microbes can make a significant contribution to the animals' total CO_2 production. Furthermore, a relatively large proportion of total body water in ruminants is contained in the gut where it equilibrates only slowly with the rest of the body. Consequently, Fancy, Blanchard, *et al.* (1986) designed their study as a validation trial to compare apparent rates of CO_2 production (CDP) measured by the doubly-labelled water method with rates of CO_2 expiration (VCO_2) measured by open circuit respirometry.

Fancy and his colleagues circumvented problems related to slow equilibration of water between different compartments in the body by talking serial blood samples, rather than relying on the more simple 'two point' approach (Coward, Roberts and Cole, 1988). Their results showed that both CDP and VCO_2 were affected by CH_4 production. However, loss of ^3H in CH_4 largely offset losses of CO_2 by reduction to CH_4, so that the difference between methods was less than 2%. On the other hand, while the *overall* net difference between the two methods was 1-3% in one reindeer in winter, the difference in caribou in summer ranged from 5 to

20%. Part of the differences in summer were putatively attributed to net deposition of ^3H, ^{18}O and unlabelled CO_2 in growing antlers and other tissues. The authors concluded that the doubly-labelled water technique is a reasonbly accurate method for measuring CO_2 production rates in reindeer and caribou, at least during periods of slow growth (i.e. winter), providing appropriate corrections are made.

Activity

Besides minimising heat loss in winter by means of increased insulation, reindeer and caribou can reduce energy expenditure by adopting appropriate behaviour; in particular, by reducing their total daily locomotor activity.

The daily energy cost of locomotion is influenced by three variables: the total distance which the animals travel per day, the overall distance which they climb and the nature of the surface over which they move. Two other variables, running speed and the angle of ascent, have less significance first, because the weight-specific net cost of climbing in ungulates appeares to be independent of the angel of ascent, at least on moderate slopes (Fancy and White, 1985) and second, because in reindeer and caribou, like other terrestrial mammals, the relationship between running speed and the rate of energy expenditure is effectively linear (Taylor, Heglund and Maloiy, 1982; Parker, 1983; reindeer: Nilssen, Johnsen *et al.*, 1984). Consequently, the net cost of travelling a given distance is, for an animal of a given body weight, largely independent of the speed at which it moves.

The nature of the surface over which animals travel, on the other hand, has a very important influence on the cost of locomotion. White and Yousef (1978), for example, showed that reindeer expended 30% more energy when walking on wet tundra compared to on hard-packed roads. The costs of walking across soft or crusted snow are even higher and rise exponentially as the animals sink deeper. In one case, in which a caribou sank to 60% of brisket height at each step, the relative net cost of locomotion increased almost six times (Fancy and White, 1985). The capacity of snow to support an animal depends on the hardness of the snow and the pressure (foot load) which the animal exerts on it. Thus, if snow hardness consistently exceeds foot loads, animals can walk on top of the snow or will sink to only a fraction of its total depth. The broad, spreading feet of reindeer and caribou, a well-known characteristic of this species, is clearly an adaptation to walking on snow, through minimising the extent to which they break through the crust and sink in. In fact, reindeer and caribou, with the exception of musk deer *Moschus moschiferus*, have the lowest foot load measured in any ungulate (Fancy and White, 1985).

The potential significance of reducing locomotion as a means of saving energy is made clear from Fancy and White's (1985) calculation that the costs of locomotion for a 90 kg caribou breaking the trail at the head of the spring migration will represent an increment to its minimal metabolism of 82%. For the animals following the packed trail in its wake, the incremental cost would be equivalent to about 33% of their minimal metabolism, a saving of more than half (Fancy and White, 1985). At the other extreme, Svalbard reindeer appear to be able to reduce their activity to a level at which the total daily energy cost of locomotion becomes almost negligible. These animals are typically sedentary, walking, on average, <0.7 km (net) per day in winter (Tyler and Øritsland, 1989) and rarely running at all unless provoked. The daily cost of locomotion amounts to only about 2% of their daily energy expenditure (DEE) (Tyler, 1987b). In barren-ground caribou which, by contrast, travel on average approximately 5 km per day in winter (Fancy *et al.*, 1988), the energy cost of locomotion is correspondingly higher: approximately 8% of DEE (Boertje, 1985; Fancy, 1986).

Selective cooling of the brain

The net energy cost for an animal of given body weight moving from one place to another is largely independent of the speed at which it travels. This begs the question: Why don't reindeer always run? The answer is that the insulation which enables them to survive under extremely cold conditions predisposes them to heat stress if they exercise hard and presumably the costs of thermoregulation outweigh any potential saving.

Heat production in reindeer increases very rapidly with increasing running speed. The rate of heat production in Svalbard reindeer trotting at 8 km/h, for example, is four times higher than the rate of heat production when standing (Nilssen, Johnsen *et al.*, 1984; Fig. 6). Hot reindeer can increase heat loss both by peripheral vasodilation (Johnsen, Rognmo *et al.*, 1985) and by respiration which, by making appropriate vascular adjustments in the nasal mucosa, may be used to conserve or to dissipate heat (Johnsen, Blix *et al.*, 1985). Nevertheless, if an animal runs hard during winter, perhaps because it is being chased by a predator, it can soon reach a stage at which it produces heat more rapidly that it can lose it, with the consequence that body temperature rises (e.g. Johnsen, Rognmo *et al.*, 1985). It would be advantageous, in terms of survival, to be able to prolong the length of time it can maintain a high degree of physical activity, but to do so requires that thermally sensitive tissues, such as the brain, are protected.

Several species in the orders *Artiodactyla*, including reindeer, *Carnivora* and *Cetacea* have developed a system which enables them selectively to cool their brain tissue independently of the rest of the body core (Johnsen *et al.*, 1987). The principle of selective brain cooling is illustrated in Fig. 7. During mild heat-stress, venous blood, cooled at the evaporative surfaces of the nose, flows via the facial vein directly to the caval veins and is used for general body cooling. If the heat stress becomes severe, however, the facial vein is closed off and the cooled blood is directed, instead, through the *angularis occuli* veins to a venous sinus at the base of the brain (Fig. 8). Here heat is exchanged with warm blood in the carotid artery, into which a *rete* is

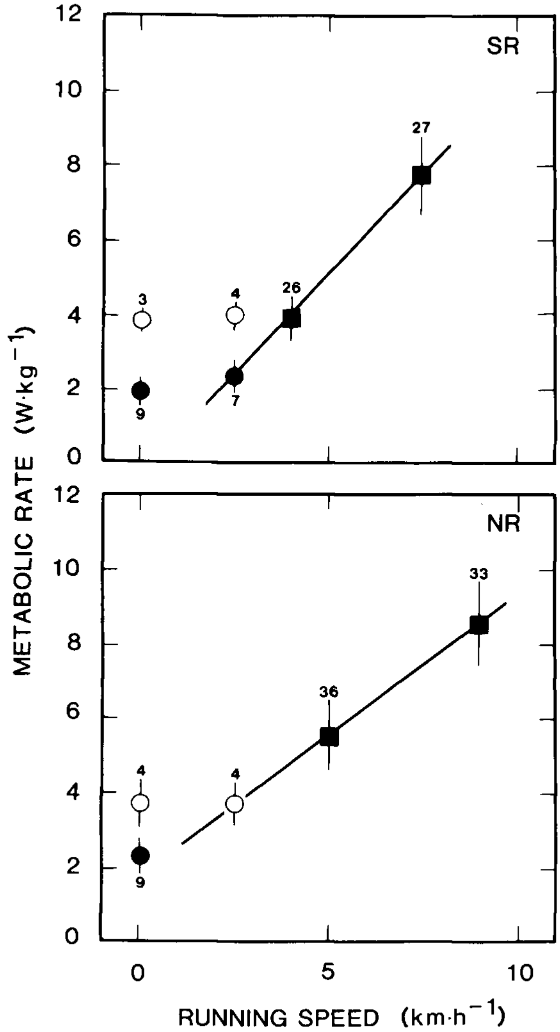

Fig. 6. Relationship between metabolic rate and running speed in Svalbard reindeer (SR) and Norwegian reindeer (NR). Symbols represent energy expenditure at different ambient temperatures: -24°C in summer (o) +9°C in summer, +8°C and -30°C in winter (●); all temperatures/seasons (■). The numbers above each symbol represent the number of measurements in two animals. Vertical bars indicate standard deviation (from Nilssen, Johnsen, Rognmo and Blix, 1984).

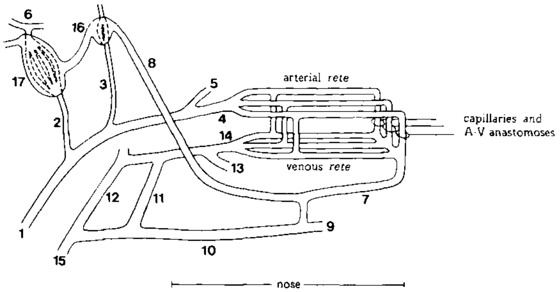

Fig. 7. Arterial and venous vasculature of reindeer nose. During heat conservation, blood may run countercurrent in the two *retia* and leave the nasal mucosa through the sphenopalatine group of veins (14), with the dorsal nasal vein (7) constricted. During heat dissipation, however, blood may run unidirectionally in both *retia* and leave the nasal mucosa by way of the dorsal nasal vein (7), and the sphenopalatine group of veins (14) would now be constricted. In this way heat dissipation by way of the respiratory tract is optimized, and cooled venous effluent may be directed, either via the facial vein (10) to the external jugular vein (15) for general body cooling or via the angular oculi veins (8) to the opthalmic plexus (16) and the cavernous sinus (17) for selective cooling of arterial blood to the brain. 1, common carotid a.; 2, arterial supply to carotid *rete;* 3, arterial supply to orbital *rete;* 4, sphenopalatine a. with its branches; 5, infraorbital a.; 6, circle of Willis; 7, dorsal nasal v.;8, angular oculi v.; 9, maxillary labial v.; 10, facial v.; 11, deep facial v.; 12, maxillary v.; 13, infraorbital v.; 14, sphenopalatine group of veins; 15, external jugular v.; 16, ophthalmic venous plexus with orbital *rete (dashed lines);* 17, carvernous sinus with carotid *rete (dashed lines)* (from Johnsen, Blix, *et al.*, 1985).

inserted to facilitate heat transfer (Fig. 9). The result of this is that the brain is cooled selectively while heat is stored (as an increase in temperature) in the rest of the body - to be dissipated subsequently when the stress is past.

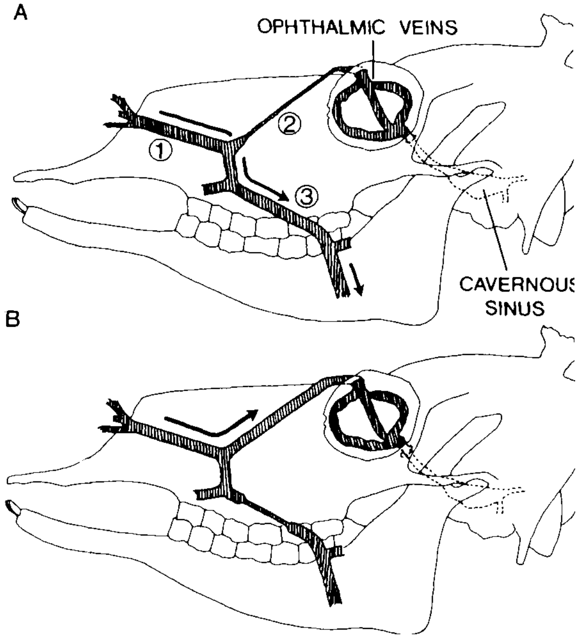

Fig. 8. Schematic diagram of superficial veins of nose and their connections with the cavernous sinus at the base of the brain in relation to the outline of the skull in reindeer. Figures illustrate the proposed mechanism for distribution of cold blood from nose of hyperthermic reindeer. A: operation of mechanism during moderate heat stress, where cold venous effluent from the mucosal lining of the nasal surfaces returns to the caval veins via the facial veins (→), thus by-passing the cavernous sinus. It is suggested that the direction of venous return through this pathway is due to sympathetic stimulation of the angular oculi and facial veins, which results in release of pressure-induced inherent myogenic tone in the facial veins and simulataneous constriction of the angular oculi veins. In contrasts, when body temperature exceeds the threshold value for onset of brain cooling, sympathetic activity to the veins in question is reduced. This will result in dilatation of the angular oculi veins and activation of inherent myogenic tone in the facial veins (B). In this situation cold blood returning from nose is directed mainly to the cavernous sinus for selective cooling of the brain (→); 1, dorsal nasal vein; 2, angular oculi vein; 3, facal vein (from Johnsen and Folkow, 1988).

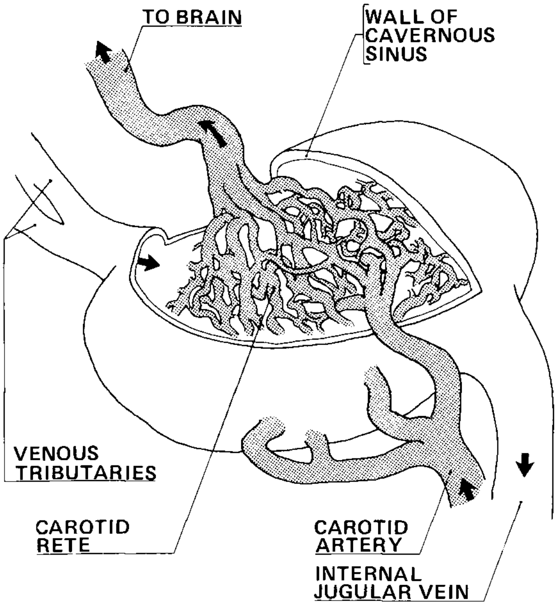

Fig. 9. Carotid *rete* of a sheep exposed in a cutaway drawing. This structure lies at the base of the brain. Cool venous blood, draining from the nose, enters an enlargement of the venous tributaries called the cavernous sinus. Here it bathes a network of small arteries callet the carotid *rete*, which is inserted into the carotid artery, and leaves via veins that enter the internal jugular vein at the right. At the same time warmer arterial blood arriving from the heart enters the *rete* via branches of the external carotid artery and is subsequently cooled by the venous effluent before continuing up to the brain. Selective cooling of the brain normally occurs only when animals sustain hard excercise and therefore are in danger of overheating (redrawn from Baker, 1979).

Appetite and growth

The central concept in most models of animal energetics is animals' 'maintenance energy requirements' (e.g. Hudson and Christopherson, 1985). This, together with the concept of 'energy balance', has become so familiar that there is sometimes a tendency to consider maintenance of energy balance almost as an end in itself, if not actually synonymous with survival. However, wild reindeer and caribou, like many other arctic species, normally lose weight throughout winter (Fig. 10, Table 2). Evidently, they can survive perfectly well despite being in negative energy balance for months at a time. Clearly, therefore, maintenance of energy balance *per se* is not a prerequisite for survival. Moreover, an important point which is often ignored, is that slowed growth and even weight loss are not necessarily consequences of undernutrition.

Loss of weight during winter is still frequntly regarded as diagnostic of undernutrition despite experimental evidence that this is not necessarily so (e.g. Mortensen and Blix, 1985; Mrosovsky and Sherry, 1980). Several species of cervids show a pronounced seasonal cycle of appetite and growth which appears to follow an intrinsic rhythm, entrained by photoperiod and associated with changes in levels of circulating hormones. These cycles, which have been discribed in detail in red deer *Cervus elaphus* (e.g. Brown *et al.*, 1979; Kay, 1985; Pollock, 1974; Suttie and Simpson, 1985), seem also to occur in reindeer and caribou. In winter their appetite falls by as much as 70% of autumn values (Larsen, Nilsson and Blix, 1985), growth slows or even stops (Ryg and Jacobsen, 1982a; McEwan, 1968) and the animals begin to mobilize their fat reserves even when good quality food is freely available (e.g. Larsen, Nilsson and Blix, 1985).

Interpretation of patterns of growth and weight loss in free-ranging animals is complicated by the difficulty of distinguishing the effects of spontaneous anorexia (a voluntary reduction in food intake) from the effects of involuntary starvation (true inanition). Nevertheless, it is interesting to note that a marked diffeence exists between the sexes in the phasing of the weight cycle (Dauphiné, 1976; Leader-Williams and Ricketts, 1982), an observation which strongly implicates the influence of some intrinsic control. Surprisingly, however, as Leader-Williams and Ricketts (1982) pointed out, the total weight of pregnant caribou kept

Table 2. Comparision of seasonal maximum and minimum mean total body weights (kg) and the proportional (%) loss of weight in adult female reindeer and caribou from different populations.

Locality/latitude	Stock/sub-species	Total body weight (kg) Max.	Total body weight (kg) Min.	Weight loss in winter (%)	Source
Svalbard 78° N	Wild reindeer[a]	63	45	29	Tyler (1987a)
Canada 62° N (Coats Island)	Barren-ground caribou	89	73	18	Adamczewski *et al.* (1987)
South Georgia (Busen) 54° S	Introduced reindeer	90	78	13	Leader-Williams (1988)
Norway 60° N (Hardangervidda)	Wild reindeer	54	48	11	Reimers (1980)
Canada 60° N (Kaminuriak)	Barren-ground caribou	90	80	11	Dauphiné (1976)
Finland 68° N	Domesticated reindeer	66	59	11	Nieminen (1980)
Alaska 65° N	Caribou	110	100	9	Boertje (1985)

[a] ≥4 years old.

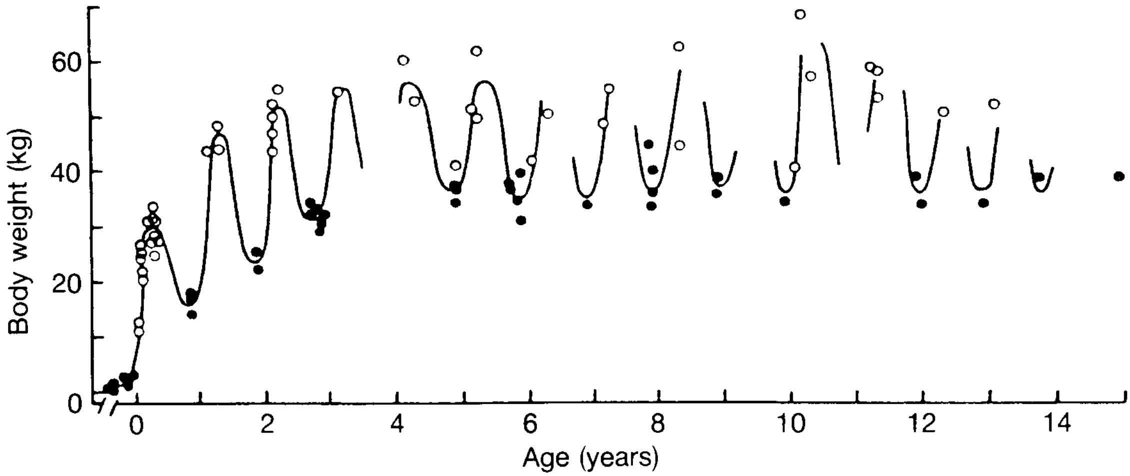

Fig. 10. Growth curve for female Svalbard reindeer. Total body weight (kg) less the weight of the reticulo-rumen (all specimens) and the weight of the uterus and its contents (winter specimens). Each point represents one reindeer. Summer and autumn (July to October) (o); late winter (April to May) (●), from Tyler, 1987b).

in captivity and fed *ad libitum* appeared to decrease at the beginning of winter, in phase with that of males. It is not clear why captive deer should differ so fundamentally from their free-ranging counterparts.

Intrinsic cycles of growth and fattening appear to be adaptations for survival in seasonal environments in which animals are confronted with long, predictable periods of potential undernutrition. Slowed rate of growth and, to an even greater extent, actual loss of weight have the effect of reducing an animal's daily

Table 3. Total fat content (% live weight) of different wild ungulates[a].

Species/breed	% fat	Source
Tropical (savannah)		
Topi[b]	1.0 D	Ledger (1968)
Impala[b]	1.2 D	Ledger (1968)
Kob[b]	2.3 D	Ledger (1968)
Thomson's gazelle[b]	2.8 D	Ledger (1968)
Grant's gazelle[b]	3.0 D	Ledger (1968)
Wildebeest[b]	3.9 D	Ledger (1968)
Temperate/sub-arctic		
Norwegian reindeer[c]	3.5 E	Reimers, *et al.* (1982)
Red deer[d]	4.5 D, E	Blaxter *et al.* (1974)
Red deer[e]	5.2 D	Wallace & Davies (1985)
Red deer[f]	5.7 E	Kay *et al.* (1981)
Mule deer[g]	6.5 E	Field *et al.* (1979)
Chinese water deer[h]	6.9 D	Pond & Mattacks (1985)
Fallow deer[i]	7.1 E	Gregson & Purchas (1985)
North American elk[j]	7.8 E	Field *et al.* (1980)
Roe deer[k]	8.3 E	Weiner (1973)
White-tailed deer[l]	9.5 E	Robbins *et al.* (1974)
Arctic		
Barren-ground caribou[m]	13.5 D	Adamczweski *et al.* (1987)
Svalbard reindeer[n]	16.8 D	Tyler (1987b)
Svalbard reindeer[o]	28.7 D	Reimers *et al.* (1982)

[a] Mostly females. Values for males are mostly post-rut; the purpose of the Table is to compare the relative size of the energy reserves prior to winter, not the maximum fatness which different species can attain *per se*.

[b] Adult females (all species), wild.

[c] Yearling males, domesticated but free-ranging, August.

[d] One 2-year-old stag, captive, post-rut.

[e] Males, captive, post-rut (% carcase weight).

[f] Yearling females, captive, autumn (% dressed weight).

[g] Females ≥ 2.5 years old.

[b] Two males & two females; mean of the fattest and thinnest, captive.

[i] Males aged 26 months, captive, pre-rut.

[j] Females ≥ 2.5 years old.

[k] Adult females, wild, February.

[l] Adult females, captive, autumn (% ingesta-free body weight).

[m] Females aged ≥ 4 years (n=4), November (island population).

[n] Females aged ≥ 4 years (n=13), September and October.

[o] One 2-year-old female, August.

D Dissectible fat.

E Chemically extractable fat.

energy requirements (see Tyler, 1987b). This may be literally vitally important in winter when food is not only scarce and of poor quality but is also energetically expensive to acquire. The endocrine control of appetite and body weight cycles in ungulates is not fully understood (e.g. Nilssen, Bye, *et al.*, 1985; Ryg and Jacobsen, 1982a,b). Nevertheless, it is clearly misleading to regard the body weight of reindeer and caribou simply as the product of some precarious balance between food intake and energy expenditure (see also King and Murphy, 1985). Seasonal changes in body weight should be thought of, instead, primarily in terms of intrinsic cycles of growth and fattening mediated by appropriate changes in appetite (Kay, 1985; Ryg, 1983; see also Mrosovsky and Powley, 1977) rather than in terms of passive responses to seasonal changes in the quality, abundance and availability of food.

Fat

Knowledge of seasonal changes in body composition of reindeer and caribou has increased considerably during the last 20 years. One of the earliest, and still one of the best descriptive studies was made on the barren-ground caribou of the Kaminuriak herd by Dauphiné (1976) in the late 1960s. Subsequently, Cameron and Luick (1972) and Ringberg *et al.* (1981) worked on reindeer in Alaska and Krog *et al.* (1976) and Reimers *et al.* (1982) studied Svalbard reindeer. Reimers *et al.* (1982) showed, in particular, that fat accounted for almost 30% of live weight in a sub-adult female in late summer; the mean total fat content of *adult* females is rather less, however, accounting for approximately 17% of live weight (Table 3). Interestingly, Coats Island caribou fatten almost to the same extent; the mean total fat content of adult females in autumn is approximately 13.5% of their live weight (Table 3).

These studies have greatly increased our knowledge of the anatomy of adipose tissue in reindeer and caribou but the actual function of fat reserves, curously, is still far from clear.

Many animals which live in highly seasonal environments store large amounts of energy as lipid droplets in adipose tissue during summer and autumn in anticipation of food shortage during winter. In hibernating species fat deposits may constitute up to 35% of the animals' total body weight (e.g. Linsdale, 1946; Pond and Mattacks, 1985; Wienland, 1925). Ungulates, by contrast, usually store relatively little fat. The fat deposits of temperate and sub-arctic cervids, for example, represent usually only between 4-10% of total body weight in autumn (Table 3).

Such low values cast doubt over the widely held view that fat is a major source of energy for deer and other ungulates in winter. Even using the most conservative models of energy expenditure it seems unlikely that the fat reserves of female Svalbard reindeer, for example, could contribute more than 10-25% of the animals' energy damands during winter (Mathiesen *et al.*, 1984; Tyler, 1987b). In practice, the contribution from fat is likely to be lower than these models predict because reindeer which survive winter do not normally use up all their fat (Tyler, 1987a,b). Moreover, there is increasing evidence that the principal role of fat reserves in ungulates is to enhance reproductive success, rather than to provide a substitute for poor quality winter forage (although the very presence of fat will necessarily also provide insurance against death during periods of acute starvation).

Substantial pre-rut fat reserves, for example, enable male deer to gather, defend and serve their harems without being distracted by the need to feed and, in several species, males hardly eat at all for two or three weeks during the rut (Clutton-Brock, Guinness and Albon, 1982; Rapley, 1985; Thomson, 1977; Skogland, 1974). Consequently, in many species, mature bulls use up much of their fat before the start of winter (caribou: Dauphiné, 1976; white-tailed deer: Johns, *et al.*, 1982; reindeer: Leader-Williams and Ricketts, 1982; red deer Mitchell, McCowan and Nicholson, 1976; Wallace and Davies, 1985). None of these species, however, usually store large amounts of fat (Table 3). Svalbard reindeer bulls are very fat in autumn. As expected, they lose weight during the rut but, unlike bulls of mainland subspecies, they still have substantial reserves when it is over (mean rump fat depth at the end of November = 42 mm, n = 3; Tyler, unpublished data). Nevertheless, the pattern of the fat cycle in Svalbard reindeer is similar to that of other sub-species of *Rangifer* and after the rut females are about 30% fatter than males.

It is more difficult to distinguish between alternative roles (reproduction and food supplement) for fat reserves in female ungulates because, in many species, these are pregnant throughout winter. Nevertheless, pregnant females may delay mobilisation of their fat reserves until the end of gestation, or early lactation, which normally occurs in spring or early summer, sometime after the period of maximum food shortage (Caughley, 1970; Dunham and Murray, 1982). Kay (1985) suggested that the principal role of fat reserves in females may be to supplement (but not to substitute for) their food intake during late pregnancy.

Recently, Tyler (1987b) found evidence of a marked difference in the pattern of mobilisation of fat between pregnant and non-pregnant female Svalbard reindeer. Pregnant animals appeared to become increasingly less dependent on their reserves as winter advanced, not only losing weight more slowly during the last two months of winter, when food availability was lowest, compared to the preceding six months but, also, losing it more slowly than non-pregnant females despite presumably having substantially increased energy requirements at that time. Thus, it appears that at the end of winter pregnant Svalbard reindeer, like certain temperate and tropical species of ungulates, spare their remaining fat reserves in anticipation of the energy demands of lactation. How they achieve this and how such a mechanism might be controlled is unknown (see Tyler, 1987b). Nevertheless, in the high arctic, where the spring melt can be delayed by several weeks, a large store of fat with which to support lactation is likely to be very important both for ensuring the survival of newborn calves and for promoting their growth.

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The ship of the desert. The dromedary camel *(Camelus dromedarius)*, a domesticated animal species well adapted to extreme conditions of aridness and heat

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Abstract: The dromedary camel *(Camel dromedarius)* is extremely well adapted to life in hot and arid lands. In terms of physiological adaptation to heat and water deprivation it surpasses by far every other large animal of which data have been collected. None of the adaptive mechanisms to cope with the environmental stresses are unique to the Arabian camel, but the efficiency of its adaptation is superior.

At high ambient temperatures the camels adapt to the scarcity of water by reducing their faecal, urinary and evaporative water losses.

During dehydration, the kidneys reduce water losses both by decreasing the glomerual filtration rate and by increasing the tubular reabsorption of water. Also their ability of regulating their body temperature from 34.5-40.7°C conserves a lot of water, when most needed.

Key words: heat-adaptation, water conservation

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Introduction

For hundreds of years the camel *(Camelus spp)* had been exploited by man in Asia and Africa in arid and semiarid areas - often being the only supplier of food and transport for people.

In the aftermath of the devastating droughts, which hit Africa during the 1970s and 1980s an interest has awakened in this beast of burden and provider of milk, meat, wool, fibres and hides. The camels are truly multi-purpose animals. They have shown to be better adapted to extreme conditions in most aspects than other domestic ruminants husbanded in the harsh environments of arid and semiarid Africa and Asia.

Camelus spp

There are two species of camels belonging to the camelidae. The two- humped or Bactrian camel *(Camelus bactrianus)* is found in Asia and thrives particularly in cold and arid regions.

The one-humped or dromedary camel *(Camelus dromedarius)* also called the Arabian camel, because it is closely linked with Arab history and culture. The dromedary is found in almost all the hot, arid and semiarid regions of the "old world": throughout northern Africa and parts of Asia.

Origins of the Camelidae

The camels belong to the *Camelidae* in the ruminant suborder *Tylopoda* of the order *Artiodactyla* (even-toed Ungulates). The Tylopoda (padfooted) walk on cushioned pads at the end of the digits (the second and fourth).

The *Camelidae* differ from other true ruminants in not having horns or antlers. Their forestomachs are different morphologically and physiologically. A special feature of the *Camelidae* is the oval shape of their red blood-cells - unique among mammals.

Fossils show that the early evolution of the *Camelidae* took place in North America. The earliest found ancestor (Protylopus) from the Upper Eocene period was no bigger than a hare.

The *Camelus* spp appeared during the Pleistocene period, and during one of the ice ages when there was a land-bridge between Alaska and Siberia (the present Bering strait) "early camels" spread into Asia.

During the migration and evolution of the camels in the "Old World", the camel groups died out in Northern America. However, some Camelids had migrated to South America and evolved to the present South American Camelids; the three species of the genera *llama* and the one species of the genus *Vicugna*.

Distribution

The population of the dromedary camel is much more numerous then the Bactrian camel and constitutes about 90 per cent of the genus Camelus in the world.

More than 80 per cent (12 million) of the Arabian camels are found in Africa in more than 18 countries, forming an important part of the domestic livestock population.

In Asia the dromedary camels are found in the Middle East including the South Arabian peninsula, Turkey, Iran, Afghanistan, North Western India, China (Western Sinkiang) and in the south-western Soviet Union (mainly Turkmenistan).

At the northern and eastern edges of the dromedary camel's range in Asia one finds the Bactrian camel in the mountainous regions of southern Russia and in the cold deserts of China including Mongolia. The total population of Bactrians in China is estimated to be about 600 000 (some sources say over 1 million, Mason, 1984). 60% of these animals are found in inner Mongolia. The limits of the camel-breeding area follow the *isohyet* for 50 cm of rain and the Bactrian camels are not found where the mean annual temperaure is above 21° C (Mason, 1984).

The camel today is essentially a domestic animal of pastoralists and agropastoralists. However camels are also found in areas of permanent cultivation i. e. desert oases, along the Nile in Egypt or in Indian and Pakistani villages.

The dromedary camels have very special anatomical and physiological characteristics, which enables the animals to live, reproduce and produce milk and meat and to work under extreme conditions of heat and aridness - even during periods of drought when cattle, sheep and goats barely survive.

Anatomical advantages

Skin and coat

Insulation from high environmental temperature depends on the quality (i.e. density, thickness, texture, colour) of the coat of the animal, the colour and quality of the skin and the presence of layers of fat in the subcutis.

In theory animals exposed to high levels of solar radiation should preferably have a smooth reflective coat, which should not be too thick to prevent evaporation at the skin surface nor too thin, in order to avoid too much heat striking the skin surface.

Most types (breeds) of dromedary camels living in hot arid environments conform to the above requirements. The "summer" coat of dromedary camels are usually light in colour, rather thin and sleek, effectively reflecting the solar rays.

Size

The large size and height of the camel can be of some advantage in heat regulation. (The Arabian camel stands over 2 meters at the shoulders and an adult camel weighs about 400-700 kg). A large body mass heats up much more slowly than a smaller mass exposed to the sun (Yagil, 1985).The long legs and the large humps, containing adipose tissue, gives to the camel a large skin surface in relation to the body mass, which is another advantageous feature in regards to heat regulation.

The height above the ground (long legged) allows the desert winds free access to the body thus in some circumstances cooling it effectively. It also enables the camels to browse high above the ground reaching 3.5 meters into the canopies of trees and bushes. This characteristic together with their preference to browse on many kinds of bushes makes them an excellent complement for multi-species herds in different kinds of rangelands, increasing the productivity of the land without really competing with other livestock (Evans and Powys,1984). The camels graze and browse in ways similar to some wild ungulates. They keep moving while feeding, nibbling a few bites here and there from one plant to another. Their long muscular legs allow them to cover vast distances in search of water and food. Even on rich pastures they may cover five kilometres in two and a half hours while grazing and browsing (Gauthier-Pilters and Dagg, 1981)

Water conservation

The camels' ability to survive long periods without water is legendary. This ability varies between breeds, and is influenced by climatic factors, the quality and quantity of the forage, and its water content, the age of the animal and the type of work it is subjected to (Gauthier-Pilters and Dagg, 1981; Schmidt-Nielsen, 1964). It is also influenced by training (management).

During the rainy season the herbage is often rich in water and the camels will also find surface water in natural dams. During the winter and cool season (6-7 months) in the Sahara the camels can go without water. They do not even drink when offered water. The fodder has enough moisture for the maintenance and productive requirements (Gauthier-Pilters and Dagg, 1981)

During the dry season when pastures have dried up camels are taken to water every 6-10 days. In extreme situation they can go without water for over a month (cattle have to be watered every 2-3 days).

When the mean temperature reach 30-35°C in the Sahara and in the Sahel, camels can go 10-15 days without water but when the temperature exceeds 40°C, shorter periods between watering is necessary (Gauthier-Pilters and Dagg, 1981).

According to Schmidt-Nielsen et al. (1956) a camel can lose water (dehydrate) of more than 25% of its body-weight. Gauthier-Pilters and Dagg (1981), when studying camels in the Sahara during the summer, saw camels of 500 kilos body-weight drinking 150-200 litres of water after being without it for 5-7 days. The camels compensated their dehydrated state by drinking over 30% of their weight. This they usually do very quickly. In a couple of minutes they have drunk most of what they need. A well nourished camel will drink 10-20 litres per minute.

The more dehydrated a camel becomes the more it conserves water (Schmidt-Nielsen et al., 1956; Charnot, 1958; Clair, 1962). Camels do not store water as was thought not so long ago. They conserve it by help of many different physiological mechanisms.

Temperature regulations

Body-temperature

Instead of dissipating most of its heat through loss of water during the hot part of the day by sweating, the camel, when dehydrated can store some of the heat allowing its body temperature to rise as high as 40.7°C. During the evening and cooler part of the night the temperature of the body can fall to a little above 34°(Schmidt-Nielsen, 1964). This difference in temperature (34.5-40.7°C) of 6.2° of a camel weighing 500 kg is equivalent to approximately 2 500 kcal, which by dissipation via evaporation would require nearly five litres of water (sweat), which is thus saved,

Evaporation

Camels have sweatglands in their rather thick skin (Sekles et al., 1979). There are an average of 200 per cm^2 on the body, the same amount as found in man. (Cattle have 4-8 times as many.) Sweating is said to be one of the major mechanism for increasin evaporation in camels (Schmidt-Nielsen et al., 1981). However, the camels do not start sweating when dehydrated until their upper limit of heat storage is reached.

At high ambient temperatures the respiratory rate increases slightly in the camel from 6-11 to 8-18 breaths per minute (in the Sahara, Schmidt-Nielsen, 1964) and in Australia from 10-12 to 20-24 (Macfarlane, 1968). This raise in respiration rate does not significantly increase evaporation or loss of water (compare the panting in the dog).

The sweat evaporates directly from the skin surface in the dromedary camel rather than from the tip of the hairs as it does on heavily furred animals. Latent heat of vaporization is therefore drawn directly from the skin. Evaporation that takes place directly on the skin saves more energy and cools the skin more effectively than if the evaporations took place at the tip of the hairs.

It has been estimated that during the cooler months (Sahara) 50% of the total water loss of camels are from evaporation (Schmidt-Nielsen, 1956). During midsummer 85% of the total water losses were from evaporation declining to 65% in the dehydrated animal.

Water conservation via kidneys and gut

Another water conserving adaptation mechanism of the camel is the capacity to produce very little urine and dry faeces.

The alimentary tract in the camel is regarded to be the main provider of fluids for the body and the kidneys are vital in retaining as much water as possible by helping in maintaining the extracellular fluid composition and volume brought about by glomerular filtration, tubular reabsorption and tubular secretion. Macfarlane (1977) calculated that the daily urine volume excreted by dehydrated camels was one thousandth of the animals body weight. Dehydrated sheep living in the same environment excreted one two-hundredth of its body weight. If an adult man (80 kg) would excrete urine as the dehydrated camel does, it would mean a daily volume of 0.08 litres.

In the literature a wide variation of data on the volume of urine excreted by camels are found. In Algeria urine volumes declined from 0.75 litres a day when water was given ad libitum to 0.5 litres when the camels where dehydrated (Schmidt-Nielsen et al., 1956). In Kenyan camels urine volumes declined from 0.8 to 0.2 litres per day (Maloiy, 1972). Siebert and Macfarlane (1971) reported declining volumes from 2.9-8.6 litres to 0.7-1.7 liters per day in camels in Australia and in Morocco Charnot (1958) found urine volumes declining from 5 liters to 1.5 litres per day in the camels studied. This great reported variation in urine volumes are not only due to the different methods (accuracy) in collecting the urine by the researchers but also due to the type (breed) and size of animal studied , what climatic stress (temperature, solar radiation etc) the animal investigated was exposed to and the quality and water content of the fodder given and for how long the animal had been deprived of water (dehydrated).

During dehydration the kidneys reduces urinary water loss both by decreasing the glomerular filtration rate and by increasing the tubular reabsorption of water (Maloiy, 1972). Sperber (1944) found that animals who efficiently conserve water via their kidneys have a proportionally thicker medulla (higher ratio of the medulla/cortex) than animals who are less efficient in concentrating their urine. Abdalla and Abdalla (1979) could verify that the kidneys of the dromedary camel possessed anatomical structural requirements to produce hypertonic urine. The medulla to cortex ratio was 4:1.

The small quantites of urine produced are also well utilized by the animals for cooling by urination onto the backlegs and tail.

Craving for salt

The ability to concentrate its urine enables the camel to tolerate even to require water and plants with high salt content, thus salt (NaCl) is a very important part of the camels diet. Traditional grazing management by most camel beeeders involve regular supplementation of salt, usually by taking the camels to saline pastures, saline wells or salty earth, at least twice a year. It is believed that they will loose condition, abort, give less milk and will be prone to diseases like skin necrosis and arthritis (Peak, 1939), if not given enough salt.

Conservation of urea

The kidneys of the camel excrete small amounts of urine when it is necessary to conserve water. the animal can also produce urine with extremely low concentration of urea, when fed a diet low in proteins (Read, 1925; Schmidt-Nielsen et al., 1957). The urea in the camel formed during protein metabolism is thus not necessarily excreted. It may pass back into the rumen from the blood plasma via the saliva and through the rumen wall. Thus the camel can conserve and recycle urea for protein synthesis when food is low in protein or when growing or pregnant. This mechanism of recycling urea is also found in true ruminants. Valtonen (1979) found in reindeer (confirming Schmidt-Nielsen findings in camels) that the recycling mechanism of urea is coupled to a decrease in water intake.

Metabolic rate

Another adaptive mechanism of this extraordinary animal includes its metabolic activity, which is sensitive to temperature fluctuation. Like all other mammals, exposed to high ambient temperatures, the metabolic rate increases with increasing body temperature. However, in camels dehydration leads to a reduction in the metabolic rate. There is inhibition of thyroxin production during periods of dehydration which decreases pulmonary water loss and reduced metabolism (Yagil et al., 1978).

The metabolic rate of dromedary camels has been shown in the desert and sub-desert of Australia to be about half of that of cattle living in the same environment (Macfarlane et al., 1971). The turnover of water is also low in camels grazing during summer in the desert - about half of the turnover rate of cattle studied in the same area of Australia. The water turnover rate for the camels in the hot season is twice as high as in winter and it is higher in lactating than in non-lactating camels.

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Melatonin secretion in reindeer *(Rangifer tarandus tarandus* L.)

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Abstract: Seasonal breeding cycles in many mammalian species in polar or temperate latitudes enable optimal survival of the offspring. This, however, is obtained only by adjusting the whole reproductive cycle to respond to environmental cues. The cue most frequently used is the annual change in photoperiod. The environmental photoperiod regulates the secretion of melatonin through two effects on the daily rhythm of melatonin synthesis and secretion. Firstly it suppresses melatonin production and secondly it sets a circadian pacemaker in the suprachiasmatic nuclei to the light-dark rhythm. In this study circadian and circannual variations of serum melatonin were investigated in ten adult female reindeer and five calves housed outdoors in the latitude 69 ° 10' N. Samples were taken 4- hourly for 24 h every 3 months. Serum levels of melatonin were determined by the RIA developed by Vakkuri et al. (Acta Endocrinol. 106:152. 1984).Serum melatonin levels exhibited a pronounced seasonal rhythm ($F = 5.88$, $P < 0.001$). A circadian rhythm in melatonin secretion was discernible in autumn, winter and spring in adults with acrophases at night ($P < 0.001$/vs. day). However no circadian rhythm was observed in summer. In calves the circadian melatonin rhythm was observed in autumn and spring, but in the autumn the peak levels were lower than those of adults ($P < 0.05$). In winter and in summer the melatonin levels were equal and no circadian melatonin rhythm was observed. Our present results indicate that a large circannual change in the secretion of melatonin occurs in Finnish reindeer in all age groups. No summer diurnal rhythm in melatonin is seen.

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Abundance of warble fly larvae *Hypoderma tarandi* (L.) *(Diptera:oestridae)* in reindeer *Rangifer tarandus tarandus* (L.) and its relation to reindeer postcalving migration

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Abstract: Intensities of warble fly larvae *Hypoderma tarandi* (L.) were examined in slaughtered reindeer *Rangifer tarandus tarandus* (L.) from different summer grazing areas of Finnmark county, Northern Norway. To test the hypothesis that larval abundance decreases as post-calving migration distance increases (i.e. distance from calving- grounds), herds with differing migration lengths were sampled. The prevalence of infection in the total sample of 1232 animals was 99.9%. The study reveals significant differences in larval abundance between herds from different summer grazing areas. Herds with post-calving migrations have significantly lower larval abundances than herds remaining on the calving grounds the whole summer. The between herd variation in *H.tarandi* larval abundance was assumed to reflect differing densities of the infective stage on the herd's summer ranges. Larval abundance, in turn, is negatively correlated with the distance between the main larval shedding area (i.e. calving grounds) and the area of infection (i.e. summer pastures). This has led to the new hypothesis that the post-calving migration, common in wild reindeer, is a behavioural adaptation which reduces levels of warble fly infections.

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Sympathetic control of brain cooling in reindeer

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Abstract: The cold venous blood returning from the nose of the heat stressed reindeer *(Rangifer tarandus tarandus)* may be distributed both through the angular oculi veins for selective cooling of the brain, and through the facial veins for general body cooling. *In vitro* experiments indicate that the adrenergic receptors of the angular oculi veins are exclusively of the ß- adrenergic type, while the facial veins contain mainly ß - adrenergic receptors. We suggest that the antagonistic neuroeffector organization of these veins play a major role in the control of brain cooling. Thus, simultaneous sympathetic stimulation will result in constriction of the angular oculi veins and release of a pre-existing stretch-induced tone in the facial veins. In this situation the cold venous blood is directed via the facial veins and used for general body cooling. Reduction of sympathetic activity, on the other hand, will result in dilatation of the angular oculi veins and constriction or the facial veins, due to development of myogenic tone in the latter vessels. In this situation the cold venous blood is distributed via the angular oculi veins and used for selective cooling of the brain.

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Reindeer breathe less and save water in the cold

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Abstract: Simultaneous measurements of metabolic rate, respiratory minute volume, respiratory frequency, and oxygen extraction from the inspired air were obtained during treadmill exercise in Svalbard reindeer *(Rangifer tarandus platyrhynchus)* and Norwegian reindeer *(Rangifer tarandus tarandus)*. The experiments were carried out both in summer and winter at ambient temperatures and running speeds ranging from +12 to -30°C and 3.7 to 9.0 $km \cdot h^{-1}$, respectively. We found that respiratory minute volume was generally lower in summer than in winter for a similar ambient temperature, and also that respiratory minute volume was reduced at low ambient temperature both in summer and winter. The change in respiratory minute volume was inversely related to oxygen extraction, the latter being at its highest at the lowest ambient temperature and running speed in summer. Reduction of respiratory minute volume, and hence respiratory water loss, at low ambient temperature is likely to contribute significantly to the survival of these species, particularly in winter when the animals can only replace body water with snow at low temperature.

Key words: *Rangifer tarandus*, temperature regulation, oxygen extraction, arctic

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Introduction

The Svalbard reindeer and the Norwegian reindeer both survive under the most austere nutritional conditions in the arctic and subarctic regions, where energy conservation is a matter of supreme importance. In winter, ambient temperature often rises above freezing followed by long periods of bitter cold. Such weather produces a crust of ice which severely limits the animals access to the already poor winter range. Thus, with plant quality as well as availability much reduced, energy economy attains a substantial survival value. To that end both the Svalbard and the Norwegian reindeer are equipped with fur of unsurpassed quality during winter, while respiratory heat and water loss are reduced by nasal heat exchange in the resting reindeer (Blix and Johnsen, 1983; Johnsen, *et al*, 1985a).

Since oxygen consumption, and hence heat production, is largely independent of variations in ambient temperature in the exercising reindeer (Nilssen, *et al*, 1984), the overall oxygen extraction in the lungs must be altered in accordance with the changes in minute volume that are normally associated with variations in thermal load. In order to elucidate further the respiratory adjustments which are accompanied by variation in thermal load, we have measured simultaneously respiratory minute volume, respiratory frequency, and oxygen extraction in exercising Svalbard and Norwegian reindeer subjected to different ambient temperatures in winter, when fur insulation is prime, and in summer when fur insulation is at its minimum.

Methods

Two adult female Svalbard reindeer *(Rangifer tarandus platyrhynchus)* and two adult female Norwegian reindeer *(Rangifer tarandus tarandus)* were used in this study. Between experiments the animals were kept outdoors at the Department of Arctic Biology, University of Tromsø, where food (RF-71; Jacobsen and Skjenneberg, 1979) and water and snow were available *ad libitum.*

The experiments were carried out in a climatic chamber at temperatures of -24 and +12°C in summer (late July) and -30 and +9°C in winter (February and March). Thus, the summer values were obtained with fur insulation at a minimum, while the winter values were obtained with fur insulation at its prime. The temperature of the chamber was controlled within ±1°C in time and ±2°C in space with a constant wind speed of 0.6 m·s^{-1}. Barometric pressure inside the chamber was the same as outdoors.

The climatic chamber contained a 3.5 m long and 1.0 m wide level treadmill driven by a variable-speed motor providing constant speed regardless of load. The noise level inside the chamber was 63 dB (A) when the treadmill was running at 9 km·h^{-1}. The animals were accustomed to run fully instrumented on the treadmill over a period of 6 months before any measurements were made.

For calculations of respiratory minute volume and oxygen consumption the animals expired into an airtight face mask with two one-way valves, with the outlet valve connected to a 150 liter spirometer. The system was arranged in such a way that the mask could be connected to the animal while it was running. After a sample of air was obtained the air was dried before it was passed through an O_2-analyser (Model S-A, Applied Electrochemistry, California, USA) and a CO_2-analyser (Model Binos 1, Leubold Heraus GmbH, Hanau, West Germany) for measurements of O_2 and CO_2 concentrations, respectively. Respiratory frequency was calculated by use of a thermocouple fixed into one of the valves, monitoring changes in temperature associated with changes in airflow direction.

Rectal temperature was obtained by use of a copper/constantan thermocouple inserted 15 cm into the rectum and connected to a Fluke 2190A digital thermometer (accuracy ±0.1°C).

During experiments the animals were allowed a 60 min equilibration period before exercise began. After 5 min of exercise, when O_2-consumption and CO_2-production had reached equilibrium, the airtight mask was connected to the animal and approximately 100 liters of air was collected. Based on this air sample values for respiratory minute volume, respiratory frequency, tidal volume, metabolic heat production and oxygen extraction were determined. Oxygen extraction was calculated as the percentage partial pressure of oxygen in the inspired air minus that of the expired air.

All volumes have been converted to STPD,

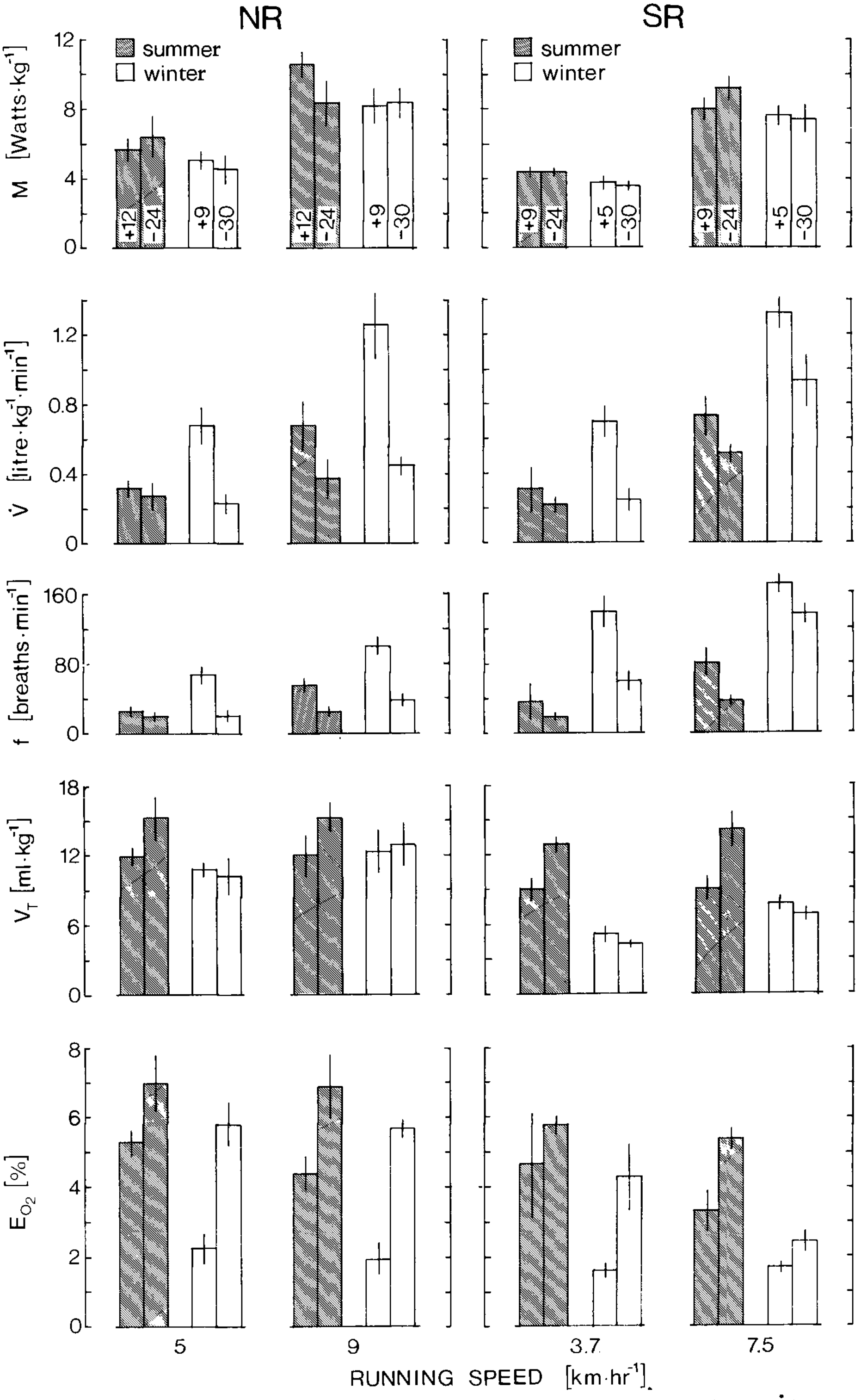

Fig.1. Simultaneous measurements of metabolic rate (M), resporatory minute volume ($\dot{V}$) respiratory frequency (f), together with calculated values for tidal volume (V_T) and oxygen extraction E_{O2}, in Norwegian (NR) and Svalbard reindeer (SR). The values were obtained at various ambient temperatures (indicated within the columns of the top panel) and running speeds both in summer and winter.

and a caloric equivalent of 20.17 J·mlO_2^{-1} have been used for calculation of heat production.

Results

The results from both the Norwegian reindeer and the Svalbard reindeer are presented in Fig. 1. The values for metabolic heat production have been presented in a previous paper (Nilssen *et al*, 1984).

In general, respiratory minute volume was higher in winter as compared to summer for a similar ambient thermal load, but lower at low, as compared with high, ambient temperature within the same season. Reduction of respiratory minute volume in response to cold was especially pronounced at low ambient temperature and running speed in the winter insulated animal. Reduction of respiratory minute volume in response to low ambient temperature was predominantly due to reduced respiratory frequency accompanied by increased tidal volumes in the Svalbard reindeer, but not in the Norwegian reindeer. It appeared, however, that tidal volume at the lowest ambient temperature in summer was elevated in both the Svalbard and the Norwegian reindeer, regardless of running speed.

Reduction of respiratory minute volume in response to cold was always accompanied by a significant ($p < 0.001$) increase in oxygen extraction in both Svalbard and Norwegian reindeer (Fig.1.). This relationship is illustrated in Fig.2.

Discussion

Previous studies in reindeer indicate that respiratory heat loss is low at low ambient temperatures, both during rest (Blix and Johnsen, 1983) and during short periods of exercise (Folkow and Mercer, 1986; Johnsen *et al.*, 1985b). The present results support this view and suggest that respiratory minute volume and frequency, and hence respiratory water and heat loss, are low during exercise at low ambient temperature both in winter and in summer (Fig. 1). Reduction of respiratory minute volume was always accompanied with an increase of oxygen extraction from the inspired air. Our results in exercising reindeer are consistent with previous observations in resting sheep (Joyce and Blaxter, 1964) and pigs (Ingram and Legge, 1969/70) which respond to cold stress by increased oxygen extraction.

The increased oxygen extraction observed

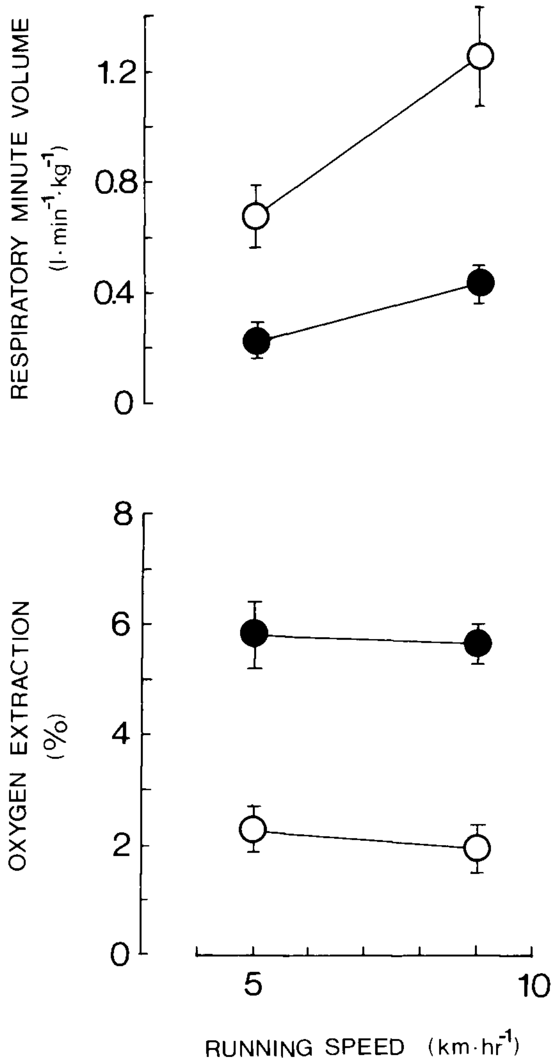

Fig.2. Respiratory minute volume and oxygen extraction in relation to running speed in Norwegian reindeer. The values were obtained in winter at ambient temperatures of +9 (open circles) and -30°C (filled circles).

during exercise at low ambient temperatures in the reindeer may, at least in part, be explained by an increase in tidal volume (Fig.1), but a combination of respiratory and circulatory adjustments, such as those described by Bech *et al.* (1984) in the pekin duck *(Anas platyrhynchos),* may also contribute to this end.

We suggest that reduction of respiratory minute volume, and hence respiratory water loss, in response to cold contribute significantly to the survival of reindeer, both at rest and during running. This would be particularly important in winter when the animal has to replace body water with snow at low temperature.

Acknowledgements

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Hoof and foot loads for reindeer *(Rangifer tarandus)*

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Abstract: Hoof and foot measurements and body weights were taken from 60 living semi-domesticated reindeer *(Rangifer tarandus tarandus* L.) (8 female and 13 male calves, 10 young females (age 2 yrs), 9 young males (age 2-3 yrs) and 20 adult hinds) at the Kaamanen Reindeer Research Station during the winter 1988. The outline of the hooves and the feet (hoof + dew claws) from front and hind legs were drawn when pressed down on a hard substrate in a natural position. Measurements were taken also from foot prints of 26 wild forest reindeer *(R. t. fennicus* Lönn.) (7 calves, 11 hinds and 8 stags) made on hard snow surfaces in Kuhmo and Salamajärvi national park during 1985-88. Reindeer had bigger hooves and feet on front than on hind legs, and male calves had bigger hooves and feet than female calves. Hoof and foot areas of wild forest reindeer (means 74.6 and 200.3 cm^2 for calves, 79.4 and 230.4 cm^2 for hinds and 83.6 and 258.6 cm^2 for stags) were bigger than those of semi-domesticated reindeer (means, front legs, 60.9 and 165.3 cm^2 for calves and 78.9 and 214.1 cm^2 for hinds, respectively). There were significant correlations between live weight and hoof areas ($r = 0.839$ and 0.792), between live weight and foot areas in front and hind legs ($r = 0.714$ and 0.664) and between live weight and foot area when supported by 4 legs ($r = 0.726$) in semi-domesticated reindeer. Load on ground and foot load in semi-domesticated reindeer when supported by 4 legs were 235 and 85 g/cm^2 in calves and 268 and 102 g/cm^2 in hinds.

Key words: snow

Rangifer, Special Issue No. 3, 1990: 249-254

Introduction

Reindeer and caribou *(Rangifer tarandus)* spend over 40 per cent of each year in snow. They are true *chinophiles* (Formozov 1946, Pruitt 1959), which means that they are highly adapted to snow. They have blunt toes, crescent-shaped hooves with a sharp edge for grip on hard snow and ice and functional lateral digits, or dew claws. A heavy growth of bristle-like hairs surrounds the hoof, and the joints of the middle toes can be bent sharply to assume an almost horizontal position. In fact, the reindeer hoof can be considered in a state of transition toward a plantigrade foot (see Nasimovich 1955). Those adaptations greatly increase the surface area of the hoof and help the reindeer to float on soft snow.

External morphology and behavior reflect adaptation to snow. The measurements of the foot area is a prerequisite in the determination of load on ground and, hence, an important measure of the adaptability of mammals to snow of various depths, densities and hardnesses. The load on ground can be divided up into hoof load and foot load (Thing 1977). The hoof load is the measurement most frequently used in the literature (Nasimovich 1955, Kelsall 1969), but the foot load seems to be a more realistic measurement since the whole hoof-pastern-dew claw area offers support in snow (Telfer & Kelsall 1979).

The ability to move in snow not only depends on the snow characteristics, but also on the load on ground and length of legs of the animals. No comparative studies are available on the load on ground between the various reindeer populations. This paper describes hoof and foot measurements for semi-domesticated and wild forest reindeer and calculated hoof and foot loads for semi-domesticated reindeer in Finland.

Material and methods

Hoof and foot measurements and body weights were taken from 60 freely grazing and supplementary fed semi-domesticated reindeer (8 female and 13 male calves, 10 young females (age 2 yrs), 9 young males (age 2-3 yrs) and 20 adult hinds) at the Kaamanen Reindeer Research Station during winter 1988. Hoof and foot characters of living reindeer were measured to the nearest millimetre with a steel metric rule. Broken hooves were omitted. The outline of the hoofs and the feet (hoof + dew claws) from the left front and hind legs were drawn when pressed down on a hard substrate and in a natural position. Hoof and foot areas were calculated according to Kelsall & Telfer (1971) (Fig. 1). To be sure that the hoof and foot areas were as correct as possible, control measurements were taken on distinct reindeer foot prints on hard snow surfaces to determine space between the hooves and the distance between hind edge of hooves and dew claws (Thing 1977). Measurements were taken also on distinct foot prints of 26 indentified wild forest reindeer *(Rangifer t. fennicus* Lönn.) (7 calves, 11 hinds and 8 stags) on hard snow surfaces in Kuhmo and Salamajärvi national park during 1985-1988.

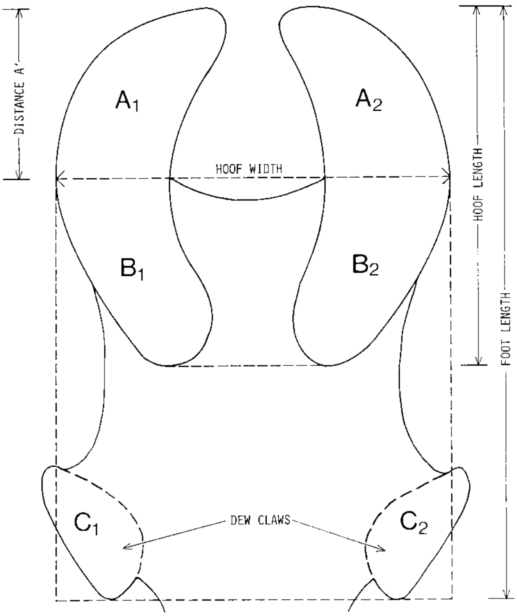

Fig. 1. Diagram of a reindeer foot seen from below showing hoof and foot lengths and hoof outline. Hoof area = A1 + A2 + B1 + B2 cm^2 and foot area is obtained by adding to A1 + A2 area the area of the rectangle (foot length — distance Ax hoof width (see Kelsall & Telfer 1971).

Hoof and foot loads were calculated for each reindeer by dividing live weights by the combined area for all 4 hooves or feet. The load on ground was calculated also for moments when the reindeer was supported by 4, 3, 2 or 1 foot (Fig. 2).

Results and discussion

Results are given in Tables 1 and 2. Reindeer had bigger hooves and feet on front than on hind legs, and male calves and young males had bigger hooves and feet than female calves and young females. According to McCullough (1965) no significant differences existed between sexes in measurements of hooves in black-tailed deer fawns *(Odocoileus hemionus)*, but differences in yearlings and adults were significant. Hoof and foot areas of wild forest reindeer (means 74.6 and 200.3 cm^2 for calves, 79.4 and 230.4 cm^2 for hinds and 83.6 and 258.6 cm^2 for stags) in present study were big-

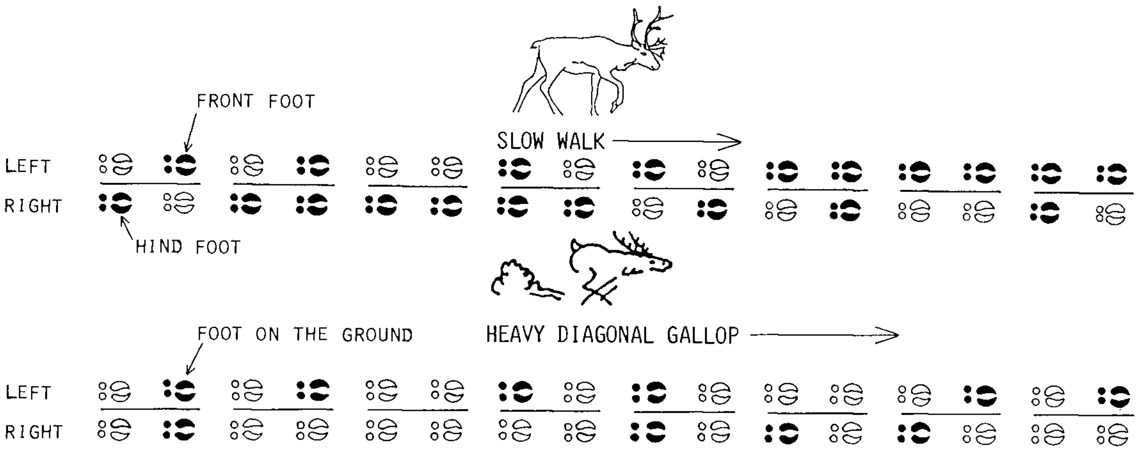

Fig. 2. Graphic representations of the symmetrical normal walk and heavy diagonal gallops of reindeer and their support graphs.

ger than those of semi-domesticated reindeer (means, front legs, 60.9 and 165.3 cm^2 for calves and 78.9 and 214.1 cm^2 for hinds, respectively). The length of the dew claws in wild forest reindeer was also bigger than that of semi-domesticated reindeer (Table 1, Fig. 3).

There were significant correlations between live weight and hoof areas ($r= 0.839$ and 0.792, $n=60$, $P<0.001$) between live weight and foot areas of front and hind legs ($r= 0.714$ and 0.644, $n=60$, $P<0.001$) between live weight and foot area when supported by 4 legs ($r= 0.726$, $n=60$, $P<0.001$) in semi-domesticated reindeer (Fig. 4). The hoof load and the foot load in semi-domesticated reindeer, when supported by 4 legs, was 235 and 85 g/cm^2 in calves and 268 and 102 g/cm^2 in adult females (Table 1).

In the present study, hoof and foot measurements of wild forest reindeer were taken from distinct foot prints on hard snow surfaces. Thus it can be supposed that there appear to be some measurement errors in this material. However, it has long been known that both in wild and semi-domestic stocks in Finland and Sweden the differences are clearest between the mountain and forest reindeer forms (Lönnberg 1909, Klemola 1928, Itkonen 1948). The wild forest reindeer is 10-15 cm taller than the mountain reindeer and semi-domesticated reindeer. It has significantly longer legs, both relatively and absolutely, than the wild Norwegian mountain reindeer and semi-domesticated reindeer (Nieminen 1980, Nieminen & Helle 1980). According to Banfield (1961), the hoof size in wild Fennoscandian mountain reindeer males is 60 x 60 mm and in wild forest reindeer males 110 x 95 mm, which may indicate considerably lower load on ground in the wild forest reindeer. It is concluded, that the long legs and low load on ground of the wild forest reindeer are important adaptations to taiga conditions, where the snow cover is usually very deep and soft (see Nieminen & Helle 1980).

The lowest hoof loads and foot loads were calculated in present study for calves and young reindeer (Table 1). The hoof load and the foot load are important when one wants to know how hard the snow cover has to be in order to support a reindeer. If it is too soft, the reindeer will sink through and therefore have to use more energy when walking than if it was walking on top of the snow cover. Usually the load on ground is calculated by dividing total body weight with total hoof or foot area, and it will then only refer to an animal standing still on all 4 feet and not to an active and moving animal. However, information on load on ground has practical value only when given for 1, 2, 3, or 4 feet as according to the different ways of locomotion used by the animal in uestion. As can be seen in Fig. 2, the reindeer

Table 1. Hoof and foot measurements, live weights and hoof and foot loads ($\bar{x}$ ± S.E.) in semidomesticated reindeer. Measurements of wild forest reindeer were taken from foot prints on hard snow surfaces.

Species	Sex	N	Leg	Hoof length (cm)	Hoof area (cm^2)	Dew claw length (cm)	Dew claw area (cm^2)	Hoof width (cm)	Foot length (cm)	Foot area (cm^2)	Live weight (kg)	Hoof load (g/cm^2)	Foot load (g/cm^2)
Semi-domesticated reindeer													
Calf	F	8	Front	8.6 ±0.1	58.2 ±1.2	6.0 ±0.1	18.9 ±0.4	11.0 ±0.1	16.3 ±0.1	158.4 ±1.2	50.3 ±1.4	234.2 ±2.2	85.2 ±1.2
			Hind	8.4 ±0.1	49.7 ±0.6	4.7 ±0.1	12.6 ±0.4	9.5 ±0.1	16.3 ±0.1	136.9 ±1.3			
Calf	M	13	Front	8.7 ±0.3	62.6 ±2.5	5.8 ±0.3	19.1 ±0.8	11.2 ±0.2	16.9 ±0.3	167.5 ±5.4	54.5 ±5.4	235.1 ±4.1	84.4 ±2.2
			Hind	8.5 ±0.3	53.2 ±1.8	4.7 ±0.2	12.4 ±0.5	10.3 ±0.1	17.1 ±0.3	154.8 ±3.4			
Calf	F+M	21	Front	8.7 ±0.2	60.9 ±2.1	5.9 ±0.2	19.0 ±0.7	11.2 ±0.1	16.8 ±0.2	165.3 ±4.0	52.9 ±2.1	234.8 ±3.5	84.7 ±1.9
			Hind	8.5 ±0.2	51.3 ±1.4	4.7 ±0.2	12.4 ±0.6	9.9 ±0.2	16.6 ±0.2	144.2 ±3.0			
Young	F	10	Front	9.0 ±0.1	63.0 ±0.8	6.2 ±0.2	18.7 ±0.7	11.7 ±0.1	17.3 ±0.2	166.3 ±6.1	60.2 ±1.6	264.3 ±8.1	94.2 ±4.7
			Hind	9.0 ±0.1	51.3 ±1.3	4.6 ±0.1	11.5 ±0.8	11.0 ±0.2	17.3 ±0.3	156.9 ±4.2			
Young	M	9	Front	9.2 ±0.2	70.5 ±3.0	6.6 ±0.2	23.8 ±1.4	12.2 ±0.3	17.7 ±0.4	186.3 ±7.0	69.6 ±2.6	268.0 ±10.2	98.8 ±3.9
			Hind	9.1 ±0.2	60.1 ±2.4	5.1 ±0.2	16.1 ±1.0	10.9 ±0.2	18.1 ±0.3	167.8 ±5.2			
Adult	F	20	Front	9.4 ±0.3	78.9 ±2.7	6.6 ±0.1	20.0 ±1.0	12.6 ±0.1	17.9 ±0.2	214.1 ±4.1	76.2 ±1.2	267.8 ±5.4	101.9±1.8
			Hind	9.3 ±0.1	63.4 ±1.4	4.9 ±0.1	14.6 ±0.6	11.2 ±0.2	17.6 ±0.2	173.4 ±3.9			
Wild forest reindeer													
Calf	F+M	7		10.7 ±0.4	74.6 ±4.8	8.3 ±0.6	21.4 ±0.5	11.8 ±0.6	18.4 ±0.7	200.3 ±9.9			
Adult	F	11		11.4 ±0.5	79.4 ±3.8	8.7 ±0.4	26.2 ±1.4	12.9 ±0.4	19.2 ±0.5	230.4 ±7.8			
Adult	M	8		13.2 ±0.3	83.6 ±5.7	9.5 ±0.8	28.0 ±0.8	13.3 ±0.6	23.6 ±0.7	258.6 ±8.3			

Table 2. Foot load values (g/cm²,x̄ ± S.E.)of semi-domesticated reindeer supported by 1, 2, 3 or 4 feet.

Front foot ↘ Left / Right ↖ Hind foot	Calves (N=21)	Young females (N=10)	Young males (N=9)	Adult females (N=20)
Left ●● Right ●●	84.7 ± 1.9	94.2 ± 4.7	98.8 ± 3.9	101.9 ± 1.8
○● ●●	111.0 ± 2.4	124.7 ± 6.5	129.6 ± 5.2	132.6 ± 2.3
○● ○●	161.1 ± 3.5	184.9 ± 11.6	188.3 ± 7.8	191.0 ± 3.6
●○ ●●	115.0 ± 2.7	126.6 ± 5.5	134.1 ± 5.3	140.5 ± 2.9
●● ○○	169.4 ± 3.8	188.6 ± 8.8	197.6 ± 7.8	203.9 ± 3.7
○● ○○	322.5 ± 7.0	370.8 ± 23.1	376.6 ± 15.8	378.9 ± 6.7
●○ ○○	358.3 ± 10.0	386.6 ± 14.8	417.5 ± 17.5	442.9 ± 9.9
●○ ●○ ↗ Foot on the ground	179.2 ± 5.0	193.3 ± 7.4	208.8 ± 8.8	221.5 ± 4.9

will be supported by only 2 or 3 feet at any time when it is walking. When the reindeer is moving in a heavy diagonal gallop it is supported by 1 or 2 feet only at any movement (Fig 2). Reindeer hoof load is only about 125 to 180 g/cm² when standing (Nasimovich 1955, Thing 1977), 500 g/cm² when walking, and 1 000 g/cm² when trotting (see Thing 1977), compared with 390 to 659 g/cm² for standing moose (Telfer & Kelsall 1979). In the present study the foot load of semi-domesticated reindeer was only about 85 to 102 g/cm² when standing and maximally 358 to 443 g/cm² when the reindeer was moving in a heavy diagonal gallop and supported by 1 foot (see Table 2). The effects of speed on the foot loads were not taken into consideration.

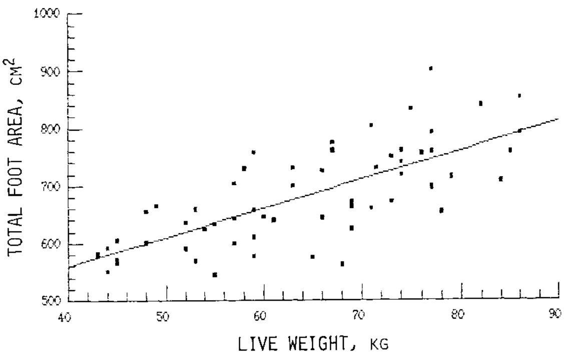

Fig. 4. Regression between live weight and total foot area supported by 4 legs in semi-domesticated reindeer (r=0.726, n=60.

Fig. 3. Wild forest reindeer (*R. t. fennicus,* Lönnb.) have bigger hooves and feet and is also 10 - 15 cm taller than wild mountain and semi-domesticated reindeer. Photo L. Rautiainen.

Conclusions

Semi-domesticated reindeer, and especially wild forest reindeer are well adapted to travel through deep and soft snow. Hoof and foot areas and length of dew claws are bigger in wild forest reindeer than in semi-domesticated reindeer. Reindeer hind legs have bigger hooves and feet, and males have usually bigger hooves and feet than females. There are significant correlations between live weight and hoof and foot areas in reindeer. The results indicate that information on load on ground has a practical value only when given for 1, 2, 3 or 4 feet as according to the different ways of locomotion.

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Activity budgets, food habits and habitat selection of the Porcupine Caribou Herd during the summer insect season

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Abstract: The effects of insect harassment on the activity budgets, food habits and habitat selection of caribou can have a profound effect on physical condition of individuals entering winter. The proportion of time animals spend feeding and lying declines with increasing harassment levels with a subsequent increase in time spent standing. Fecal analysis revealed no discernable alteration in diet during the insect season although indications are that a decrease in food intake is significant. Members of the Porcupine Herd seek insect relief on windswept slopes of mountain complexes within the region. Groups favoured lower insect "risk" habitat types as insect harassment increased and use of higher "risk" as well as diminishing in importance, were located in lower "risk" terrain locations. The implications on the ecology of the herd during this critical time period is discussed in relation to proposed development within the summer range.

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Age-specific fecundity of the Beverly herd of barren-ground caribou

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Abstract: The age-specific fecundity of the Beverly herd of barren-ground caribou *(Rangifer tarandus groenlandicus)* was monitored each winter from 1979-80 through 1986-87. Fecundity in 840 females increased with age from 12% in yearlings to 86% at age 5 years and it did not decline in old (> 11 yr) females. Significant variations occurred among winters and even between two subherds in one winter. Reproductive abnormalities were detected in 2 of 840 females and a probable resorption in 1 of 420 females collected in March. Only about 5% of the fetuses were conceived late, possibly by repeat ovulators. Combining survival and fecundity data yielded age-specific calf production, which indicated that, for example, 54% of calves were born to females 3-6 years old.

Key words: age, calf production, *Rangifer*, reproduction

Rangifer, Special Issue No. 3, 1990: 257-263

Introduction

The results in this paper are part of a study conducted from 1980 through 1987 on the effects of forest fires on the winter range of the Beverly herd of barren-ground caribou. This herd winters largely in the south central Northwest Territories (NWT) between Great Slave Lake and the NWT-Saskatchewan boundary. Caribou were sampled primarily to assess the quality of the winter range by monitoring changes in fat reserves from December to March (Thomas and Kiliaan, 1990a).

Fecundity is a measure of the energy reserves and nutrition of caribou at the time of breeding in late October (Dauphiné, 1976; Thomas, 1982; Reimers, 1983; Tyler, 1987) and of their general well-being, which is related to environmental conditions including the quantity and quality of summer and winter ranges. Estimates of fecundity are needed as part of the formula to derive herd size estimates from counts of caribou on the calving grounds (D. Heard, pers. comm., NWT Wildlife Service). The best information on age-specific fecundity of barren-ground caribou in Canada was the results of Dauphiné (1976) for the Kaminuriak herd.

The purpose of this paper is to further document the age-specific fecundity of barren-ground caribou; to record annual variations in fecundity over several years; to document variability between subherds in one winter; to estimate the relative production of male and female calves by each age class of females; to assess the extent of reproductive disfunction; and to estimate the proportion of late breeders.

Methods

Caribou were sampled from the Beverly herd each March from 1980 through 1987, in late November 1982, and in early December from 1983 through 1986. The usual procedure was to establish a field camp where the caribou were in greatest concentration or near the front of it if the caribou were in migration or travelling from one part of the range to another. These camps were cooperative ventures with the Fort Smith Hunters and Trappers Association.

Reproductive tracts of females obtained in November and December were frozen in the field and returned to the laboratory for examination. In the November 25 - 28 sample, the uteri of some females were enlarged but in others pregnancy was confirmed by the presence of filamentous membranes and early embryonic stages, some detectable by eye and others microscopic. The uteri of pregnant females collected in early December were distended with fluid and the embryos were visible to the unaided eye. In a few late conceivers, pregnancy was assumed if one or more corpora lutea were present. Ovaries were sliced transversely at about 2 mm intervals after fixing them for several days in AFA (ethanol, formalin, and acetic acid). A book of slices was produced by not cutting through the hilum.

Ages were estimated from eruption schedules (0.5 - 2 yr) and from counts of annuli in stained sections of the first incisor and first molar. Among- and within-year (1984) variation in fecundity was analyzed by modified Chi-square (Zar, 1984), as was variation among age classes in low and high fecundity samples and in all samples. We calculated variation (SD and CI) about mean fecundity after Zar (1984:377).

Results

Age-specific fecundity and annual variability

Pooled data for all years provided average fecundity data for 840 females in seven standard age classes used throughout the study and four larger age groupings (Table 1). Two females with reproductive abnormalities were excluded

Table 1. Fecundity of age classes of caribou sampled from the Beverly herd from 1979-80 through 1986-87.

Age class (yr)	Fecundity[a] (%)	Standard deviation[b]	Confidence interval[b]	Sample size
0.5-1	0.0	0.0		37
1.5-2	12.0*	3.4	6.1-20.4	92
2.5-3	71.7	4.1	62.7-79.5	120
3.5-4	81.5	3.8	72.9-88.3	108
4.5-5	85.5	3.9	76.1-92.3	83
5.5-11	87.5[c]	1.8	83.5-90.8	343
>11	90.9	3.9	80.0-97.0	55
>2	83.7[d]	1.4	80.8-86.3	711
>3	86.1[d]	1.4	83.1-88.8	591
>4	87.2[d]	1.5	83.8-90.0	483
>5	87.5[d]	1.7	83.9-90.6	400

[a] The pregnancy rate in unweighted data from all collections.

[b] After Zar (1984:377 and 378).

[c] Excludes one barren female and one female with no uterus.

[d] Includes barren females.

from the 5.5 - 11 year class but included in the larger age groups, e.g., >2 years. We excluded them from the standard age classes because their chance occurrence could unduly influence relative age-specific fecundity. We included them in the large groupings of age classes because they affect overall calf production. Fecundity stabilized by the 4.5 - 5 year class (binomial test, P<0.05).

Fecundity of yearlings averaged 12% with yearly values ranging from 0 to 31% where minimum n=10 (Thomas and Kiliaan 1990b). Fecundity of females 2.5-3 years old varied from 47 to 90 % and from 64 to 92 % in 3.5-4 year females where n ≥10. In females >4 years old, pregnancy rates varied significantly (P <0.01) from 1981-82 through 1986-87, ranging from 78 % (n=50) to 94 % (n=51) (Thomas and Kiliaan, 1990b). The pregnancy rate was 98% in 60 females >4 years old in a subherd sampled in March 1984, excluding one female with no ovaries.

Annual fecundity, including two disparate rates in 1983 - 84, fell into low (1982 - 83; 1983 - 84, subherd A; 1985 - 86; and 1986 - 87) and high categories (1981 - 82; 1983 - 84, subherd B; and 1984 - 85). Fecundity in females 2, 3, 4, 5, 6 - 11, and >11 years old were 2, 64, 77, 80, 81, and 86% (n = 28 - 181) and 34, 86, 90, 95, 94, and 96% (n = 27 - 142) in the low and high groups, respectively (Thomas and Kiliaan 1990b). Fecundity in 1979 - 80 was low (50 and 86% pregnancy rates in 2.5 - 3 and >3 year age classes, respectively) in a segment sampled in the NWT. In 1980 - 81, 14 of 15 females in our sample were pregnant.

Subherd variations in fecundity

In December 1983 and March 1984, a subherd (A) was sampled that straddled the tundra/taiga ecotone all winter. Another subherd (B) sampled in March, remained in the taiga all winter. Yearling pregnancy rates were 0% (n = 10) and 33% (n = 9) in the two subherds; 80% (n = 45) and 99% (n = 74) in older females (Thomas and Kiliaan 1990b). The lower fecundity in subherd A was present in the December sample and was related to poorer fat reserves. For example, average depths of back fat in females >2 years old in the subherds were 10 and 21 mm, respectively (Thomas and Kiliaan, 1990a). This variability was attributed to unknown events on the spring and summer range before the rut in October.

Age-specific calf production

Relative calf production by each age (Table 2) was the product of the frequency of each age class in the breeding population and the fecundity of that class (Table 1). Frequencies were derived from a quadratic regression equation for females >2.5 years old in all collections (mean date February 21) adjusted to the June 8 "birth pulse" (Caughley, 1977) and extrapolated to include females 2 years old (Thomas and Barry, 1990. Our shooters selected against small, lean caribou and therefore calves and yearlings were excluded from the survivorship data.

Relative calf production was highest in females 3 and 4 years old with progressive decreases in older females. Over half (54%) of the calves are produced by age classes 3 through 6 years.

Young females (2 - 4 yr) produced more female than male offspring and the reverse occurred in old females (>10 yr) (Thomas *et al.*, 1989). Apparently 3 - 6 year-old caribou produce 59% of the female calves.

Reproductive abnormalities

A 7-year-old female collected in March 1984 had a small, pale uterus characteristic of calves and nulliparous (never pregnant) yearlings. Ovaries were absent. A female nearing 6 years old, collected in March 1986, had no detectable uterus though its ovaries had developed. A 5-year-old female in the same group as the female with no uterus had about a liter of yellow

Table 2. Relative age-specific production of caribou calves in the Beverly herd from 1980 through 1987 based on estimated frequency of female age cohorts in the breeding population, their mean fecundity, and fetal sex ratios.

Age class[a] (yr)	Frequency[b]	Fecundity (%)	Calf production/100F Males & females	Females only
2	16.2	12.0	1.9	1.2
3	14.4	71.7	10.3	6.4
4	12.8	81.5	10.4	6.5
5	11.3	85.5	9.7	4.7
6	9.8	85.9[c]	8.4	4.1
7	8.4	79.7[c]	6.7	3.2
8	7.1	94.9	6.7	3.3
9	5.9	92.3	5.4	2.7
10	4.7	88.6	4.2	2.1
11	3.7	85.0	3.1	1.0
12	2.7	90.0	2.4	0.8
13	1.8	91.7	1.7	0.5
14	1.0	100.0	1.0	0.3
15	0.2	100.0	0.2	0.1
16	0.0	50.0	0.0	0.0
Totals	100.0		72.1[d]	36.9

[a] Age when calf produced (conceived when 7 months younger).

[b] Based on a smoothed survival curve at June 8 (Thomas and Barry, 1990).

[c] Excluding two females with reproductive tract malformations.

[d] Total is 72.3 where calculations carried to three decimal places.

Table 3. Statistics of three female caribou with reproductive abnormalities in relation to mean values for others in the same sample from the Beverly herd of barren-ground caribou.

Month/ year	Age class (yr)	Condition	Weight (kg)	Back fat (mm)	Kidney fat (g)	Femur length (mm)
Mar 84	7	No ovaries	97	26	163	297
Mar 84[a]	6-11	Pregnant	88.1	21.5	127	274
Mar 86	6	No uterus	111.5	1	114	304
Mar 86	5	Resorption	91.5	21	119	271
Mar 86	6-11	Pregnant	87.6	12.8	107	279
Mar 86	6-11	Not pregnant	76.8	5.8	63	276

[a] Subherd B, 1984, in which all other females 6-11 years old were pregnant.

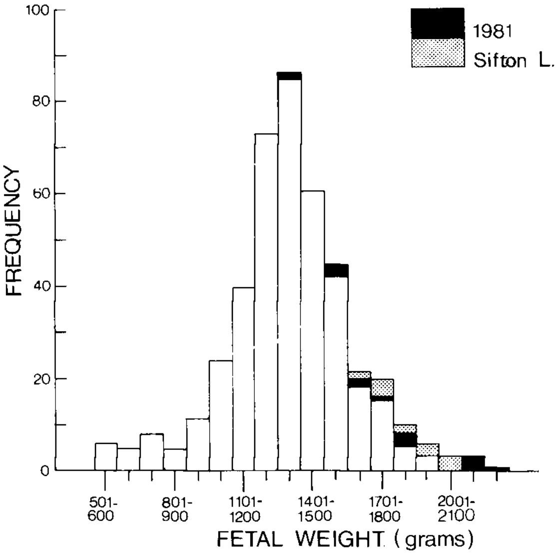

Figure 1. Distribution of fetal weights of barren-ground caribou sampled from the Beverly herd in March, 1980 through 1987.

fluid in its uterus and no fetus. A resorption was suspected. Statistics for the three females (Table 3) reveal that the female with no ovaries was heavier, larger, and fatter than average. The female with no uterus was the heaviest of 591 females >3 years old that we collected over the 8 years, even though it had little mantle fat.

Fetal weights and late conceptions

The frequency distribution of fetal weights (Fig. 1) included late-March samples obtained in 1981 and 1984 (Sifton Lake sample). Fetuses less than 800 g were attributed to late breeders, probably females that cycled more than once before they became pregnant. Late breeders accounted for 4.8% of 420 females. Their exclusion and exclusion of the 1981 and Sifton Lake samples produced a normal distribution of weights. One female aged 5 years had conceived in January based on its 9.2 g fetus collected in March.

Fetal weights were unrelated to age of dam (Table 4). Only in the >5 year class was fetal weigh influenced ($P<0.01$) by sex. Weights increased through the first four age classes but not significantly so (Table 4).

Discussion

Fecundity of the Beverly herd from 1980 through 1987 was similar to that of the adjacent Kaminuriak herd in 1966 - 68. Fecundity was

Table 4. Weights of male and female fetuses sampled from the Beverly herd of caribou in mid-March, 1980 through 1987.

Age class (yr)	Fetal weight (g)					
	Males			Females		
	Mean	SE	n	Mean	SE	n
1.5-2	1160	32	6	1021	61	2
2.5-3	1287	55	22	1294	46	35
3.5-4	1454	57	18	1321	46	29
4.5-5	1435	31	25	1401	39	21
>5	1397	19	120	1318	21	108
>1	1387	16	191	1320	17	195
>2	1395	16	185	1323	17	193
>3	1409	16	163	1330	18	158

[a] Excludes fetuses probably conceived late (<800 g) and fetuses in samples obtained late in March (1981 and 1984, subherd A).

higher in young females in the Beverly herd but slightly lower in older (e.g., >5 yr) caribou compared with Dauphiné's (1976) results. Parker (1981) reviewed age-specific fecundity in several caribou herds. His values for the George River herd in April 1980 were higher than the others: 43% in 21 yearlings, 90% in 20 females 2.5 - 3 years old, and 95% in older females. Messier *et al.* (1988) gave fecundity values of 12, 70, and 80% for 2, 3, and >3 year females in the George River herd. The previous estimate for the Beverly herd (McEwan, 1963) did not deviate from the present results among females >3 years old. Limited data in the younger age classes prohibit comparisons.

There was no decline in fecundity with age in the Beverly herd (McEwan, 1963; this study) in contrast with declines in the Kaminuriak herd (Dauphiné, 1976) and apparently in the George River herd in 1980 (Parker, 1981). Parker's results were influenced by the chance sampling of 3-year-old females with superior energy reserves and insufficient numbers of old caribou.

The observed low and high fecundity could not be explained by environmental conditions on the winter range, as the caribou maintained their fat reserves in all five winters (Thomas and Kiliaan, 1990a). The fecundity of Svalbard reindeer *(R.t. platyrhynchus)* was either low or high and, with one exception, alternated between the categories (Tyler, 1987).

The incidence of resorptions and abortions is difficult to obtain. Early loss of embryos would go undetected. Our rate of 1 resorption or abortion in 420 would apply to the gestation period between about months 2 and 5. Dauphiné's (1976) rate of 0 - 2% may have been artifacts because of poor fixation or multiple cycling. McEwan (1963) listed 3 cases in 52, but criteria used to identify absorptions were lacking. Tyler (1987) suspected that abortions were common in undernourished Svalbard reindeer.

The >5 year age class ofifemales best reflects annual variations in fecundity caused by environmental factors. Females in young age classes (2-4.5 years) may have their energy reserves depleted by successfully rearing a calf and fail to breed the following October (Dauphiné, 1976). High pregnancy rates in young females in one winter could be followed by low rates the following year with equivalent environmental conditions. Therefore, assessing environmental conditions by the performance of females 2 - 5 years old must be done with caution. The pregnancy rate in yearlings probably is a sensitive barometer of the environment in the preceding 2 years.

Conclusions

1. Average fecundity (pregnancy rate) of the Beverly herd from 1980 through 1987 increased progressively with age. Overall, fecundity was comparable to that of the Kaminuriak herd in 1966 through 1968, being somewhat higher in young females and lower in those over 5 years old.
2. There was no decline in fecundity in old (>11 yr) females in contrast with the results from some previous studies.
3. Fecundity varied considerably from year to year where n≥10: from 0 to 31% in yearlings, 47 to 100% in the 2.5 - 3 year class, 64 to 90 % in the 3.5 - 4 year class, and 79 to 98% (in a subherd) in the >4 year class.
4. The fecundity of two subherds varied significantly in 1983 - 84.
5. Intrauterine mortality between 2 and 5 months of gestation was exceedingly low, involving one suspected resorption in 420 (March samples).
6. Light (<800 g) fetuses, possibly arising from failure to conceive at first estrus, comprised 4.8 % of 420 fetuses obtained in March collections. A fetus weighing 9.2 g was estimated to have been conceived in January by the 6-year-old female.
7. Estimates of age-specific calf production

were obtained by combining data on survivorship of females and of age-specific calf production.

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Veterinary Medicine/Growth, Lactation and Reproductive Physiology

Key note address:

Management stress in reindeer

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Abstract: The general mechanism and biological effects of stress are dealt with. Investigations performed on semidomesticated reindeer concerning the stress response under different herding and management conditions are presented and discussed.

The findings indicate that:

Reindeer are susceptible to management stress and that their degree of tameness plays an important role in the development of stress lesions such as muscular and myocardial degeneration and abomasal haemorrhages, etc.

The animals are not favoured by rests between events of stress exposure as the effects produced tend to be cumulative.

Depletion of muscular glycogen stores, increased catabolism of muscular protein, muscular degeneration and increased blood-urea levels can not be excluded as a cause of an altered and bad taste of the meat, i.e. a bad meat quality.

Thus prolonged and repeated manual handling and transportation of live animals should be avoided. The use of helicopters or other motor vehicles must be correlated to the tameness of the animals and to environmental conditions.

Stress due to incorrect management methods may, by means of stress induced lesions, severly affect the productivity of reindeer.

Key words: stress lesions, meat quality

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Introduction

During many years of work with reindeer under different circumstances, I was taught by several very experienced herdsmen the importance of careful handling of the animals. When selecting for slaughter these herdsmen were experts in "reading the behaviour" of reindeer, picking out animals with abnormal breathing, movements, etc. I also learned the importance of careful handling and early slaughter of animals intended for consumption, in order to obtain the best meat quality. (Hanssen et al 1984). Obviously, the best meat is obtained from animals shot with a rifle when grazing or resting, i.e. totally undisturbed. It was also obvious that harsh and rough treatment under unsuitable conditions, such as gatherings during hot sunny summer days could be fatal, first of all for young animals and calves. In fact, the combined effects of heat, insect harassment and gatherings seem to be able to contribute to a considerable calf mortality (Rehbinder 1975). Today, the demands of rationalization are valid also for the reindeer industry. The "old methods" of intensive herding and relatively tame animals are not practiced any more but have been replaced by an extensive herding of semidomesticated or almost wild animals, and the use of modern equipment such as motorcycles, snow mobiles, lorries for transports, etc.

The objective of this report has been to compare some common knowledge of the effects of stress in animals with results obtained from four different investigations concerning management stress in reindeer.

What is stress and how does it affect the organism?

According to Selye (1956, 1974) stress is the nonspecific response of the body to any demand upon it. The exposure to different stressors is, as such, not harmful and not producing disease. Stress becomes harmful to the body when the normal level of resistance is exceeded by any stimulus or succession of stimuli of such magnitude as to tend to disrupt the homeostasis of the organism. Thus, a stage of exhaustion is initiated when the capacity to adapt to the sum of all nonspecific systemic reactions of the body, is exceeded, which ensue upon long-continued exposure to systematic stress. This has been known as the General Adaption Syndrome of Selye (loc cit) and points out that the body's adaptability is finite. Hence, when mechanisms of adjustment fail or become disproportionate or incoordinate, the stress may be considered an injury, resulting in disease, disability, or death.

Selye's concept of the non- specific stress response has later on been refuted. It is now widely accepted that there are unique but different endocrine responses to different physical, chemical, and psychological stress factors (Mason 1968, Dantzer and Mormide 1988, Griffin 1989). The effect of stress may be influenced by the severity of the stressor the time during which it is applied (acute vs chronic) or whether there is a possibility to escape the stressor or not or if it is applied repeatedly (escapable vs inescapable, Griffin 1989). Any external stimulus that challenges homeostasis can be viewed as a stressor and the changes in biological function which occur as attempts to maintain homeostasis consitute the stress response (Moberg 1985). Capture of wild animals, restraint and transport of wild or semidomesticated as well as domesticated animals may consitute considerable stress factors to which the animals can adapt with difficulties only or not at all. Failure of the animal to express the flight-fight response results in the expression of ange or rage, and if the stimulus persists, in frustration or helpless. (Griffin 1989).

In man and animals with a highly developed nervous system, emotional stimuli are in fact the most common and important stressors (Levi 1967, Seley 1974, Stephens 1980, Becker 1987).

Animals have a genetically determined behaviour which includes defense mechanisms and warning signals (Fabricius 1973). Animals do also have space requirements which are depending upon many factors such as living habits, size, species, strain, etc. The space requirements may be divided into zones or distances of different size (Fox 1974, Fig 1). When humans or animals regarded as a threat, enter into the different zones, the response elicited may vary from alertness, over anxiety and distress to fear, depending on how close the threat comes. Approach or intrusion within the flight distance will provoke anxiety and/or distress, and the animal will flee in order to try to keep or regain the flight distance. An intrusion into the personal or critical distance will make the animal frightened and it will, if proximity becomes intolerable, make all efforts to escape, and if necessary, it will attack and fight.

The size of the zones and the lenght of the

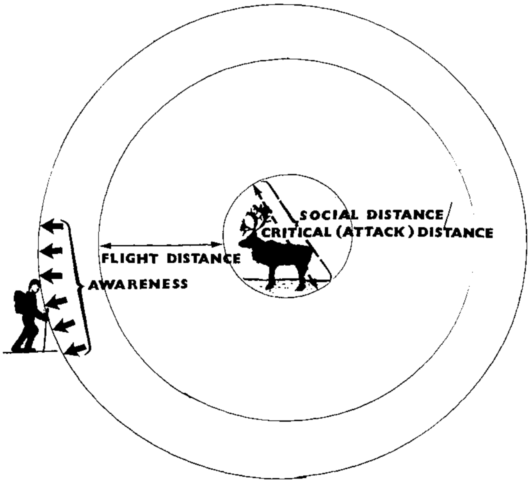

Fig.1. Animal's space zones. Approximate concentric zones in the spatial world of a reindeer are arbitrarily depicted (Adapted from MW FOX, Envir. Var.Anim. Exp., H. Magalhaes, ed., 1974).

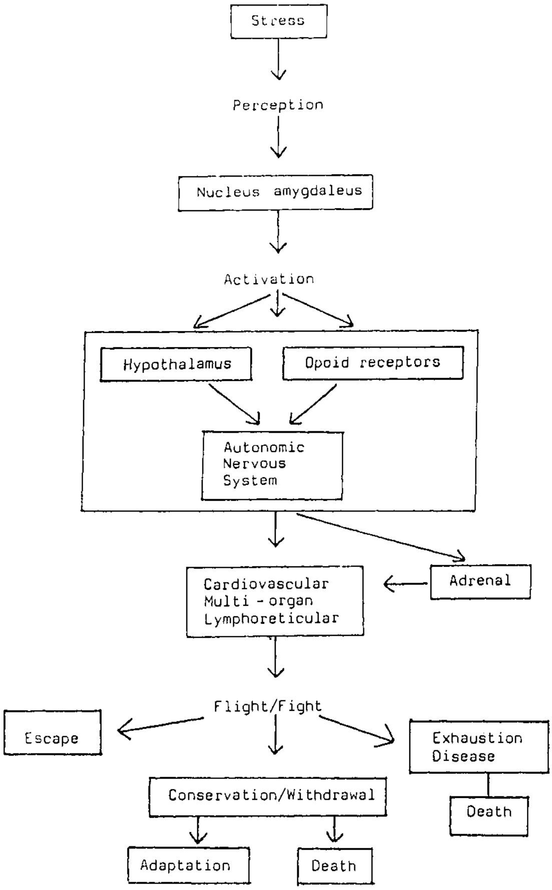

Fig. 2. Sympathetic adreno-medullary response to stress.

distances, however, are depending upon the tameness of the animal. Socialization of animals with man not only facilitates handling but also increases tolerance to proximity. Tame, socialized species do even seek human contact. Tameness also eliminates the flight response and defensive aggression so characteristic of wild non-socialized animals (Fox loc cit).

There are two major pathways for the effect of stressors on the individual; the sympathetic - adrenomedullary response to stress (Fig 2) and the hypothalmic-pituitary-adrenal response to stress (Fig 3).

The sympathetic-adrenomedullary response is an immediate response to cognitive stimuli resulting in a direct flight or fight situation, caused by a stimulation of the autonomic nervous system.

The somatic response to the catecholamines released is characterized by increased cardiovascular function and metabolism, vasoconstriction and splenic contration (Axelrod and Reisine 1984).

The flight-fight system mediates the active response whereby the animal struggles to escape from an external danger. The conservation - withdrawal system comes into play when the active response is fruitless, and it serves to conserve energy and reduce contact with the environment (Engel 1967). The hypothalamic-pituitary-adrenal response is a slow response to stress. Failure of the sympathetic-adrenomendullary system to resolve stress leads to the activation of the hypothalmic- pituitary-adrenocortical response which is manifest behaviourally by the conservation-withdrawal reaction and displacement activities (Stephens 1980, Griffin 1989). The persistence of the hypothalamic-pituitary-adrenocortical activation will

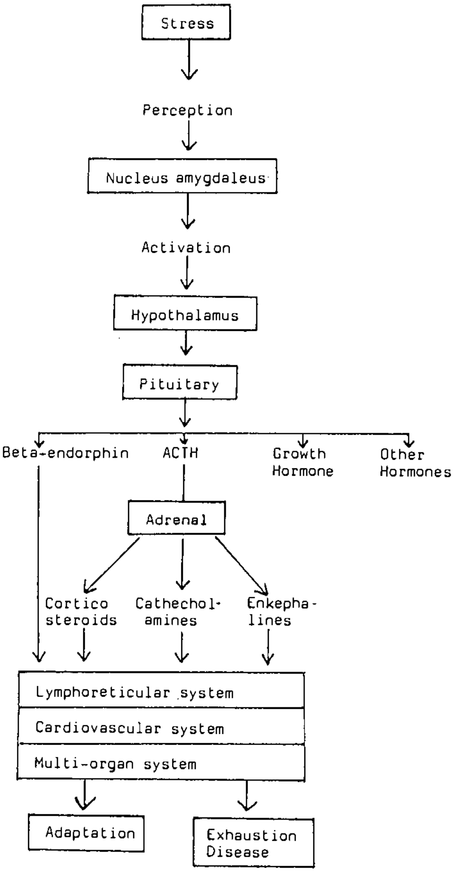

Fig. 3. Hypothalmic - pituitary - adrenal (HPA) response to stress.

produce prepathological or pathological changes (Kagan & Levi 1974) and may cause the death of the subject (V. Holst 1985).

To develop a stress response the animal must be able to identify the external stimuli which represents a threat to its homeostasis, and then when appropriate, make those adjustments in its biological balance which will provide the best biological defense against the threat. Perception of an external threat, whether a change in temperature, a social conflict or the experience of pain is thus of crucial importance, considering the fact that the first controlling component of an animal's response to an external event is the manner in which the animal perceives a stimulus (Moberg 1985). Experience of different factors and situations plays an important role in the response of the animal to a stressor.

When wild or semidomesticated animals are captured, restrained, and immobilized, this is a very definite intrusion into their personal distances and produces a severe emotional stress response. The animals may then behave differently. Some may fight desperately trying to escape, while others may exhibit different displacement activities. The latter animals may act as if they had surrendered, accepting the situation, while others may show other and more obvious kinds of abnormal behaviour, such as biting themselves, gasping, etc. Neverthenless, animals that seem to adapt to the situation may thus suffer from severe emotional stress. Immobilization is in fact a common and effective method to produce gastric stress ulcers, and there is a progressive increase in the incidence of lesions correlated to the duration of immobilization (Brodie 1963, Ader 1971). Servere, prolonged and repeated stress exposures may also produce muscle degeneration (Bartsch *et al.* 1977) and myocardinal degeneration (Jönsson & Johansson 1974) and a number of other important physiological changes (Harthoorn 1977). By amygdalectomy, Johansson et al (1982) demonstrated the importance of the amygdaloid part of the limbic and the sympathetic-adreno- medullary system. Hence, by preventing the animal's conception of fear, by amygdalectomy, the production of restraint-stress induced lesions was prevented. In laboratory animals it is found that even minor changes in the environment may affect several physiological parameters (Gärtner *et al.* 1980) but also that warning signals sound and smell, may produce a considerable state of emotional stress (Sadjak *et al.* 1983). Thus situations thought to be fearsome, i.e. intrusions wihtin defence distances, warning signals, restraint situations, transports, etc are all considerable stress factors.

It is obvious that rationalization and the changes in herding methods it produces are connected with several factors causing stress in reindeer. Therefore, the investigations carried out by us were initiated in order to study the influence of different factors such as handling, transports, herding conditions, tameness, ect, on the stress response of extensively herded, semidomesticated animals.

Own investigations

I. Influence of stress on some blood constituents in reindeer (Rangifer tarandus L) (Rebbinder & Edquist 1981).

Blood samples from 3 different groups of animals were compared. The first group consisted of 10 animals; 6 bulls (3-5 years), 2 females (2 and 4 years); and 2 calves (1 female and 1 male). They were killed, by means of a rifle-shot in the head, when resting or grazing. These animals were considered an undisturbed control group.

The second group consisted of 5 female reindeer (1-4 years and 1 calf) kept for experimental purposes in a corral. These animals were confined during feeding. After the initial sampling they were released into the corral and kept moving during a 2 hour period, whereafter they were recaptured with a lasso for final sampling.

The third group consisted of 10 animals selected at a slaughter event; 4 bulls (2-7 years), 3 females (3-7 years) and 3 calves (2 females and 1 male). The animals had been subjected to one day of gathering and herding into a large grazing corral where they rested during the night. The next day they were driven into a small (60 cm in diameter) selection corral where they were captured with a loop on a pole and put into a small pen from where they were taken out by hand and slaughtered.

The blood picutre of the shot, unstressed animals (Group I) appeared different from that of the groups subjected to different kinds of stress (Fig. 4). In the unstressed animals the blood leucocyte composition was found to be comparable to normal values of domestic ruminants (Schalm *et al.* 1975).

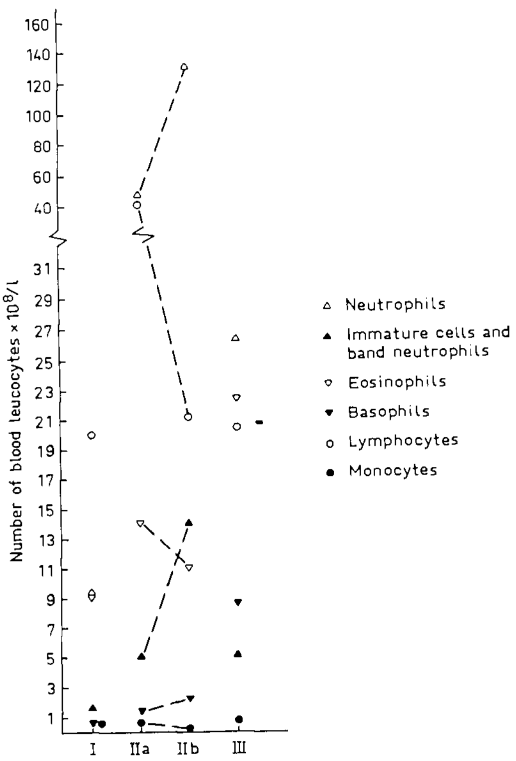

Fig. 4. Mean values of number of blood leucocytes in unstressed and stressed reindeer.
I = Unstressed animals: Group I
IIa = Experimental animals: Group IIa. Captured by hand and sampled animals.
IIb = Experimental animals: Group IIb. Animals recaptured by means of lasso and sampled after being persued, kept moving, during 2 hours.
III = Reindeer exposed to management stress. Group III. Samples obtained at slaughter event.

In the experimental animals (Group IIa captured and sampled and Group IIb recaptured with lasso and sampled after being kept moving, during 2 hours) there was seen a marked increase of segmented neutrophils, band neutrophils, and immature cells. The changes were still more pronounced at the second sampling with an obvious decrease in the number of lymphocytes and eosinophils. In the group of slaughter animals (Group III) the same values were found as for the experimental animals except for very high values of eosinophils, reflecting a heavy burden of endo- and ectoparasites. Of the noncellular constituents,

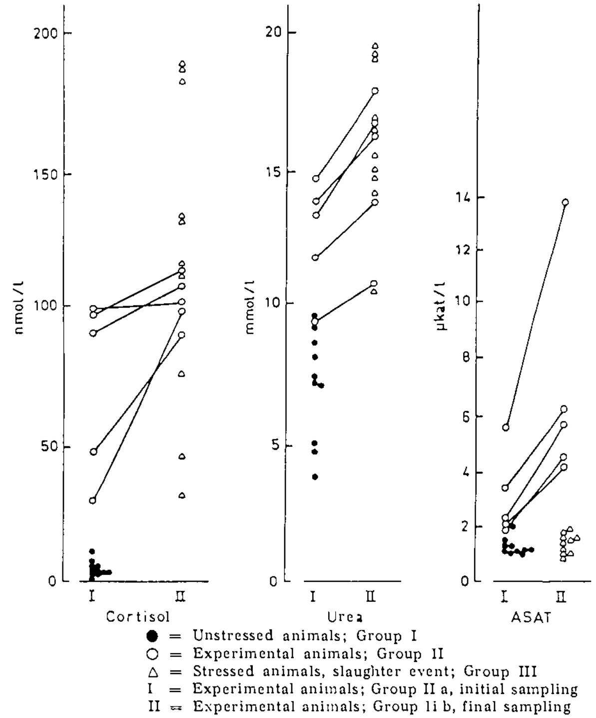

Fig.5. Cortisol, urea and ASAT values in stressed and unstressed reindeer.

marked differences were noticed between unstressed an stressed animals in the levels of cortisol and urea. In addition, a pronounced increase between samplings was found in Group II concerning ASAT, (Fig. 5). All animals in the study were exposed to a low level of physical stress. The major stress event was mental stress, obviously due to the manual handling as such.

II. Skeletal muscle characteristics of reindeer (Rangifer tarandus L.) (Essén-Gustavsson & Rehbinder 1985).

Fiber type composition, fibre areas, capillaries, enzyme activities, and intramuscular substrates were analysed in skeletal muscle samples (triceps, gluteus, semitendinousus, and longissimus dorsi). Two eleven-month-old reindeer, one male and one female, were used in the study. The animals were killed by means of a rifle-shot in the brain when resting or ruminating. These animals also served as controls for a similar investigation on animals exposed to stress. Muscle samples were obtained within 10 min. of death. The samples were immediately frozen in liquid nitrogen. The muscles were analysed for fibre composition, fibre areas, capillaries, enzyme activities (citrate synthase, CS), 3-OH-acylCoA dehydrogenase (HAD), lactate dehydrogenase (LDH), triose phosphate dehydrogenase (TPHD), glycogen, and triglyceride levels.

The muscles contained 10-20% Type I fibres (slow twitch fibres). The percentage of Type IIB fibres (40-60%) was higher than the percentage of Type IIA fibres (20-40%). All fibre types revealed medium or dark staining intensity for oxidative capacity. Glycolytic capacity was greatest in Type IIB fibres. All fibres stained for glycogen, while Type I and IIA fibres stained for lipids.

The mean number of capillaries in contact with fibres of each type, relative to fibre type, were high in all muscle types. The metabolic profile of reindeer muscle indicates that energy to a great extent is produced via oxidative pathways, and that both carbohydrates and lipids are important for energy production.

III. The influence of stress on substrate utilization in skeletal muscle fibres of reindeer (Rangifer tarandus L) (Essén-Gustavsson & Rehbinder 1984).

The same animals as in Investigation I were used and the same investigations as in Investigation II were performed. The animals of Investigation II served as controls. It was found that even moderate stress in connection with handling, sampling, and herding caused a very pronounced depletion of glycogen in mainly II A and II B fibres (Table 1) as compared to the control animals. Type II B fibres are fast-fatiguable and largely involved in maximal efforts (Burke *et al.* 1973), providing high speed and thus part of flight behaviour. Also, intramuscular triglyceride levels decreased, but mainly so in type I fibres. Muscle lactate levels increased in all animals. Reindeer muscles appear to have a great capacity to oxidize both car-

Table 1. Glycogen in the semitendinosus of stressed and unstressed reindeer. A = initial samplings. B = final sampling. Controls were killed by means of a rifleshot in the head.

Groups	Animal No	Glycogen /μmol/g A	B
Experimental animals	Calf	174	164
	759	217	155
	758	256	187
	52	120	32
	994	17	15
Controls	106	523	
	184	464	

bohydrates and lipids.

The experimental animals, as compared to the controls, showed increased cortisol, ASAT, und urea-values (Table 2).

IV: A field study of management stress in reindeer (Rangifer tarandus L), (Rehbinder, Edquist, Lundström & Villafané 1982).

The objectives of the investigation were to perform a field study of the pathological and haematological responses in different reindeer herds subjected to different management methods.

The investigated herds were:

A. ÖSTRA KIKKIJAURE (22. Aug.): Ten animals were killed, resting or grazing in the forest, by means of a rifle-shot in the head. These animals were considered as unstressed controls and served as such also in the previous investigation A.

B. ROMPERHEDEN (22. Jan.): About 1800 animals were herded into a large grazing corral of about 1,5 km^2. The animals were gathered by men on snowmobiles and on skis. The following day the herd was driven into an ordinary corral. (Romperheden, Fig. 6:1), using the same method. The herd was very calm. Parts of the herd where driven into a selection corral were those to be slaughtered were picked out and lassoed, dragged out of the corral and stunned. The remaining animals were let out into a smaller grazing corral.

C. ROMPERHEDEN (23. Jan.): The same herd as for B had been kept overnight in a small (0,25 km^2) grazing corral. In the morning the animals were driven by herdsmen in skis and by snowmobile back into the ordinary corral. This time the animals were rather reluctant to enter the corral. The average drive distance of less than 1 km took about 40 min. Most of the snow was trampled into a dry slush and did not hinder the movements of the animals. Selection for slaughter was done in the same way as on the previous day (see B).

Table 2. Cortisol, ASAT and urea levels in the blood of stressed and unstressed reindeer. A = initial sampling. B = final sampling. Controls were killed by means of a rifleshot in the head.

Groups	Animal no	Cortisol nmol/l A	B	Asat μkat/l A	B	Urea μ/nmol/l A	B
Experimental animals	Calf	90	106	2,3	5,7	13,4	16,8
	759	30	97	1,9	4,5	9,3	10,7
	758	48	89	2,1	4,2	11,7	13,9
	52	99	100	3,4	6,2	13,9	16,3
	994	97	112	5,6	13,8	14,8	17,9
Controls	106	15	—	1,9	—	5,2	—
	184	2	—	1,2	—	5,1	—

Plate 1. Animals of herd B inside the corral. The animals are seized with panic. The picture is taken 1 hour after the animals entered the corral, but they are still running senselessly. Photo C. Rehbinder.

D. BRÄNDVALLEN (31. Jan.): Around 3000 animals of a mountain herd were grazing in the forest not far from the corral. They had been gathered 3-4 days earlier by snowmobile borne herdsmen. On Jan. 31, about 1200 of these animals were driven into a corral by means of a helicopter and, at the end of the drive, by snowmobiles. The average herding distances was approximately 3-4 km. During the drive the animals were obviously seized with a panicky fear of the helicopter, but were prevented from escaping or stampede by a thick snow cover. The drive took nearly 2,5 hours. Inside the corral the animals continued to run and most of them never calmed down (Plate 1, Fig. 6:2). Six animals were found dead or dying. After about 1 hour in the corral, parts of the herd were driven into a small selection corral, 15 m in diameter, where the animals were captured by hand (Plate 2). Those picked out for slaughter were put into a rectangular pen (Fig. 6:2) from which they were taken by hand for slaughter, or driven into lorries for transport to a slaughter-place (Brändåsen), 71 km away.

Plate 2. Reindeer dragged out of the corral after being selected for slaughter. A typical example of restraint stress added to other stress events. Photo C. Rehbinder.

Several persons stood around and inside the selection corral. Most of the animals inside the selection corral and pen were seized with fear and panic and showed abnormal behaviour such as hyperactivity, attempts to escape by jumping the fences, aggressiveness, but also lethargy.

About 4 hours after the start of the drive the first slaughters took place. No other than animals slaughtered at the corral were examined.

E. BRÄNDVALLEN-BRÄNDÅSEN (1. Feb.): Out of the same main herd (D) around 1800 animals were driven by helicopter and snowmobiles to the corral. This means that a mixture of animals that had and had not been in the corral the day before was driven for selection. The drive by helicopter lasted around 2,5 hours. The animals showed similar signs of panic as in the day before. Animals for slaughter were selected in the same way, but only animals transported by lorries to the slaughterplace at Brändåsen were examined. The transport distance was 71 km and took, on an average, 1,5 hours. The unloading took about 30 min. The animals were let out into a small corral (Fig. 6:3). From there they were taken out by hand for slaughter.

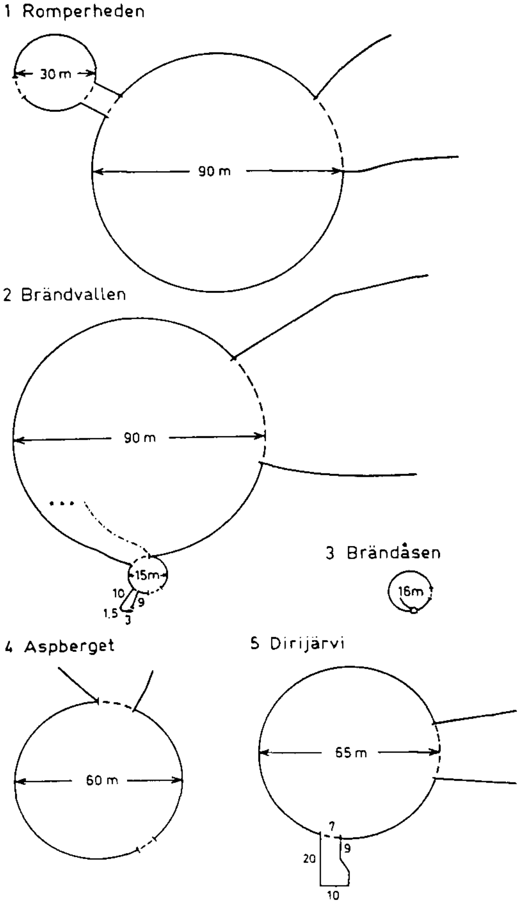

Fig. 6. The construction and shape of the corrals used for the different herds investigated.

F. BRÄNDÅSEN (2. Febr.): The reindeer examined were the last to be brought in by lorry around midnight the day before. These animals had been allowed to rest during the night in the small corral at the slaughterplace (Fig. 6:3) and reindeer had been exposed to handling for more than 24 hours including the overnight stay in the corral.

G. MAUSJAURE (2. July): A herd of around 400 animals was driven into a corral for calf marking. Blood samples were drawn from 10 herded by herdsmen on foot.

H. ÅNGSÅ (19. Sept.): A small herd of around 300 animals was scattered in the forest. An attempt to herd them into a corral had failed in the morning. Instead, a few bulls were killed by a rifle-shot in the neck after the animals had been cautiously driven out of the forest by slowly walking herdsmen.

I. ASPBERGET (19. Sept.): Around 300 animals were herded into a small corral (Fig. 6:4) during a period of around 4 hours. Slaughtering started at once. The animals were lassoed, taken out of the corral, and slaughtered.

J.DIRIJÄRVI (20. Sept.): A herd of about 300 animals had been herded into a large grazing corral on September 18. The following day an additional 400 animals were driven into the same grazing corral. On September 20 the animals were driven into the ordinary corral (Fig. 6:5). The handling was calm. The animals were lassoed and put into a pen from which they were taken out by hand or by lasso, dragged out and killed. Numerous spectators, herdsmen, ect, stood around the slaughterplace and pen, and also inside the corral and the pen.

At slaughter, macroscopical inspection of carcasses and viscera was undertaken. From randomly chosen animals, blood samples were taken and material for histopathological examination was taken from M.semitendinosus, M.longissimus dorsi, myocardium, liver, kidney and abomasum. The gross examination of slaughtered animals revealed a major patho-

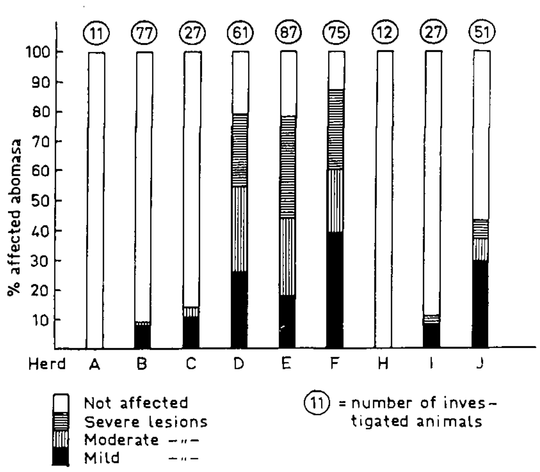

Fig. 7. Distribution of abomasal lesions

logical finding to be haemorrhages in the abomasa (Plate 3). These lesions were classified as mild, moderate, or severe according to their appearance in size and number (Fig. 7). Haemorrhages were found in the abomasa of animals from all herds except A and H. They were fewest in herds B, C, and I, while herd J had more than these, but fewer than herds D, E, and F. It should be noted that haemorrhages were present in the material even as early as only within 4 hours of handling and herding (Plate 3).

Microscopically, most of the lesions consisted of a local mucosal haemorrhage, oedema, and constriction of submucosal vessels. These changes varied from minor mucosal haemorrhages to severe haemorrhages, coagulative necrosis and submucosal haemorrhages (Plate 4). Ulcers penetrating to the submucosa were not found. A marked inflammatory reaction with infiltration mainly of neutrophils was present in cases of more pronounced mucosal lesions.

Lesions in the skeletal muscles and myocardium were not observed at the gross examination. The histopathological examination of muscular

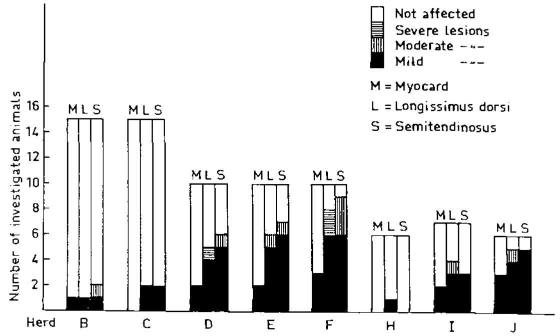

Fig. 8. Distribution of degenerative muscular lesions

Plate 3. Abomasum with several mucosal haemorrhages. The animal was slaughtered 4 hours after the beginning of a helicopter drive.
Photo C. Rehbinder.

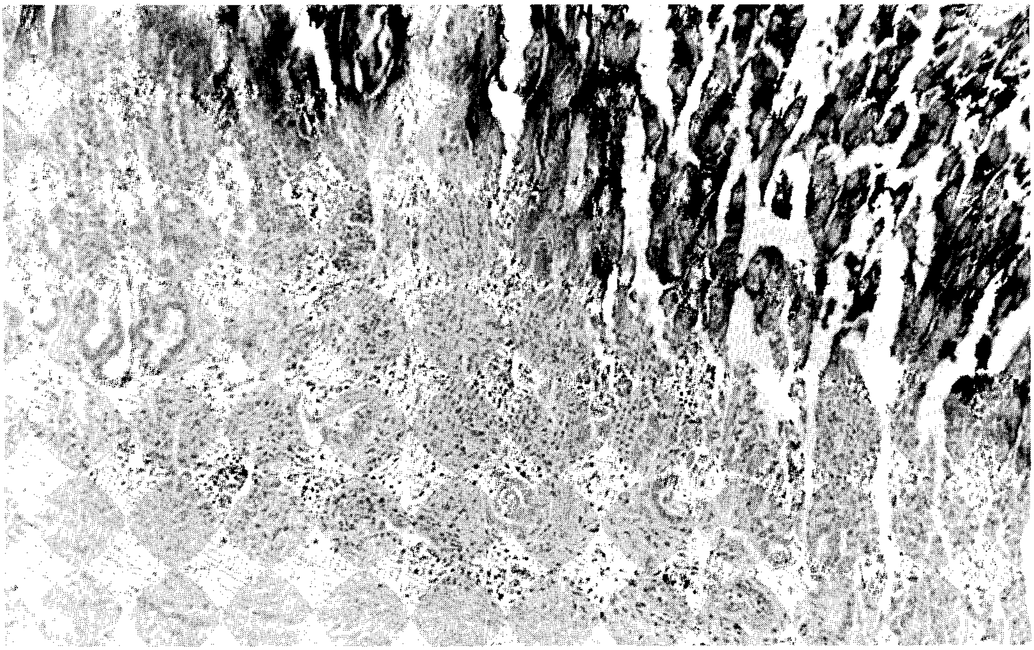

Plate 4. Extensive mucosal haemorrhage. Note coagulative necrosis and infiltration of neutrophils HE x 130. Photo C. Rehbinder.

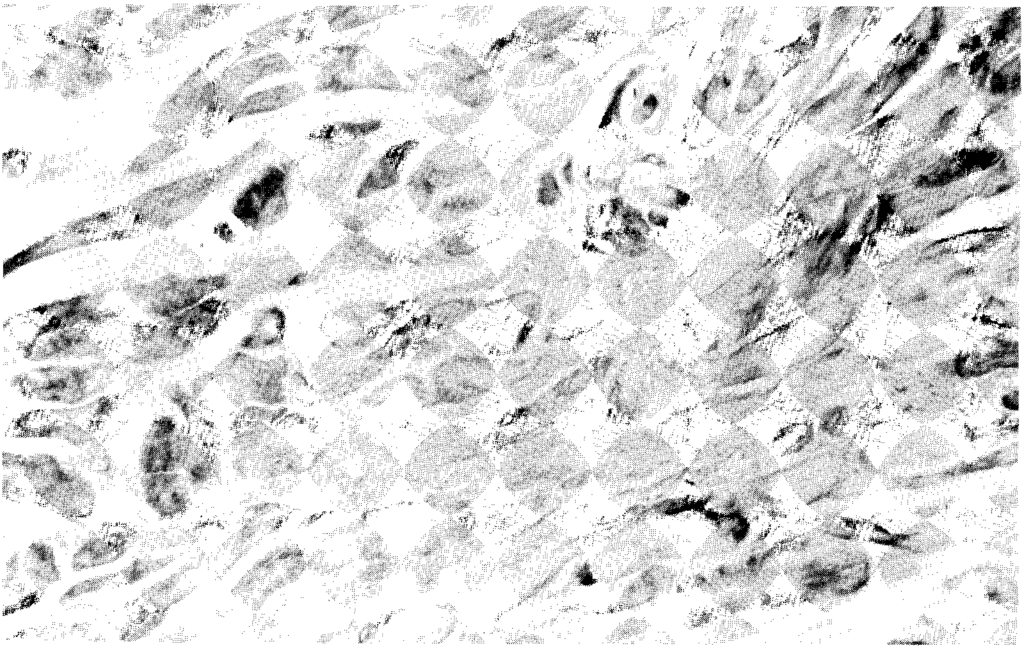

Plate 5. Skeletal muscle (semitendinosus). Note the almost complete destruction of the normal configuration by fragmentation, necrosis, fibrosis and histiocytic reaction. Histiocytes HE x 270. Photo C. Rehbinder.

tissues, revealed degenerative lesions in both skeletal muscles and myocardia. These changes ranged from loss of striation and fragmentation, to hyalinization and necrosis, and the extent of the lesions varied from minor focal lesions to larger areas of necrosis (Plate 5).

Degenerative muscular lesions were not found in herd A. Herds B, C, and H were considerable less affected than herds D, E, F, I, and J (Fig. 8).

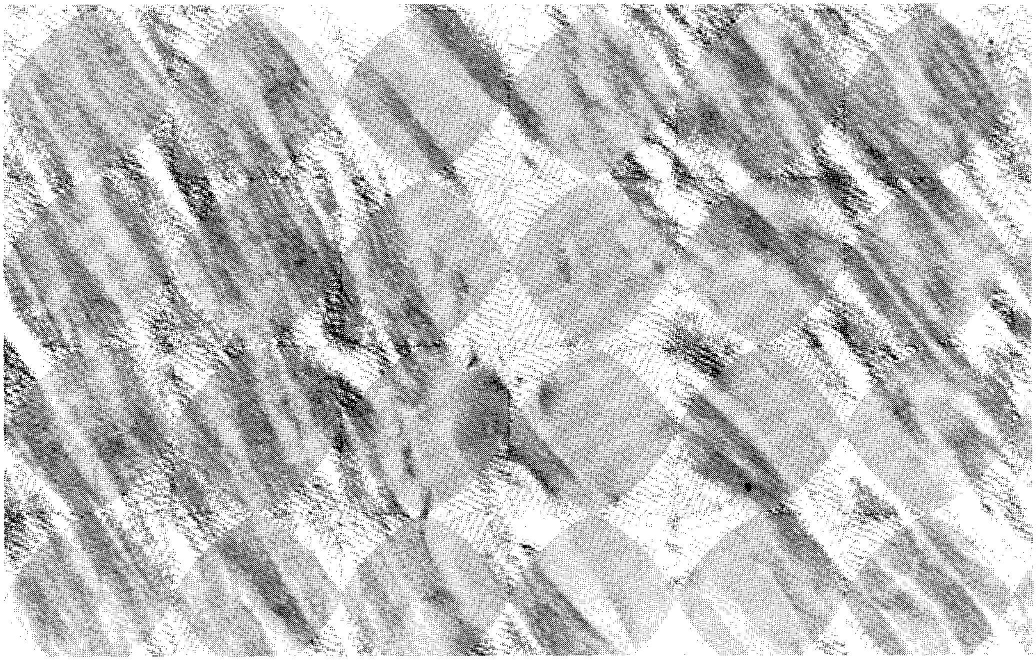

Plate 6. Myocardium. Note loss of striation, swelling and hyalinization of affected muscle cells. PTAH. x 440. Photo C. Rehbinder.

The differential counts of leucocytes revealed marked differences between the control group and handled animals. The most striking effects of handling stress was an increase in immature and mature neutrophils and a decrease in lymphocytes correlated to the degree of stress to which the animals had been exposed. Prolonged exposure to stress produced a considerable decrease in the number of eosinophils. In addition, in herd I, paired blood samples were taken at 3-5 min intervalls between samples. These animals were lassoed (1:st sample) in the corral and dragged out for slaughter (2:nd sampled). Changes in the blood picture appeared fast. (Fig. 9).

The corticosteroid levels were found to be considerably lower in animals shot (herds A and H) than in handled animals (Fig. 10). The shot animals of herd H, however, showed a wider range. The lowest cortisol levels in handled animals were found in herds B and C, and the highest in herds F and J. The very quick response in the corticosteroid levels of the animals from herd I between initial sampling (I_1) and sampling at slaughter (I_2) was remarkable.

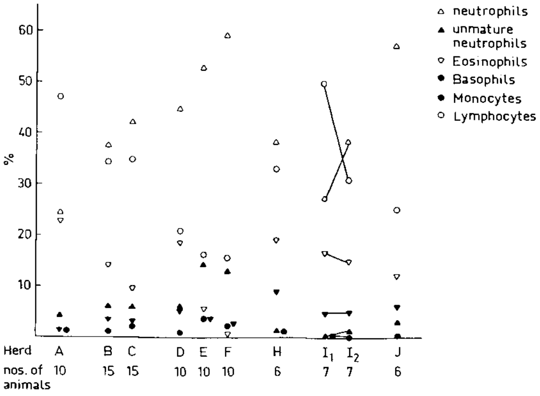

Fig. 9. Differential counts of leucocytes

Urea levels were found to be lower in herds B, D, H, and I than in animals shot in August (herd A), while animals kept overnight in grazing or resting corrals (herds C, F, and J) revealed significantly higher values than animals from all the other herds (Fig. 11).

Significantly increased ASAT values were found only in herd F; but individual animals with high levels were found also in herds B, C,

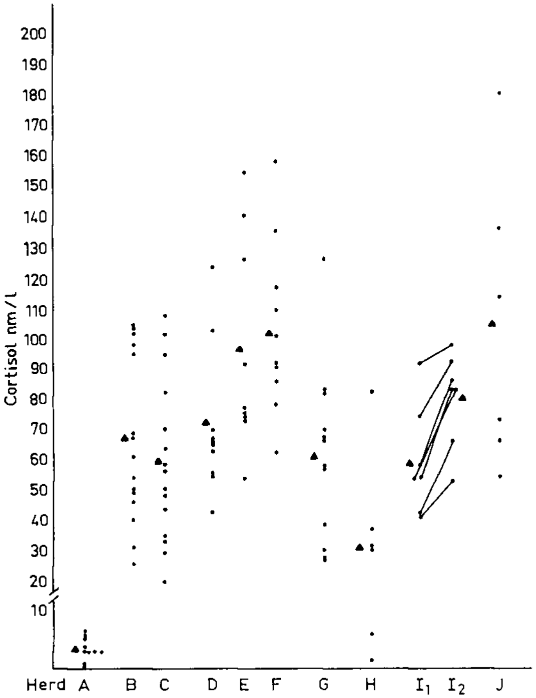

Fig. 10. Peripheral blood plasma levels of cortisol

and E. A tendency toward comparatively higher levels of ASAT was found in herd E (Fig. 12).

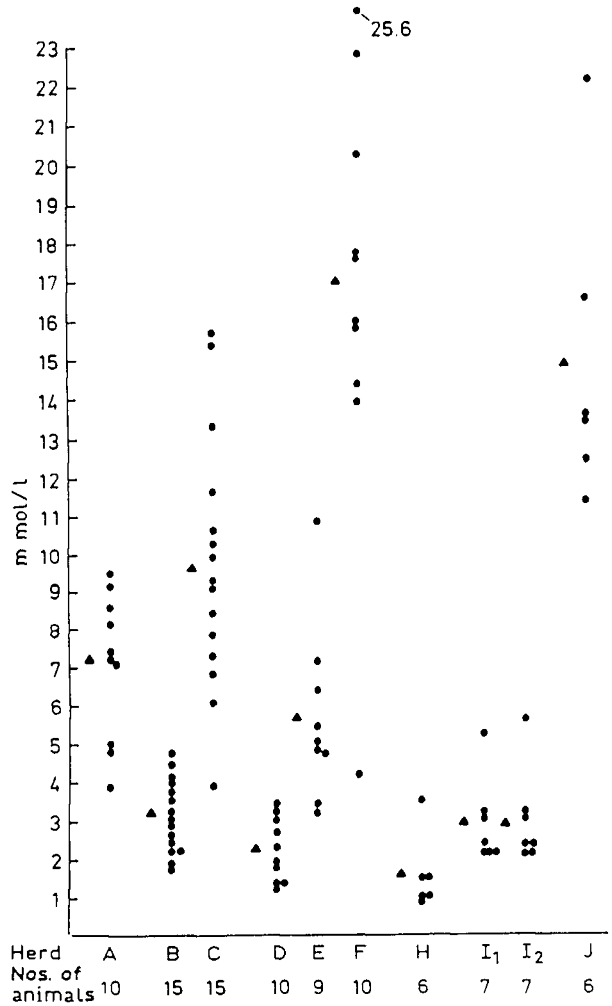

Fig. 11. Periferal blood plasma levels of urea

General discussion

Modern methods of reindeer herding differ considerably from the traditional old herding methods. The latter involved a rather intimate relationship beween the herdsmen and their reindeer, which contributed to the creation of comparatively domesticated animals. Furthermore, the animals were kept in relatively small herds in those days. Present herding methods imply larger herds of less domesticated animals. The traditional methods, which involved daily contact with the animals by herdsmen on foot or by skiis, have given way to territorial surveillance and round-ups of large herds, often with the aid of snowmobiles and sometimes even helicopters. In addition, transport of reindeer by lorry for different purposes is a common practice.

Thus, numerous stress factors are involved in the management of reindeer, inherent in the methods of gathering and herding them, other conditions under which they are herded, the extent of manual handling and contact with people, transportation, etc. All these factors imply intrusion into the flight and critical distances. (Fox 1974). *Hence, in the reindeer, the degree of its tameness should be considered an important factor.*

The field study of management stress largely confirmed the results of earlier investigations. The animals investigated, except those of herd A, had all been subjected to varying levels of stress. The animals of herd A which were shot while resting or grazing were considered un-

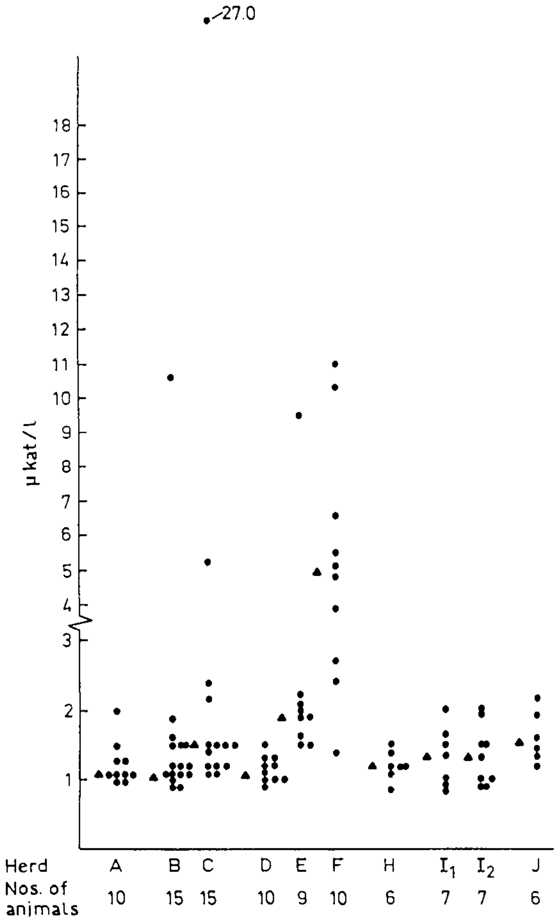

Fig. 12. Periferal blood plasma levels of ASAT

stressed. The animals of herd H were also shot, though some of them apparently did not die immediately when shot in their necks, but were only paralysed, as shown by the presence of blinking reflexes. This fact may explain the wide individual differences in the blood parameters encountered in theses animals.

Herds B, C, and I were subjected to a comparatively mild herding stress and a breif handling stress. Herd J was exposed to a moderate degree of herding stress but a pronounced handling stress.

The effects of management stress were reflected in the blood samples by an increase in both immature and mature neutrophils and a decrease in lymphocytes, and these changes were positively correlated to the degree of stress to which the animals had been exposed. Prolonged exposure produced a remarkable decrease in the number of eosinophils (Fig 9).

The results correspond well with the investigation on blood constituents (Investigation I, Fig 4). Considerable variations are found within and between reports on differential counts of blood leucocytes in reindeer and caribou (*e.g.* Yagimoff & Mitzkewitsch 1931, Gibbs 1960, McEvan 1968, McEvan & Whitehead 1969, Dieterich 1970, Drescher-Kaden & Hoppe 1973, Timisjärvi *et al.* 1976, Nieminen 1980). Apparently, stress has an influence on several blood parameters which may explain the differences found in literature. It must be considered almost impossible to obtain normal values for blood constituents of reindeer as many of these will reflect the state of stress in the individual animal, which results from the capture and handling necessary for sampling.

In the experimental investigation (investigation I) there were small variations among the unstressed animals (Group I), yielding a higher number ofi lymphocytes than that of neutrophils. In the stressed animals the relation between lymphocytes and neutrophils was that of neutrophilia. In the experimental animals (Group II) a decrease in the number of lymphocytes and eosinophils with a simultaneous increase in segmented, band, and immature neutrophils is evident (Fig 4). This interchanged distribution is well known from other animals in connection with different kinds of stress (Winqvist 1954, Dvorak 1968, Gartner *et al.* 1969, Hartman *et al.* 1973, Jacobsen *et al.* 1978).

The cortisol levels found in the unstressed animals (Group I) were markedly low as compared to the levels found in the experimental animals at the initial sampling, (Fig. 5), indicating that the hypothalmic-pituitary- adrenal system of the latter animals rapidly responded to handling (Fig 3).

The generally high cortisol values and the wide range found in them thus reflect the individual response to herding and handling.

Apparently, the manual handling of reindeer provokes a rapid stress response as judged from the elevated cortisol levels.

The elevated urea levels in the stressed animals may be explained by an increased catabolism of protein from cellular depots, probably muscle tissue. It is known that cortisol exerts such a catabolic effect (Wilkinson 1980), and that skeletal muscle in several species such as the rat (Dahlberg *et al.* 1980) and the pig (Snochowski et al. 1981) contains specific glucocorticoid receptors mediating the hormone action. The finding of elevated cortisol levels in the stressed animals further supports this assumption.

The animals of Groups I and III showed the same magnitude of ASAT activity as reported by Bjarghov *et al.* (1976) and by Nieminen (1980). The experimental animals showed a higher activity at both sampling occasions with a pronounced increase between the two sampling events.

Elevations of ASAT activities have been reported in connection with muscular disorders and capture myopathies (Cardinet III & Stephens-Orvis 1980). The higher activity in the experimental animals probably indicates that these animals were physically less well adapted to running exercise as they were kept in a corral and artificially fed, which should have limited their need for physical movement. The skeletal musculature in these animals is therefore probably more vulnerable to physical exercise and handling, resulting in leakage of ASAT from muscle cells to the general circulation (Table 2).

The differences established, in certain blood parameters between unstressed animals and animals subjected to stress, i.e. the change of the white blood cell composition and the elevation of cortisol and urea values in the stressed animals indicate that reindeer are markedly stress susceptible. This is underlined by the striking changes in these values in the experimental animals and in the handled animals of the field study. The lower lymphocyte and higher eosinophil counts found in older animals might be attributable to a more pronounced parasitic infestation in these animals *(Elaphostrongylus rangiferi, Setaria tundra* and *Onchocerca tarsicola,* Rehbinder et al., 1979).

Abomasal haemorrhages (Fig. 7, Plate 3) are also characteristic of stress in many different species (Brodie *et al.*, 1963; Iversen *et al.*, 1972; Johansson *et al.*, 1973; Krisst & Freimark, 1973), and gastric ulcers due to acute and prologned stress have been observed in cervidae (Anon., 1981; Presidente, 1978).

The muscular and myocardial lesions (Fig. 8) and the heamatological values in animals subjected to prolonged herding and handling are all charateristic of physical exertion and acute mental stress (Jönsson and Johansson 1974; Bartsch *et al.*, 1977).

The results of the studies of the blood constituents are presented in Figs. 9-12. When analysing pathological changes and haematological variation in relation to treatment (stress), sex, and age it is obvious that stress significantly influences most parameters studied. Consequently, even the degree of stress applied is more or less directly reflected in pathological lesions and in changes in blood constituents. Thus the distribution of abomasal and muscular lesions and the changes in blood constituents must be considered to reflect a general response correlated to the stress to which the animals had been exposed. The higher urea levels in younger animals could be due to the comparatively more vigorous physical exertion of these animals.

The herding stress applied to herds B, C, and I in the field study was comparatively mild, and the handling stress was low. Even herd H had been subjected to a very low degree of herding stress. The handling stress applied was also of short duration. Consequently, the lowest rates of pathological lesions and the least pronounced haematological changes were found in these herds.

Herd G, from which only cortisol values

were obtained, was exposed to a moderate herding and handling stress. The cortisol values are comparable to those of herds B, C, and I, indicating herd similarities under stress exposure. If there is any difference in the adrenocortical function between seasons as stated by Yousefi et al (1971), such differences are most probably masked by stress induced changes.

When repeated handling is applied as in the case of the seven animals of herd I, this is reflected in a significant increase in immature and segmented neutrophils and a decrease in monocytes and lymphocytes (Fig. 9), accompanied also by a marked increase in cortisol levels (Fig. 10). These changes apparently were attributable to the short period of restraint stress. Prolonged and repeated handling - but moderate herding stress - was applied to herd J and was reflected in a marked increase in pathological lesions and alterations in the blood constituents studied. *Thus prolonged and repeated manual handling as such appears to be the most important factor producing stress lesions.* Consequently, in reindeer, mental stress, sheer fear as reported in pigs (Johansson *et al.*, 1982) and seen in restrained (Ader, 1971; Franzmann *et al.*, 1975) or trapped animals (Iversen *et al.*, 1972; Jacobson *et al.*, 1978) appeares to be the most significant factor in the development of stress induced lesions.

The use of helicopter or snowmobiles when herding animals (herds D, E, and F) can cause severe mental stress owing to the animals' attempts to escape (from these vehicles). Overstraining when trying to escape is bound to contribute to the kind of pathological lesions found. It has been reported earlier that low-flying aircraft provokes a strong escape on panic response (Calef *et al.*, 1976; Miller & Gunn, 1979). When this effect is used in herding the animals, the response may be severe mental and exertional stress, especially when escape attempts are hindered by snow, and when deep snow also prevents early escape.

Capture myopathies in wild ungulates usually develop within 4 hours (Harthoorn 1977; Bartsch *et al.*, 1977), but capture stress and capture myopathy may be inflicted in a matter of a few minutes (Harthoorn, 1977).

Fowler (1977) stated that non-specific responses involving the hypothalamic-pituitary-adrenocortical axis are cumulative. Thus, repeated stress, viz. handling and/or herding, may result in more pronounced and advanced stress induced lesions. *The increase in abomasal and muscular lesions and the marked changes in the blood constituents seen in the herds subjected to prolonged or repeated handling or herding are strongly indicative of such a cumulative response in the semi-domestic reindeer.*

Whether the muscular degeneration observed by others as well as myself can be related to an increased catabolism exerted by cortisol remains to be elucidated. The remarkable depletion of glycogen and lipids in many of the fibres may be a major factor involved in the development of reindeer skeletal muscle degeneration in connection with exertion and mental stress. Apparently, repeated and prolonged stress may result in elevated urea and ASAT values (Figs. 11, 12), the latter probably due to a progressive muscular degeneration. Both urea and, ASAT values were correlated to the distance of the drive and the time spent in the corral. These findings are consistent with the values found here for herds B, C, and D, E, F, and for herd J. The comparatively high urea values in the unstressed control animals (herd A), sampled in August were probably related to a higher protein intake (Bjarghov *et al.*, 1976).

No kidney lesions such as described by Harthoorn (1977) and Bartsch *et al.* (1977) were recorded. However, the animals were killed within 24 hours after provocation of herding and/or handling stress, and chronic lesions are not likely to appear in such a short time.

The fact that manual handling elicits a marked stress response in reindeer also stresses the importance of correct selection methods and consequently of a suitable construction of the corral system. When the various corral system used are compared, B and C (Romperheden Fig. 6) represent a construction which is the most likely to reduce handling stress exposure of the animals. In fact, the animals allowed back to the herd are rarely captured and in most cases are not handled manually.

Consequently, *the use of a selection corral and pens in which manual handling is enforced should be avoided.*

Transportation is found to cause severe stress in domesticated animals (Dvorak, 1975; Simensen *et al.* 1980; Mitchell *et al.* 1988), and most likely provokes an even more severe stress response in semidomesticated animals. In connection with the transportation of reindeer, traumatic lesions are commonly found (Andersen, 1978) and were observed even in the transported animals of herds E and F in the present study. A trauma will *act* as a stress factor, but as it is often the result of aggression shown by other animals in transport crates it may be considered a *result* of stress behaviour as well.

Repeated or prolonged handling must be regarded as unfavourable for the semidomesticated reindeer, as is the case with wild ungulates (Harthoorn, 1977). Consequently, *the degree of tameness is of importance.* Harthoorn (1981) reported of considerably reduced death rates due to capture myopathies when wild ungulates were trained (*i.e.* partly tamed) to accept the presence of humans before being crated and transported. It is apparent from the field study that stress is not alleviated in animals allowed to stand overnight in an ordinary or grazing corral. It is also obvious that stress can affect the health of all animals exposed to it and not only the meat quality of those slaughtered.

A severe stress response with gastric lesions will affect the digestive tract and its utilization of fodder. A considerably lower weight gain in reindeer calves subjected to intensive herding, as compared with wild reindeer calves, was reported by Reimers (1972). Handling stress was considered the major factor underlying the differences in growth. Similarly, a significant negative correlation between cortisol levels and growht rate was observed in cattle (Purchas et al., 1980). Moreover, stress has a detrimental effect on the immune system (Gisler & Schenkel-Hullinger 1971, Simensen *et al.*, 1980, Kelly 1980, Riley 1985, Griffin 1989) and therefore animals suffering from stress may have an increased susceptibility to infectious diseases. Ulcerative and necrotizing lesions of the nose and upper alimentary tract caused by a herpes virus infection in connection with transportation and handling stress has been reported. It was suggested that lesions caused by herpes virus may be the background to outbreaks of necrobacillosis of the alimentary tract in reindeer reported earlier (Rockborn *et al.* 1989).

In wild ungulates, death due to capture myopathy has been reported to occur as late as 30 days after capture. The possibility that severely stressed reindeer may succumb even later after being released from the corral, cannot be excluded.

A marked depletion of glycogen and lipids in many muscle fibres may be a factor involved in the development of skeletal muscle degeneration in connection with mental stress and exertion. There seems to be a correlation between high ASAT-values and substrate depleed muscle fibres as seen in investigation III (Table 1). A connection therefore seems to exist between high intramuscular substrate stores and the ability of a muscle to tolerate stress. A further connection may be that of "stress taste" and meat quality, as the quantity of (number of animals yielding) low quality meat increases during autumn-winter, when energy deposits are depleted (Petäjä *et al.* 1982).

Summary

It is evident that herding and handling stress is an important factor (to be considered) in reindeer management. Therefore herding must be undertaken as carefully as possible, especially when motor vehicles are used.

To obtain a good meat quality, animals should be selected almost directely from the herd and subjected to a minimum of handling, i.e. slaughter should take place with as little delay as possible. *Transportation of live animals and the confining of animals in corrals overnight or in pens or crates while awaiting slaughter should be avoided.* (Stephens 1980).

The relative lack of tameness, as different from that of the reindeer herded according to "old days' herding methods", and the intrusion into the animals' critical distance, i.e. manual handling producing mental stress is a factor which seems to have a great impact on the animals' stress susceptibility.

As mental stress, sheer fear, thus appears to be the most significant kind of stress affecting reindeer it has to be taken into consideration in the planning of herding and other kinds of activities, and especially so when new methods are to be introduced in reindeer herding.

It appears that the idea of letting the animals rest for periods during and/or between stress-events is wrong. If lesions are produced, a "restitutio ad integrum" always requires a very long time, many days or several weeks, depending upon the severity of the lesions produced. The restoration of the hormonal balance of the rat adrenal after a major stress event takes 8 days (Schalling *et al.* 1988). Careful measures applied without delay are necessary to avoid cumulative effects upon the organ systems. *This fact again underlines the importance of avoiding prolonged and repeated manual handling.* When motor vehicles such as motorcycles, snowmobiles, and helicopters are used the importance of not producing stess and fear by unexpectedly intruding into the animals' flight distance or critical distance has to be borne in mind. *The use of vehicles or any other means of transport must be correlated to the tameness of the animals.* In order to obtain a good meat quality, animals should be selected for slaughter with as little intrusion as possible, into their critical distance i.e they should be manually handled and restrained as short time as possible. The herd as a whole must be keept calm.

It is reasonable to assume that animals, if let out severly stressed after slaughter, or other kinds of gatherings, have a hard time to face restoring their physical fitness. Their digestion and food conversion rate might be hampered by gastric lesions, their search for food by muscular lesions and their blood circulation and oxygen consumption by myocardial lesions. In addition, they have to restore their energy supplies and adversely affected immune systems. All these effects are causes of production losses even if the reindeer do not actually die.

To avoid the pitfalls of faulty equipment and herding methods we should take advantage of the expert knowledge of experienced old herdsmen in reading and interpreting the behaviour of reindeer.

It is evident form the results obtained that:

1. Reindeer are very susceptible to management and restraint stress.
2. Their degree of tameness is very important for their susceptibility to different kinds of stress.
3. Reindeer subjected to stress may develop abomasal, muscular, and myocardial lesions and changes in blood constituents. There is reason to conclude that repetition of stress events tend to increase such responses in a cumulative manner.

3:1. Therefore, prolonged an repeated manual handling should be avoided.

3:2. Letting animals rest in between events of stress exposure has no beneficial effects if it means an increase in the total amount of stress to which the animals are exposed.

3:3. The use of selection corrals and pens in which manual handling is enforced should be avoided.

3:4. Preferably, animals intended for slaughter should be captured and killed as fast as possible (without any delay).

4. It can not be excluded that the depletion of muscular stores of glycogen, increased catabolism of muscular protein, muscular degeneration, and increased blood-urea levels may be stress produced effects resulting in altered and bad taste of the meat - i.e. in a bad meat quality.
5. Transportation of live animals and keeping animals over night on corrals, pens or crates while awaiting slaughter should be avoided.
6. The use of helicopters, or other motor vehicles for transports, must be correlated to the tameness and condition of the animals and to environmental conditions, such as snow cover, temperature, insect harassment, etc. The less tame the animals are, the weaker their bodily conditions is, the more unfavourable the environmental circumstances are, the more careful management methods are required and the more the use of motor vehicles should be restricted.
7. It is obvious that animals, though not selected for slaughter but exposed to a severe and prolonged stress situation, when let out grazing, will need a considerable time to reach a "restitutio ad integrum". I.e., will take considerable time before stress induced lesions have healed. These animals may suffer from circulatory disturbances and muscle pains preventing them from normal grazing. The may also suffer exhaustion and, due to gastric lesions, be incapable of properly digesting their feed. In addition, their immune system can be negatively affected paving the way for outbreaks of parasitic and/or infectious diseases.

Stress due to incorrect management methods may thus severly affect the productivity ofi reindeer.

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Contaminants in caribou tissues from northern Québec

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Abstract: Recent findings that cadmium, an atmospheric pollutant, was present at relatively high concentration in cervids from southern Québec triggered a study on contamination of caribou tissues. Following the Chernobyl accident, caribou tissues were also investigated for radionuclides. Cadmium concentrations varied according to organ, age, sex and time of collection. In fall, it averaged 27.5 (S.E. = 3.5; n = 50), 2.3 (0.3;40), and 0.1(0.01;17) $\mu g \cdot g^{-1}$ (dry weight) in the kidneys, liver and rumen wall respectively; in skeletal muscles and the heart, mean concentrations reached 0.002 (0.001;33) and 0.003 (0.003;7) $\mu g \cdot g^{-1}$. Lead and mercury were measured in the liver for a smaller number of animals; concentration averaged 1.4 (0.2;41) and 0.7 (0.03;41) $\mu g \cdot g^{-1}$ (dry weight) for the first and the second element respectively. In general, cadmium and mercury levels were higher in Québec animals than in those from Norway, while concentrations were comparable for lead. Only 10-15 percent of cesium 137 present in northern Québec originated from Chernobyl, the rest being due to earlier atmospheric nuclear weapon testing. Among tissues examined, kidneys contained the highest cesium level, followed by skeletal muscles. Mean cesium concentrations in caribou meat varied between 166 (16;4) and 1129 (74;9) $Bq \cdot kg^{-1}$ (wet weight) according to area and month of collection. Caribou feeding habits and regional variation in lichen contamination may explain oberved differences. Those cesium levels were the highest observed throughout northern Canada in 1986-1987. In Québec, the consumption of caribou kidneys and liver is not recommended mainly because of cadmium; consumption of caribou meat poses limited risks with respect to heavy metals or cesium but other natural and artificial radionuclides must be measured before making final recommendations.

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The method by which *Cephenemyia trompe* (Modeer) larvae invade reindeer *(Rangifer tarandus)*

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Abstract: Laboratory electrostimulated *C. trompe* (Modeer) females forcefully expelled (sprayed) larvae for 5-20 cm. The watery spray consisted of about 20 tiny droplets containing two to several larvae. Crawling first-instar larvae exhibited negative geotactic and phototropic responses; they were subject to rapid desiccation and became immobile as the tiny droplets dried within a few seconds. When 5-50 larvae from dissected females were dropped in physiological saline onto different areas of the muzzle of restrained reindeer, only larvae placed deep within the nostrils and on the lips crawled out-of- sight down the nostril passage or into the mouth. Drops of larvae placed elswhere quickly desiccated and the larvae became immobile. Larvae deposited by wild females onto a CO_2-baited reindeer model with the muzzle, lips and nostrils coated with insect trapping adhesive all were stuck only along the dorsal lip below the philtrum. All experimental evidence supports a natural *per os* mode of invasion.

Key words: attack, larval invasion, Norway

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Introduction

Speculation on how *Cephenemyia trompe* (Modeer), the larviparous female nasopharyngeal bot fly of reindeer, *Rangifer tarandus*, infects its host has ranged from folklore statements about flies flying into the nostrils to reports of females spraying, squirting or depositing larvae onto the hosts' nose or into the nostrils (Bergman 1917; Natvig, 1917; Hawden, 1927; Grunin, 1957; Espmark, 1967). More recent research on two species of nasopharyngeal bot flies of California blacktailed deer *(Odocoileus hemionus columbianus)* revealed that larvae of *C. apicata* (Bennet & Sabrosky) and *C. jellisoni* (Townsend), when placed experimentally on various parts of the muzzle of deer, always immediately crawled ventrally and entered the mouth of the host (Cogley and Anderson 1981). Subsequent research in California with deer models baited with carbon dioxide revealed that larvae expelled naturally by wild *Cephenemyia* females always were stuck to the lower surface of the muzzle and the lips (Anderson, 1989).

The objective of our research with *C. trompe* was to study how its larvae were expelled and how they invaded reindeer, and to make comparisons with the other *Cephenemyia* species studied.

Methods of study

The first phase of our research involved laboratory electrostimulation of live *C. trompe* females. The females used in these experiments were host-seeking flies that had been captured in Finnmark, Norway, in CO_2-baited insect flight traps like those used by Anderson and Olkowski (1968) and Anderson and Hoy (1972). Captured females were transferred to glass holding vials ventilated by several small holes in their snap caps. The females were held at about 5° C until used from 2-5 days later.

Females were glued to microscope slides that were positioned so the head and body of an electrostimulated female was aligned at a 60-75° angle from the microscope stage. The reactions of such females could then be observed with a dissecting microscope as they were electrostimulated. As described by Cogley and Anderson (1981), a Grass® # S88 electric stimulator adjusted to 40-80 volts (duration of 8 ms, frequency of 50 pulses/sec.) was used to induce females to expel larvae. Females were stimulated along the ventral nerve by touching the exposed leads to the ventral surface of the intersegmental area between the thorax and abdomen.

Groups of about 5-15 expulsed larvae were picked up from uterine fluid on the bristles of a camelhair brush or an insect pin, and their crawling behavior and time to desiccation observed while viewed with a dissecting microscope. To determine the effect of desiccation time on larval recovery, larvae that had dried on brush bristles were placed in physiological saline or human saliva at different intervals after drying. Larval tropisms were determined by holding saline moistened brushes with groups of larvae on them towards a bright light and at different angles, and observing in which direction larvae crawled.

Other larvae were obtained when the uterus of females was dissected in physiological saline. Groups of 25-50 such larvae were pipetted to spot plate depressions and held in the saline for up to 30 minutes.

Semi-tame reindeer females were restrained by hand and in a squeeze box while larvae in drops of physiological saline were experimentally placed onto their muzzle, in and around the nostrils, and on the lips. Groups of about 25-50 larvae were picked up with a 1.5 cc bulbed pipette and delivered to the muzzle of the host 8 times in a single drop of saline. In six other instances just 2-10 larvae were delivered to the hosts'muzzle in a smaller drop of saline. Four times drops of about 25 larvae were placed several cm deep into the nostrils of a reindeer (beyond the fringe of long guard hairs surrounding the entrance). Drops of from 5-25 larvae were placed onto the upper or lower lips of reindeer six times.

Figure 1. Experimental reindeer model exposed in a birch woods habitat. A curved vinyl tube leads from a styrofoam box containing dry ice into the head of the model where sublimated CO_2 was released from the mouth.

In 1987 an experimental reindeer model (Fig. 1.), similar to deer models previously used in California (Anderson, 1989), was exposed in both birch woods and highland plains habitats. The reindeer model consisted of a taxidermically-prepared head attached to a half-meter board mounted on a tree stump or wood frame. The body of the model was formed by placing reindeer hides over cardboard boxes and the frame. Dry ice was used as a source of CO_2 About 2 kg of dry ice was placed in a styrofoam insulted box that rested on the ground below the model's head. One end of a vinyl hose was inserted into the styrofoam box and the other end passed through the head and led to an opening in the mouth from where sublimated CO_2 escaped. A vinyl glove was used to spread a thin layer of Tanglefoot insect trapping adhesive (gel type)[3] over the lining of the nostrils, the surface of the muzzle and the lips of the model. This material is a weather proof, odorless insect trapping adhesive which remains sticky in all kinds of weather.

The head of the model was returned to the laboratory after a days' exposure, and small globs of adhesive were scrapped from specific areas with a forceps. Individual samples stuck to the forceps were either examined directly with a dissecting microscope to identify the trapped insect fauna, or they were spread onto a piece of clear polyethylene before examination.

Results

Seven females were electrostimulated while viewed with a dissecting microscope. Most females only responded to electrostimulation once or twice, and they usually did so by forcefully spraying a group of larvae a distance of 5-20 cm. However, for 3 of 12 larvipositions observed, a female simply extruded the larvipositor and expelled, respectively, 48,50 and 90 larvae in a single large drop of clear uterine fluid. These large drops were watery (in contrast to the sticky drops expelled by *C. apicata* (Cogley and Anderson, 1981)), and almost immediately after expulsion, they began to trickle down the larvipositor and disperse into the pile (=hairs) around the base of the larvipositor. It was from these large drops that small groups of larvae were picked up with a camelhair brush.

Most larvae were forcefully expelled in a spray of about 20 tiny droplets, with each droplet containing from two to eight larvae. Most of the sprayed droplets landed on the microscope stage 5-10 cm in front of the electrostimulated females. Many of the upwardly sprayed droplets also hit the objective (7-10 cm above the females), and some hit other parts of the microscope. A few droplets landed on the laboratory bench up to 20 cm from an electrostimulated female. Because of the way an electrostimulated female usually was positioned at the front portion of the microscops stage, the ventral surface of the objective was situated much like the hypothesized target area on the ventral surface of the upper lip of the reindeer host would be exposed (see below).

The uterine fluid in which larvae were expelled was clear and of a watery consistency. Contrary to the more viscous sticky larval packet expelled by *C. apicata* (Cogley and Anderson, 1981), the uterine fluid of *C. trompe* did not stick to the pile on females nor to an insect pin or to brush bristles. When a pin was inserted into a newly-expelled drop of larvae the larvae simply slid off in the watery fluid as the pin was raised. If a pin were held horizontally while slowly removed from a drop of larvae, some larvae crawled along the moist pin until its surface dried and they then desiccated.

When larvae were picked up from uterine fluid on the bristles of a camelhair brush which was then oriented vertically at various angles they vigorously crawled downward; when the brush was oriented laterally the larvae rapidly crawled away from a source of bright light. Larvae behaved in this manner whether they crawled as individuals or whether several larvae in a uniform drop simultaneously crawled in the

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[3] The Tanglefoot Co., Grand Rapids, MI., U.S.A. 49504.

same direction. Individually isolated larvae crawled at a speed of 4-5 mm/sec. When several larvae were picked up from the dispersed film of uterine fluid with a camelhair brush the moisture surrounding each larva often united and coalesced to form a small drop containing several wriggling larvae. When the brush was then held at even a slight angle the movement of the larvae within the drop resulted in the drop of larvae quickly "rolling" down a bristle.

Larvae individually separated on brush bristles became immobile and dried out in just a few seconds. However, after the larvae had been in a desiccated state for 1-2 minutes some revived when the bristles were immersed in a drop of physiological saline. On one occasion, 10 of 30 "desiccated" larvae began to move and quest after a few seconds in the saline. The others appeared dead. In another case, 30 of 48 such dried out larvae began to make questing movements after a few seconds in a drop of saline. A few larvae from several other groups that had momentarily dried out and stopped crawling, also revived after being put into a drop of physiological saline or human saliva. No larvae revived after 5 minutes of desiccation.

When groups of larvae obtained from dissected females were pipetted onto the muzzle of restrained reindeer in a single drop of physiological saline their wriggling and crawling resulted in the drop quickly spreading and drying. Such drops usually dried in just a few seconds as the fluid spread out on the thickly-matted hairs covering the surface of the muzzle. The smallest drops of 2-10 larvae dried in 2-5 sec., whereas the lager drops might remain moist for about 30 sec. Thus larvae were able to crawl only a few mm before becoming immobile and desiccating on the hairs of the reindeer's muzzle. Compared to their rapid locomotion along the bristles of a brush or the solid surface of a moist pin, the larvae appeared to experience more difficulty in crawling over the surface of the fine, soft hairs covering the muzzle. Perhaps it was more difficult for them to use their mouthhooks and ventral spines on a surface composed of numerous fine, loose hairs.

On several occasions captured females spontaneously larviposited in the ventilated holding vials. When this occurred the larvae continued to crawl around the interior of the vial for as long as the inside surface of the vial remained moist (as long as an hour in the maximum instance). When placed into drops of physiological saline in depression slides the larvae remained alive and active for up to 30 minutes, the longest time they remained in saline before used in experiments.

When drops of about 25 larvae were placed several cm into the nostrils (beyond the fringe of long guard hairs surrounding the entrance) the larvae were able to crawl laterally along the nostril passage. These larvae crawled more effectively along the surface of the slightly wrinkled, leather-like (hairless) lining of the inner nostril than larvae observed on the soft hairs of the muzzle. On two occasions a few larvae were seen crawling deep into the nasal passage until they disappeared from view. On these occcasions the reindeer responded with a few sneezes and snorts, and by closing and opening her nostril several times in rapid succession. These reactions appeared to be a response to irritation, probably caused by the movements of the large mouthhooks and ventral body spines used by larvae in locomotion.

When drops of larvae were pipetted onto the upper or lower lip of a reindeer the larvae quickly crawled out-of-sight into the mouth. The reindeer often responded to these larvae by licking the lips with its tongue and by rapidly moving and rubbing the upper and lower lips together. It also responded with some sneezes, snorts and head shakes. All larvae placed on the lips appeared to successfully enter the mouth.

Like deer models proviously used (Anderson, 1989), the reindeer model baited with CO_2 proved successful in attracting and inducing wild *C. trompe* females to larviposit. In two one-half day exposures of the model in 1987, we recovered 59 first-instar larvae. Only 4 of these were stuck a few cm outside the target area illustrated in Fig. 3. The CO_2-baited reindeer model thus proved successful in inducing several larviposition attackt by wild *C. trompe* females. All natural larvipositions onto the CO_2-baited reindeer model by wild females revealed that the *C. trompe* larvae were stuck only on the ventral surface of the protruding dorsal lip, usually in a small area below the philtrum (Figs. 2,3). Larvae trapped in the adhesive were compared to first instar larvae dissected from captured females to confirm their identification as *C. trompe.*

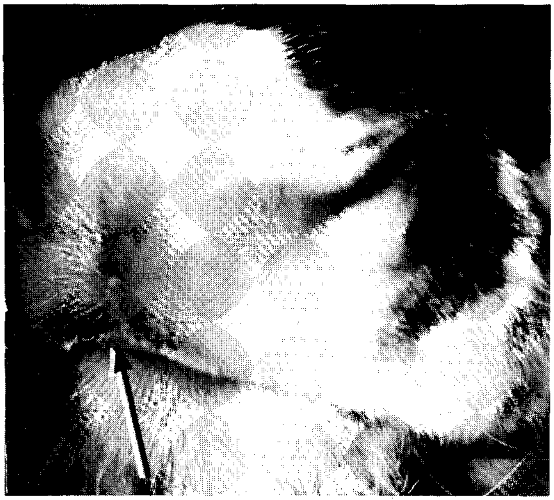

Figure 2. Close up view of the muzzle of a reindeer illustrating the exposed ventral surface of the protruding upper lip where all larvae expelled by wild female *C. trompe* were found. Arrow points to center of area where larvae were most commonly found stuck in the adhesive.

Finally, the CO_2-baited reindeer model, like the deer models used in California, appeared to also attract all parasitic Diptera that attack reindeer. Females of *Hypoderma tarandi* L. often landed and ovisposited on the hides covering the neck and body. On 10 August 1987, for example, we caught 6 *H. tarandi* females that were attracted to the model between 0900 and 1300 hrs. Members of all the blood-sucking fauna continually swarmed about, landed and crawled over most parts of the model. The numbers attracted were so large that the adhesive-coated areas soon became coverd with trapped black flies, mosquitoes and ceratopogonids (no-see-ums), whose sticky body surfaces had to be examined for *Cephenemyia* larvae after they were removed.

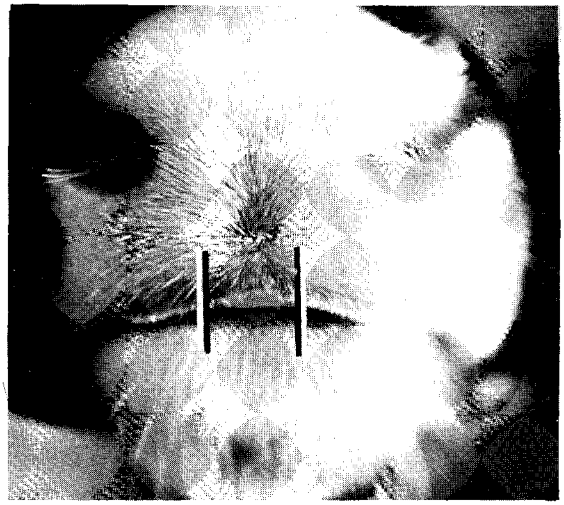

Figure 3. Same as figure 2. Almost all *C. trompe* larvae expelled by attacking females were found stuck within the target area enclosed by the two black lines.

Discussion and conclusions

Our experimental studies, plus observations of attacking females by Espmark (1961, 1967), and by us, indicate that the natural method of host attack by *C. trompe* females involves a final behavior phase in which a female flies towards the mouth of a reindeer from the ground, or a hovering position below the nose. Because the upper lip of reindeer protrudes over the lower lip, the ground-launched attacks of *C. trompe* females seem effectively adapted for spraying larvae onto the ventral surface of the exposed upper lip of its reindeer/caribou host. Electrostimulation studies indicate that as a female approaches within about 5-15 cm of the mouth she forcefully expels a group of about 25-50 larvae in a spray comprised of about 10-20 watery droplets. The spray is directed at the ventro-central area of the upper lip, and the closer the female approaches a reindeer before expelling larvae, the tighter the spray pattern will be. When landing on the lips of the host the photonegative and thermopositive reactive larvae begin to immediately crawl into the mouth. Like the larvae of other *Cephenemyia* species (Cogley and Andreson, 1981), the *C. trompe* larvae probably crawl along the roof of the mouth and the tongue toward the posterior passages to the upper respiratory tract.

In the above respects, the manner of attack and expulsion of larvae by *C. trompe* are the same as that reported for *C. jellisoni* (Anderson, 1975; Cogley and Anderson, 1981), as is their crawling speed of 4-5 mm/sec. Two other features shared by these species that are associated with the expulsion of larvae in a spray of tiny droplets are, a watery uterine fluid and a large sclerotized utero-vaginal valve (Cogley and Anderson, unpubl. data). By contrast, *C. apicata*, which expels its larvae in a single packet, has a viscous, sticky uterine fluid and a small, narrow utero-vaginal valve (Cogley and Anderson, 1981; and unpubl. data). These and other anatomical modifications associated with viviparous reproduction and expulsion of larvae by nasopharyngeal bot flies of deer are being described by Cogley and Anderson (in prep.).

Although it has now been determined that *C. trompe* is the third *Cephenemyia* species whose larvae invade the host *per os*, one cannot completely exclude the possibility of the nostrils serving as an alternate portal of entry for expullsed *C. trompe* larvae. Because, on two occasions, drops of larvae experimentally placed deep within the nostrils were seen crawling out-of-sight deep into the nasal passage, it seems remotely possible that this could occur in nature. For example, if a reindeer happened to turn its head sideways at the moment a *C. trompe* female expelled its spray of larvae, it might be possible for some of the spray droplets to elude the guard hairs and enter an open nostril with enough velocity to land deep enough inside the nasal passage for the larvae to be able to crawl to the moist inner area before they would desiccate. Since larvae were not found in the nostrils of models, however, it seems unlikely that larvipositing females selectively home in on nostrils instead of the mouth.

With respect to the *per os* invasion of the host, there is a remote possibility that larvae in droplets that miss the lips and land on the muzzle might also be able to invade the host. If, for example, groups of 3-5 larvae in tiny droplets of sprayed uterine fluid landed on the furry surface of the muzzle within about 10 mm of the lips,it might be possible for some such larvae to crawl to the lips and into the mouth before they desiccated. However, because larvae in the smallest experimental drops of uterine fluid or physiological saline dried out and became immobile in just 2-3 sec., only larvae landing in a narrow zone around the lips might have such a chance to infect a host. Larvae experimentally dropped onto the muzzle did not crawl effectively on this furry surface, and none made it to the lips of the host.

Another remotely possible mode of infection is that the crawling activity of larvae might irritate the host enough to cause it to lick such larvae off the muzzle and into the mouth before they would desiccate, but we never saw this occur when drops of larvae were experimentally placed on the muzzle of a restrained reindeer. We therefore conclude that most reindeer become infected with *C. trompe per os* after first instar larvae have been sprayed onto the lips by a larvipositing female flying towards the muzzle from a ventral position.

Acknowledgements

We thank Dr. Alex Tindall, Department of Physiology, University of Tromsø, for the use of the electrostimulator and Mr. Karstein Bye, Institute of Biology and Geology, University of Tromsø, for assisting with the experimental deposition of *Cephenemyia* larvae onto reindeer. The research was financed, in part, by a research grant from the Norwegian Reindeer Council.

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Intracytoplasmic inclusion bodies associated with vesicular ulcerative and necrotizing lesions of the digestive mucosa in fallow deer *(Dama dama* L.)

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Abstract: Intracytoplasmic epithelial inclusion bodies in the digestive mucosa of fallow deer *(Dama dama L.)* were found to most probably be the result of an unspecific degenerative or post mortal change. There are reasons to believe that this is true also for the inclusion bodies found in reindeer, roe deer and moose.

Key words: epithelial inclusion bodies, alimentary mucosa, reindeer digestive organs

Rangifer, Special Issue No. 3, 1990: 299-303

Introduction

Vesicular, ulcerative and necrotizing lesions associated with intracytoplasmic inclusion bodies, have been observed in the epithelium of the upper alimentary tract of various wild cervidae such as reindeer *(Rangifer tarandus L.)* , roe deer *(Capreolus capreolus L.)*, moose *(Alces alces L.)* and fallow deer *(Dama dama L.)*. (Rehbinder et al 1985; Feinstein et al 1987).

The type of lesions as well as the occurance of inclusion bodies were suggestive of a viral etiology. Electron microscopical studies of the inclusion bodies, however, failed to reveal virus particles. The hypothesis was raised that, irrespective of the etiology, the inclusion bodies could constitute a non-specific degenerative cell response of the digestive epithelium. In the present study we examined, by means of light and electron microscopy, alimentary tissues from clinically healthy fallow deer and also from fallow deer suffering of a disease resembling BVD/MD. To evaluate whether autolysis could play a role in the genesis of the inclusion bodies, we allowed alimentary tissues from clinically healthy fallow deer to undergo from mild to advanced autolysis by delaying the start of fixation for 24, 48 and 96 hours.

Results

Diseased animals

Erosions, ulcers, and necrotizing lesions were observed in the oral mucosa (tongue, gingiva and pallatum molle) and rumen. These lesions were deep, irregularly rounded, 5 to 15 mm in diameter with elevated margins and red bases. Some of the animals presented linear erosions

Fig. 1. Oesophagus. Fissured necrotic material covering linear erosions.

covered by a layer of fissured necrotic material in the oesophageal mucosa (Fig. 1).

Histopathology of the mucous membranes of the mouth, oesophagus and fore-stomachs revealed numerous intracytoplasmic basophilic inclusion bodies in cells of the stratum basale and spinosum (Fig. 2). Cells generally presented one inclusion body, but in occasional cells two could be seen. Inclusion bodies were round, 2 to 10 microns in diameter and surrounded by a clear halo. They often compressed the nuclei into a crescent shape and were negative for keratine and prekeratin.

Control groups

0 hs. samples:

All the animals were clinically healthy and no microscopical lesions were observed. Inclusion bodies were not observed in tissues fixed immediately after excision.

24 and 48 hs. samples:

In the oral cavity and oesophagus, of the 24 h samples, a few cells in stratum basale and spinosum exhibited intracytoplasmic basophilic inclusion bodies. In the 48 hs. samples a moderate increase in the number of inclusion bodies was observed.

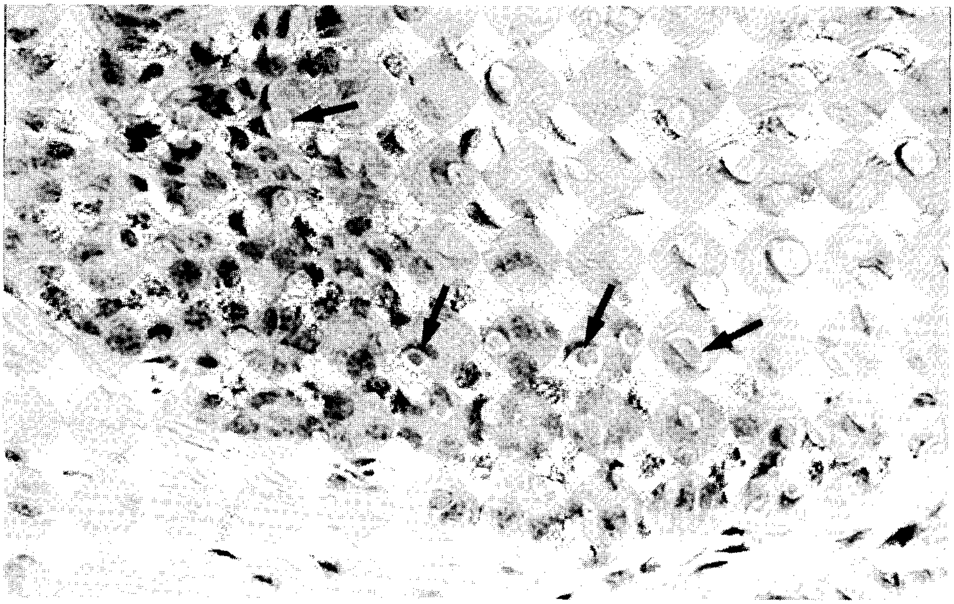

Fig. 2. Mucous membrane of the mouth. Note swollen cells and numerous inclusion bodies. H&E x 450.

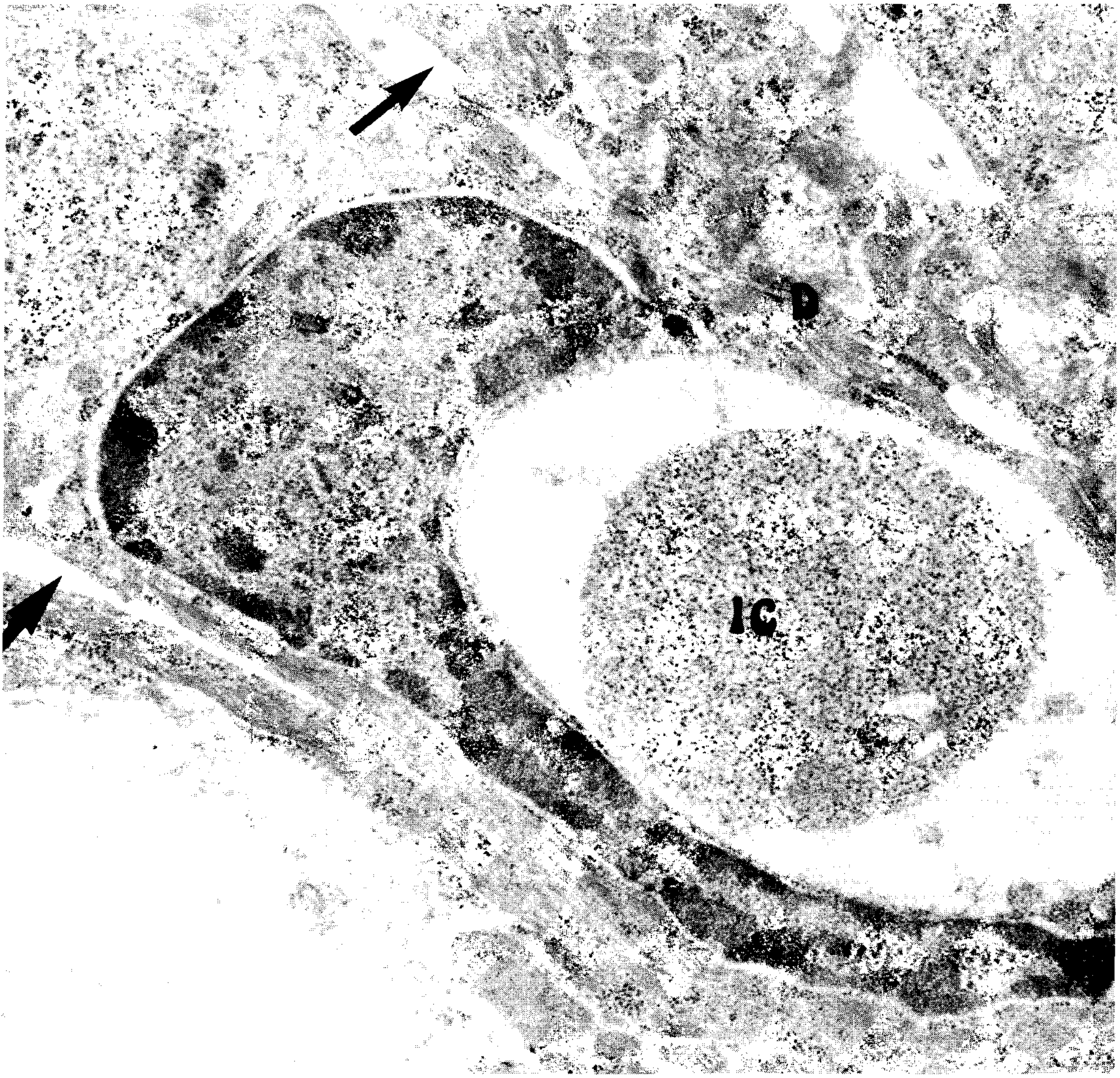

Fig. 3. Diseased fallow deer, oral mucosa. Cells with an inclusion body (IC). Note compressed nucleus (N), intercellular oedema (arrows) and desmosomes (D) x 24600.

96 hs. samples:
The autolytic changes were very advanced, the histological details of the organs being hardly recognizable. Rests of inclusion bodies, however, were still discernable in few cells of the buccal and ruminal epithelium.

Electron microscopical studies

Diseased animals
Inclusion bodies appeared round or oval with a single membrane and with granular protein-like content. Numerous inclusion bodies were only partly filled or almost empty. Inclusions were located close to the nucleus which was compressed into a crescent shape (Fig. 3). A constant feature was clumping of tonofilaments and inter- and intracelluar edema. Viral particles were not found.

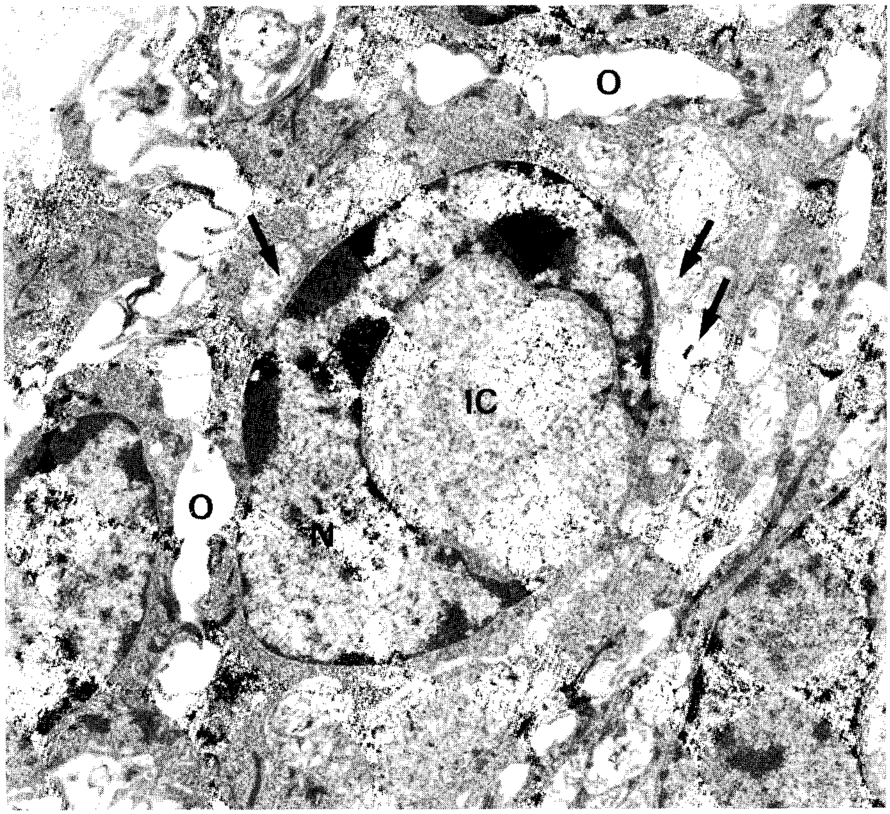

Fig. 4. Control fallow deer, 24 hs. sample. Oral mucosa. Cell with intracytoplasmic inclusion body (IC). Note intercellular oedema (O) and swollen mitochondriae (arrows) x 11700.

Control animals

0 hs. samples:

The mucous membranes of the mouth and oesophagus appeared normal exept for mild inter- and intracellular edema. Inclusion bodies were not observed.

24 hs. samples:

Autolytic changes were moderate. Inter- and intracellular edema was evident. Inclusion bodies very similar to those described for the diseased animals were observed in few cells of the stratum basale of the mucous membranes of the mouth and oesophagus (Fig. 4). Some of them contained a more loose granular protein-like material.

48 hs. samples:

Autolytic changes were more advanced, swelling of mitocondria and clumping of tonofilaments were clearly observed. Inter- and intracellular edema was pronounced and desmosomes were sharply demarcated. Inclusion bodies were very similar to those described above and more numerous than in the 24 hs. samples (Fig. 5).

96 hs. samples:

Electron microscopical studies were not performed.

Conclusion

The present study on the nature of the inclusion bodies in fallow deer have shown that they did not contain any virus, and most probably were the result of unspecific degenerative- or post mortal changes. (Díaz et al 1989). There are reasons to believe that this is true also for the inclusion bodies found in reindeer, roe deer and moose. (Rehbinder et al 1985, Feinstein et al 1985).

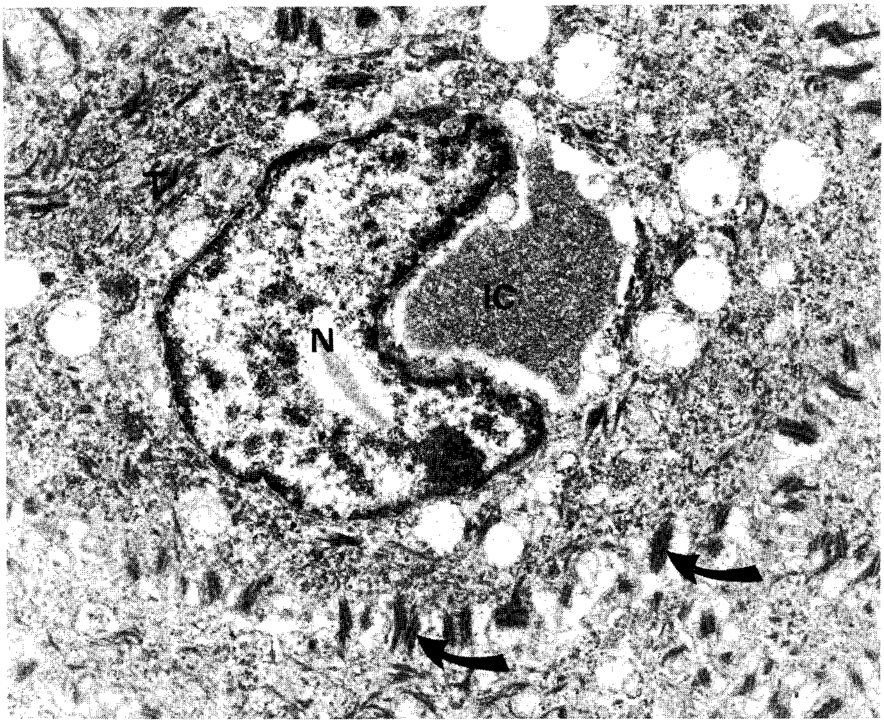

Fig. 5. Control fallow deer, 48 hs. sample. Oral mucosa. Cell with an inclusion body (IC). Note marked autolytic changes, clumping of tonofilaments (T), desmosomes (arrows) and compressed nucleus (N) x 11700.

The original an extended version of the present study is to be published in Acta Vet Scand during 1990.

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Translocation techniques used to establish pen farmed Alaskan reindeer

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Abstract: Small herds of reindeer *(Ragnifer tarandus)* frequently have been needed to be established in fenced holding pens for research or commercial reasons in Alaska and other areas. Native ranges of reindeer in Alaska were not on road systems, and the diet of the native reindeer had to be changed when they were translocated to small pens. Economics of transportation and feeding played an important role in the feasibility of translocation. Gathering and holding of reindeer for shipment, transport methods, adjustment of free-ranging reindeer to confinement, and a new diet were primary considerations to insure survival. Minimal psychologic stress of short duration, thermoregulation, and physical comfort were extremely important in carrying out a successful translocation. Receiving facilities, feed, and personnel were equally important. A minimum of one month was required to adjust reindeer to confinement and diet change.

Key words: husbandry, Alaska

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Introduction

Herding of domestic reindeer *(Rangifer tarandus)* has taken place in Alaska for nearly 100 years. The original herds were introduced from Siberia in the 1800s for use by the Eskimos located on Alaska's Seward Peninsula. Over the past several years there has been an increasing demand for Alaskan reindeer in other parts of the State or in other areas in North America.

Reindeer are needed for research purposes and for both private and commercial ventures. There are no connecting road systems to the Seward Peninsula, and sea transport of reindeer is difficult because of their remote location and the lack of proper holding facilities near ocean ports. Reindeer in Alaska roam essentially free on tundra ranges and are gathered for antler harvest and fawn marking during the summer. Most herds are gathered once again during the winter for parasite treatment, brucellosis vaccination, and for separation of animals by ownership. It is difficult to capture reindeer other than at these specific times (Dieterich, 1986).

Reindeer have been translocated to many different areas of the world for many years. Methods have varied from overland herding to air transport. Large numbers of reindeer have been

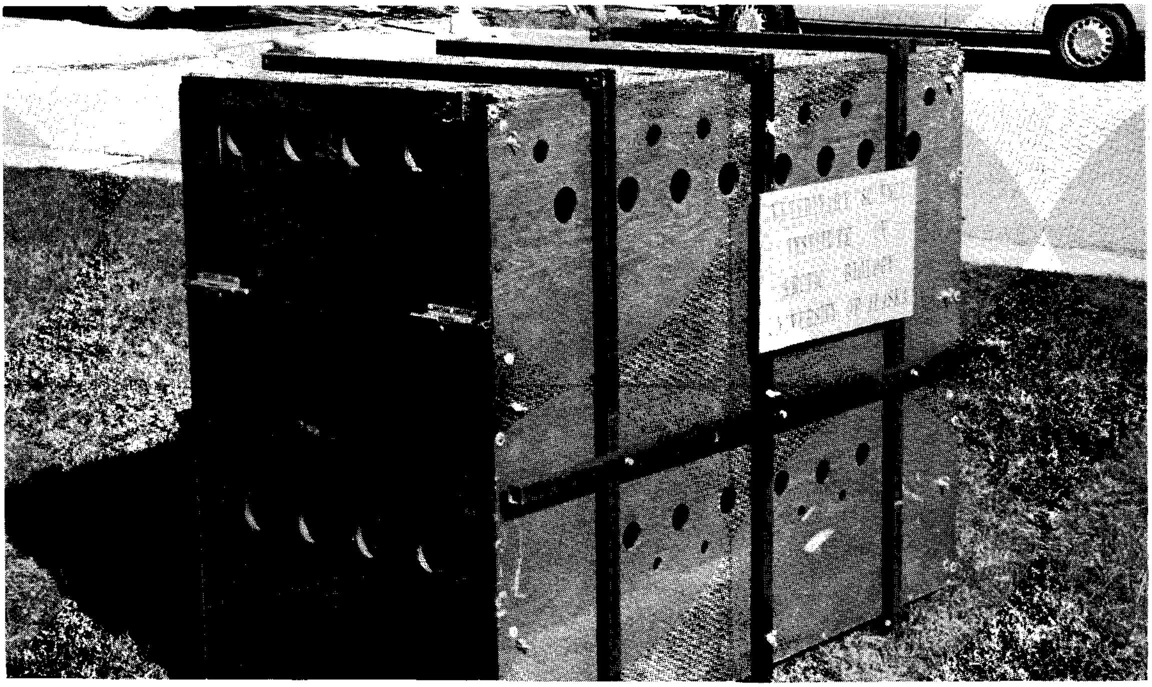

Fig. 1. Type of standard crate used for single reindeer shipments.

transported to alternate ranges in Scandinavia by semi- and tandem-trailer trucks capable of carrying up to 200 animals (Dau, 1987). The history of translocation of reindeer has varied from very successful to total failure with the deaths of large numbers of animals. Various translocation techniques used for different wildlife species and descriptions of results has been documented (Nielsen, 1988).

This report describes one method developed over the past 20 years in Alaska. Each translocation situation is unique, and it should be recognized that there is no single "correct" method. The use of good husbandry practices, an understanding of the behavior and biology of reindeer, plus consideration of the practical economics of the situation all play an important role in a successful outcome.

Materials and methods

Over the past several years, personnel at the University of Alaska at Fairbanks have translocated several hundred reindeer from Alaska's Seward Peninsula to Fairbanks, a distance of approximately 800 kilometers. Aircraft were used because no road or rail system connects these two locations.

Chemical immobilization and physical restaint were used separately and in combination. In our experience, chemical immobilization was not successful for the long duration (approximately 12 hours) of the transport because of the resultant poor thermoregulation and cardiovascular depression. Drugs were used only on reindeer which were unwilling to remain calm even after proper handling. Most transport trips required the use of no tranquilizing or immobilizing drugs.

Crates

The use of large multi-engine aircraft was very expensive, and concessions had to be made to safely move the largest number of reindeer possible in the cargo space available. There were no aircraft specifically configured to transport livestock, and the aircraft operators required control of urine and feces. Individual reindeer were shipped in large, standard, well-ventilated crates that enclosed the entire animal (Fig.1). These standard crates measured 120 cm high,

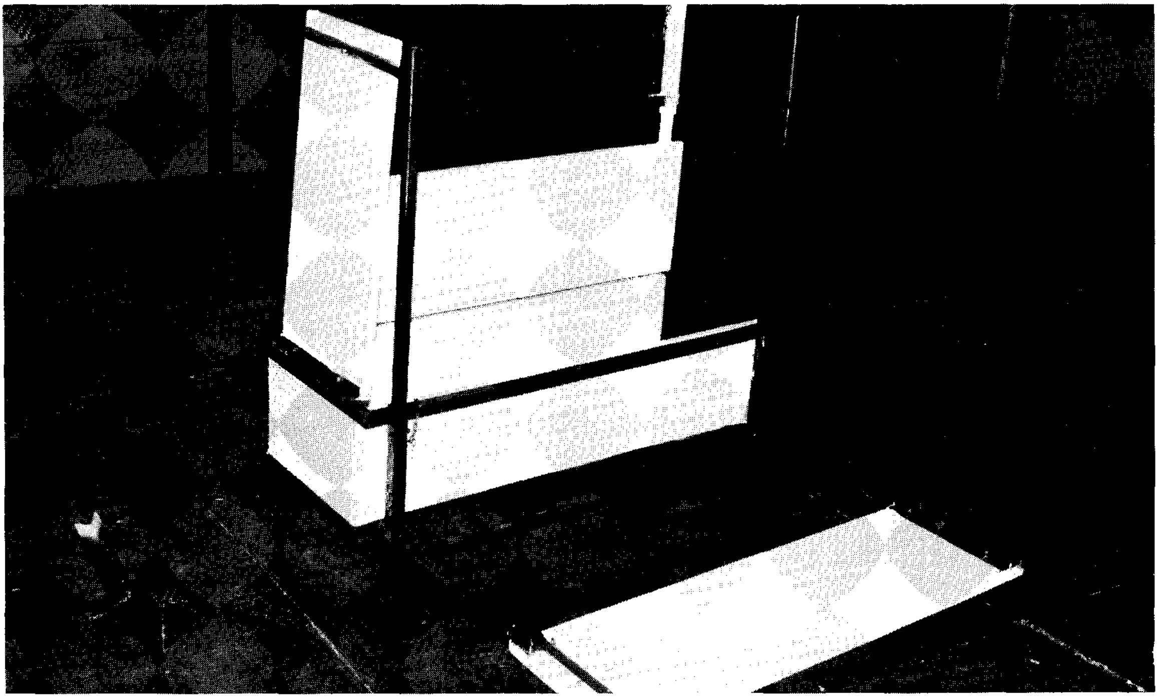

Fig. 2. Type of crate used for reindeer shipments of short durations. Partially assembled showing various parts.

76 cm wide, and 152 cm long. This system worked well but occupied a considerable amount of space and added excessive weight which further limited the number of animals an aircraft could carry.

The size of the standard crate was a limiting factor when shipping several reindeer in one load. Smaller, collapsible crates were designed that had several advantages (Fig. 2). In order to save ground-time aircraft charges, crates could be shipped to the loading site in advance so caged reindeer could be loaded into the transport aircraft as soon as it arrived. Shipping collapsible crates that could be re-assembled saved freight charges based on size-to-weight relationships. Also, more crates could be loaded on one aircraft. These crates were large enough to contain the reindeer's body but allowed the head to extend outside the crate (Fig 3). A padded stanchion which surrounded the neck of the animal aided restraint. The sides and floor of the crates were waterproof, and wood shavings were placed on the crate floors to absorb urine and fecal moisture. Inside measurements of the crates were 104 cm high, 37 cm wide, and 107 cm, long. This size was correct for mature females but small for an adult male. Crate size was minimal to prevent struggling and to conserve space. It was found that once reindeer were placed in the crates, they quickly stopped trying to escape because there was little room for movement. It should be stressed that this crate size is only suitable for trips of relatively short duration (8 to 12 hours).

Reindeer

Shipments of reindeer were carried out in November or December. Best survival was obtained during these months as the breeding season was over, and the pregnant females were early in their gestation period. Body reserves were adequate in young animals and females. Very few males were translocated. Males were more difficult to move because of relatively poorer body condition following the recent

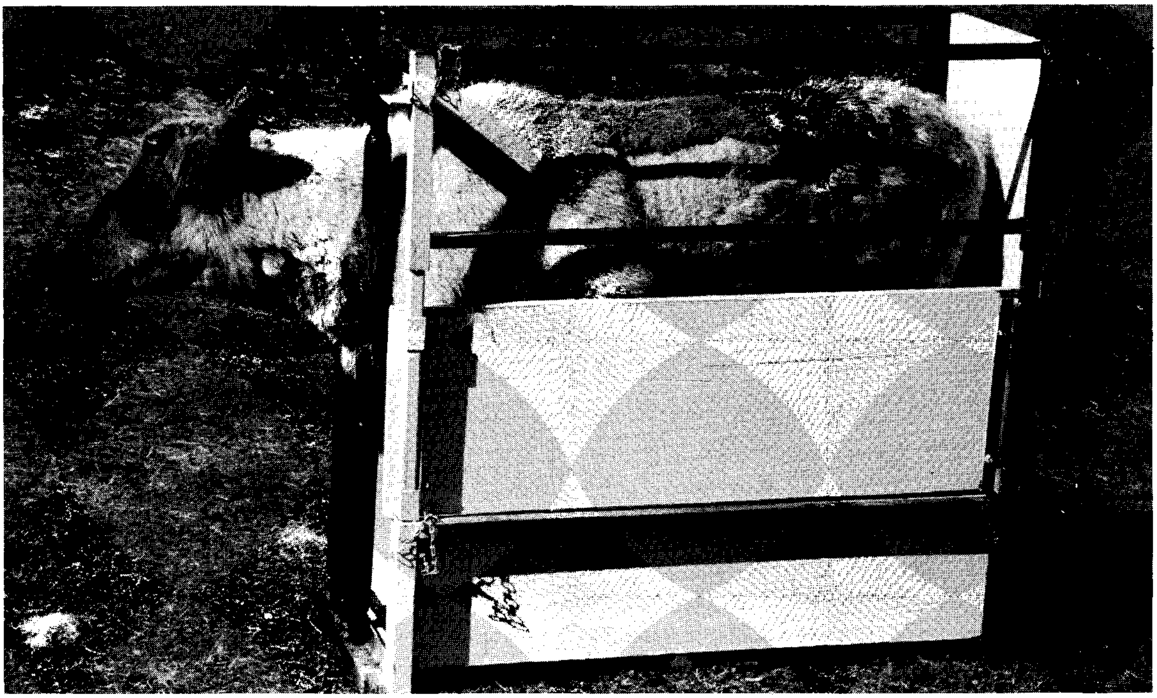

Fig. 3. Adult female reindeer in shipping crate.

completion of rut. Transports were carried out during the winter months exclusively after one attempt was made during summer months and increased mortality was experience due to heat stress.

Every effort was made to minimize the interval between the time the reindeer were first handled and the time when they were loaded into a crate. During the pre-crating period, the reindeer were held in temporary pens constructed with high sides that offered no view of the surrounding activities. Immidiately after crating, each adult reindeer was given an injection of antibiotics (900,000 units of procaine penicillin G and 900,000 units of benzathine penicillin G). Blood samples were obtained if needed. A blindfold made of surgical stockinette was placed over their eyes, and their antlers were cut near the base to prevent injury to other nearby reindeer or handlers (Fig 4).

Crates were loaded carefully and quietly into a waiting aircraft in rows such that the head of each aminal rested between the heads of animals in the next row. Thus, crates were fitted back-to-back and front-to-front which saved considerable space. This arrangement appeared to comfort the animals as they had close contact with the animals in the next row. The majority of the reindeer remained in sternal recumbancy during most of the trip and would only ocassionally stand up for short periods.

The interior temperature of the transport aircraft was maintained below freezing if at all possible to prevent moisture buildup. Ventilation was aided by opening emergency windows when possible.

Destination facilities

Upon arrival at the destination, crated reindeer were unloaded as quietly as possible, taken immediately to a dogproofed fenced field, and released (Fig 5). Within this field were natural hiding areas of trees and willows which allowed the animals to remain out of sight if they so wished. Two to four domesticated reindeer were kept in the fields to serve as "trainers" to teach the newly arrived animals where food and water were located. The newly transported reindeer had

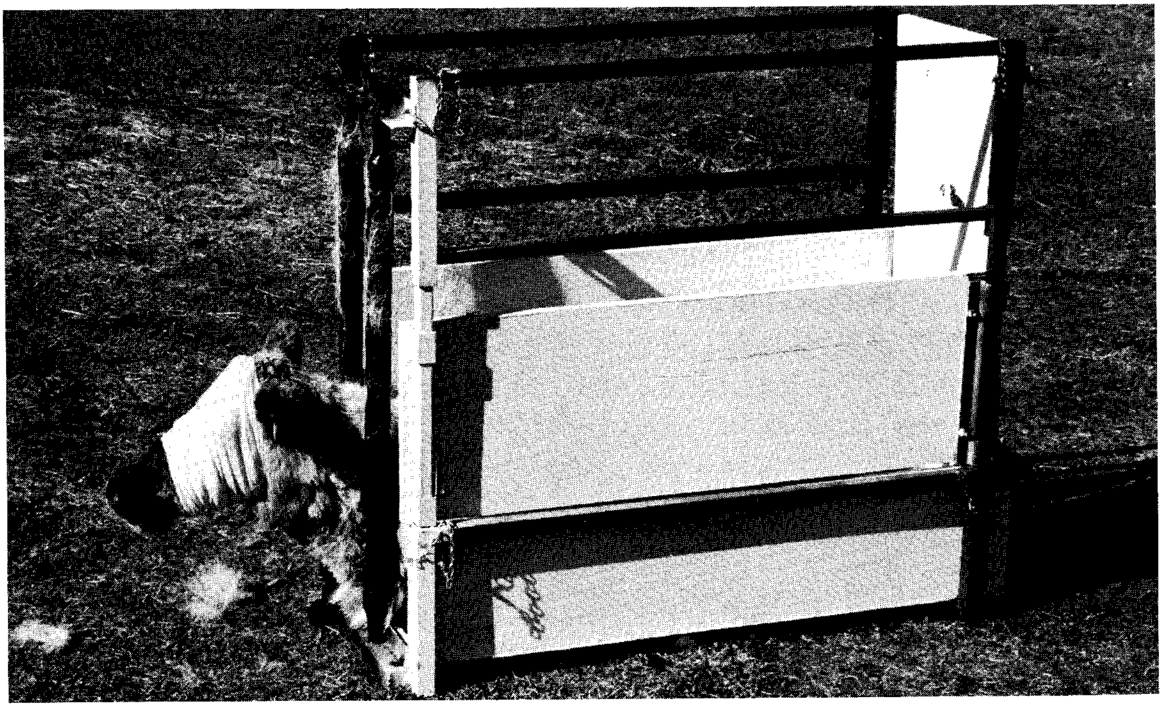

Fig. 4. Typical position of reindeer in crate during shipment. Note blindfold.

Fig. 5. Translocated reindeer in dog-proof fenced field.

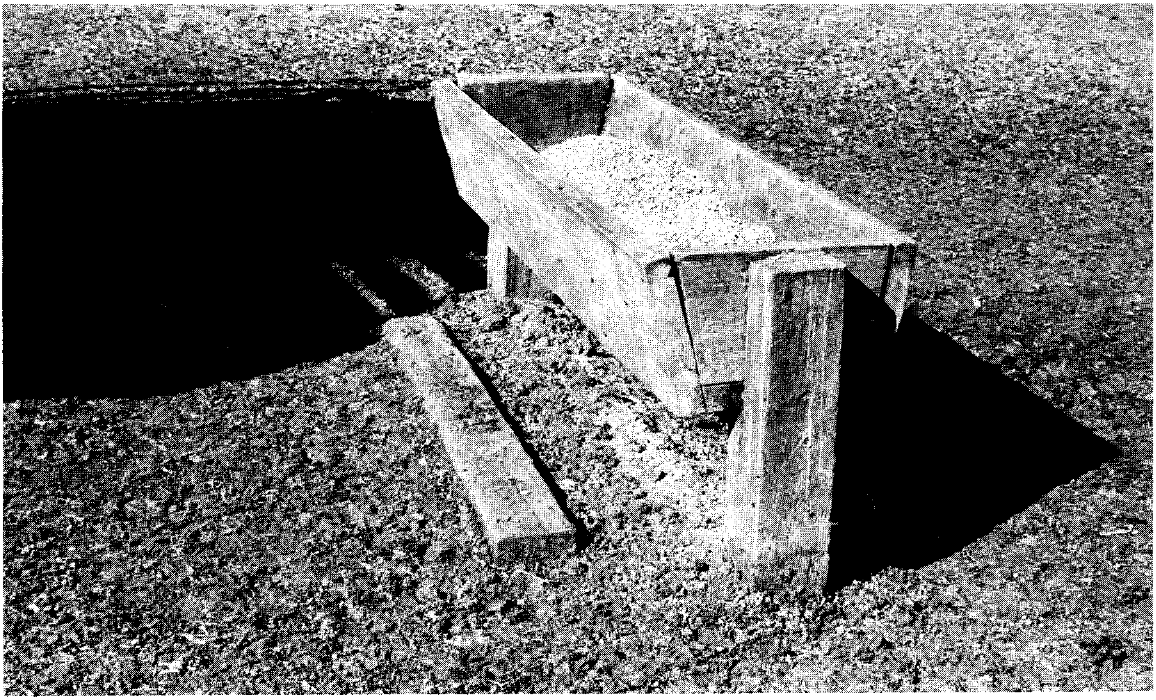

Fig. 6. Type of feeding trough used to prevent feed wastage and insure a clean feed supply free of fecal contamination.

access to natural grasses lying under snow, fine-stemmed grass hay, and a commercial grain mixture[2]. This grain mixture was first mixed with the hay and placed on the ground. The "trainer" deer soon taught the newly translocated reindeer to eat out of "V" shaped feeding troughs placed on posts approximately two feet above ground level (Fig. 6). These troughs prevented the animals from wasting feed by placing their feet in the feed and aided in parasite control by keeping feces away from food sources.

The grain mixture had been used with good results as the primary food source for several generations of reindeer held in captivity over the past 15 years. Some of these reindeer had been held in indoor rooms for infectious disease research for up to 18 months with the grain mixture as their only food source. These animals maintained excellent body condition, and those animals which were pregnant had fawns. Rumen innoculum from reindeer previously adapted to the grain mixture was not introduced to any newly translocated animals. All animals appeared to be able to adjust to the new diet without the aid of additional rumen flora.

It was observed that 90 to 95% of the translocated reindeer would successfully adapt to captivity and a commercial diet. The remaining 5 to 10% would show signs of weight loss after two to three weeks. Any deaths occurred most frequently after 3 to 4 weeks in captivity. It appeared that the time of greatest weakness in most of the reindeer occurred when their natural body reserves were depleted at 3 to 4 weeks post-transport. Unless it was absolutely necessary, newly transported reindeer were not approached or handled during this adjustment period.

After the initial conditioning period was completed, the reindeer were treated for parasites with 0.2 micrograms per kilogram of ivermectin and vaccinated with a killed bacterin-toxoid containing *Clostridium chauvaei-septicum-*

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[2] Quality Texture, Purina Mills, St. Louis, Missouri. USA

novyi-perfringens Type C and D. Reindeer that successfully adapted to captivity were used for a variety of research projects. Diet was maintained with the exclusive use of the grain mixture offered ad libitum. Care was taken to keep the food supply fresh and dry. Body condition was maintained at excellent levels for many years with good reproductive success.

Conclusions

Free-ranging reindeer can be successfully translocated and held in captivity with a low rate of mortality if the natural biology of the animals is considered and each move adjusted to fit the special circumstances of the situation. Of primary importance is the amount of stress to which the animals will be exposed, the duration of this stress, and the availability of food and water which is palatable and digestable. A fast move of only a few hours is preferable over a slow move of many hours or days even if the fast move may appear somewhat more stressful. The receiving area must be as stress-free as possible and dog-proof. The animals should not be approached or handled during the conditioning period unless absolutely necessary.

Each translocation of reindeer is unique, and no one single plan should be used for all situations. Experience and good animal husbandry techniques are essential for the succesfull completion of a move. If any one part of a translocation is not going to be completed as planned, the whole move should be adjusted or postponed until all conditions are as optimal as possible.

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Calving and lactation as fertility controlling factors in reindeer

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Abstract: The semi-domesticated reindeer *(Rangifer tarandus tarandus* L.) is extremely well adapted to the harsh arctic and subarctic environments. Patterns of growth and seasonal changes in body condition are an important aspect of deer ecology. Energy requirements of lactation and growth are the two major processes in deer elevating the metabolic rate above the levels of maintenance. For animal living in seasonal environments this means that births must be coincident with a period of food abundance. The timing of births does not however only affect calf survival but late calving is also documented as reducing the females probability of being fertile in the next year.

In this study calving and lactation stress as fertility controlling factors were studied in 836 female reindeer. The reindeer were housed outdoors during 1970-86 in the Kaamanen Reindeer Research Station (69 °10' N). The fertility rate of hinds calving in two consecutive years was clearly higher than that of those having been barren in the previous year (84.3 % and 75.4 %, $P<0.01$). Hinds calving in both years were also in better body condition in autumn than yeld hinds (71.7 ± 0.3 kg and 69.5 ± 0.7 kg respectively). Calf birth-weight was significantly related to the weight of the hind at the time of conception. The age of hind was without effect once the effect of age on body weight was discounted. Sex-ratio of calves was slightly male biased, 53.6% of calves born were male. There was a non-significant trend to male biased sex-ratio in primiparous hinds. In adult hinds the number of female and male progeny was nearly equal.

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Heavy metals in reindeer and their forage plants

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Abstract: An attempt was made to assess the level of heavy metal transfer from forage plants to reindeer *(Rangifer tarandus L.)* in an area in northern Lapland affected from dust from an open pit copper mine.

Botanical analyses of rumen contents from reindeer provided information about the main plant species in the diet. Representative plant material was collected from sample plots within an 8 km radius from the central part of the mine and from a reference area situated about 200 km upwind of the mining site.

The following plant species were analysed: *Bryoria fremontii, Br. fuscescens, Cladina rangiferina, Equisetum fluviatile, Deschampsia flexuosa, Eriophorum vaginatum, Salix glauca, Salix phylicifolia, Betula nana,* and *Vaccinium myrtillus.*

The greatest difference between metal concentrations in the plants collected from dust contaminated area and from the reference area was found in lichens. Copper is the main metallic component of the ore and was found in higher concentrations in lichens coming from the area around the mine than in lichens from the reference area. Smaller differences were found in vascular plants. Dust particles, remaining on outer surfaces after snow smelt contributed to a limited extent to the metal contents. Species—specific accumulation of metals was observed in some plants. The uptake of lead and cadmium in some vascular plants was somewhat higher in the reference area compared with plants growing in the perifery of the mining center, probably due to the metal concentrations in the bedrock.

Organ material (liver and kidney) was collected from reindeer in both areas. No noticable effect on metal concentrations in the liver of the reindeer were found. Although the lead, cadmium and copper concentrations were higher in the organs collected from animals in the reference area than in those from the mining area, the levels were still below the concentrations regarded as harmful for the animals from toxicological point of view.

The material collected during this study would also lend itselfto research into the trace element nutrition of the reindeer.

Keywords: Reindeer forage, liver, kidneys, industrial emission, pollution, heavy metal accumulation

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Figure 1. Aitik, the reference area and Gällivare Forest Saami Community.

Introduction

Copper is extracted through open pit mining at Aitik, county of Norbotten, Sweden (Fig. 1.). Blasting causes emission of metal—containing dust (Rühling, 1978 & 1979, Göransson, 1983).

Applying for permission to increase production Boliden Mining Co. Ltd. was instructed by the National Franchise Board for Environment Protection to examine whether content of certain metals in and on reindeer forage plants and reindeer organ tissues exceeded current toxicological standards as prerequisites for a good state of health. This clam was caused by the fact that the mining area is situated within the summer range of Gällivare Forest Saami Community and that fears had been uttered by the Saami Community that the reindeer (and consequently the meat market) might be affected by heavy metals deposited with the dust.

The contents of copper and zinc in the moss *Pleurozium schreberi* and reindeer lichen (*Cladina spp.*) growing around the mine were analysed by Rühling (1978 & 1979). High copper concentrations (1600 mg/kg) were observed in the moss growing in the immediate vicinity of the mine, and concentrations over 100 mg/kg were found as far as at a three kilometre distance. The regional background level of 5 — 10 mg/kg was not reached until some ten kilometres from the mine, and elevated zinc contents were observed only in the immediate neighbourhood of the mine centre. Similar conditions but with lower metal concentrations (not more than 370 mg Cu/kg) were observed in reindeer lichen *(Cladina rangiferina)*.

The Aitik area is used by the Ratukka Group of the Gällivare Saami Community (SOU 1966). Direct movements between seasonal grazing areas are made only to a limited extent. The movements of the reindeer herds are described as "roving" or migration grazing (Planverket, 1974). Grazing of the area occurs mainly when there is no snow on the ground (July through September) but reindeer herds may be present in the area even at other times of the year (Erik Lindström, the County Government; Åke Nordvall, the Ratukka Group).

Aims

This study aims at
- clarifying the reindeer's choice of forage plants in the Aitik area during summer time,
- studying the content of metals in important reindeer forage plants, and
- studying the metal content in reindeer organs.

Areas for collection of biological materials

The mining site (lat. 67° 05' N, long. 20° 55' E) and the reference area (lat. 66° 15' N, long 18° 15' E) (cf. Fig. 1) are both within the Fennoscandian subprovince of the Boreal European-Westsibirian flora province (Sjörs, 1956). The vegetation is a mosaic of coniferous forests and poor northern fens (Domänverket, 1981).

Table 1. Sampled and analyzed forage plants

Species	Plant part	Sampling date			
		May	June	July	August
Bryoria fremontii (Tuck) Brodo & Hawksw.	all	+			
Br. fuscescens coll (Gyeln) Brodo & Hawksw.	all	+			
Cladina rangiferina L. Nyl.	top third	+	+		+
Stereocaulon paschale L. Hoffm.	top third		+		+
Equisetum fluviatile L.	stem			+	+
	rhizome		+		
Deschampsia flexuosa L.	above ground			+	
Eriophorum vaginatum L.	above ground	+		+	+
Salix glauca L.	buds, leaves		+		+
S. phylicifolia L.	buds, leaves		+		+
Betula nana L.	bark, buds, leaves			+	+
Vaccinium myrtillus L.	top 5 cm		+		+

The climate is continental. The humidity index of Martone is 32 - 36 during the growing season of 140 - 150 days above + 3°C.

Yearly precipitation is 400 - 450 mm, whereof 175 - 200 mm fall during the growing season and about 150 mm, 35 - 40% fall as snow. The latter stays for 200 - 220 days (Svenska sällskapet för Antropologi och Geografi, 1953 - 1971).

Winds from W - NW and from SE are dominating throughout the year (Fig. 4).

The reference area was considered free of deposition and man-made effects, but it is situated in the periphery of an ore province (Ores, industrial minerals, and rocks in Sweden. Map, SGU, ser. Ba No. 29, 1979).

Materials

Collecting has been carried out around Aitik and within a reference area (cf. Fig. 1 and Fig. 5). The test material consists of reindeer forage plants and reindeer organs.

a) Sampling of plants

To describe the distribution pattern of heavy metals within the Aitik area metal concentrations of some important reindeer forage plants were used. For chemical analysis the plants were collected at about the same time in both Aitik and the reference area.

At Aitik sampling plots were located at a distance of 1000, 2000, 4000, and 8000 m from the centre of the mine along NW - SE and NE - SW transects. The transects coincide with dominant wind directions (Fig. 4). In addition plots were chosen in all points of the compass, right outside the fence surrounding the mine.

In mid-May, mid-June, mid-July, and mid-August 1982, plant samples were collected within all sampling plots. As shown in Fig. 3 and Table 1, stress was laid on plants of importance to reindeer during the sampling period. In July 1985 *Bryoria fuscescens* and *Br. fremontii* were once more sampled within both areas.

In August 1982, plant material equivalent to that of Aitik was collected at five locations within the reference area (Fig. 1).

Reindeer lichen from the June sampling at Aitik was used for determining wheter a metal accumulation in reindeer lichen occurred after the snow-melting period.

The plant material was classified, air dried, and packed for subsequent chemical analysis.

b) Sampling of rumen content for quantitative estimation of botanical composition.
During two periods (June 11 - 14 and August 12 - 19) five grazing reindeer, 10 animals totally, were shot in the Aitik area, and on one occasion (July 21) five reindeer were sampled during an ear-tagging session (Fig. 2).

From each animal about 2 litres of stirred rumen content was collected and preserved for quantitative botanical analysis.

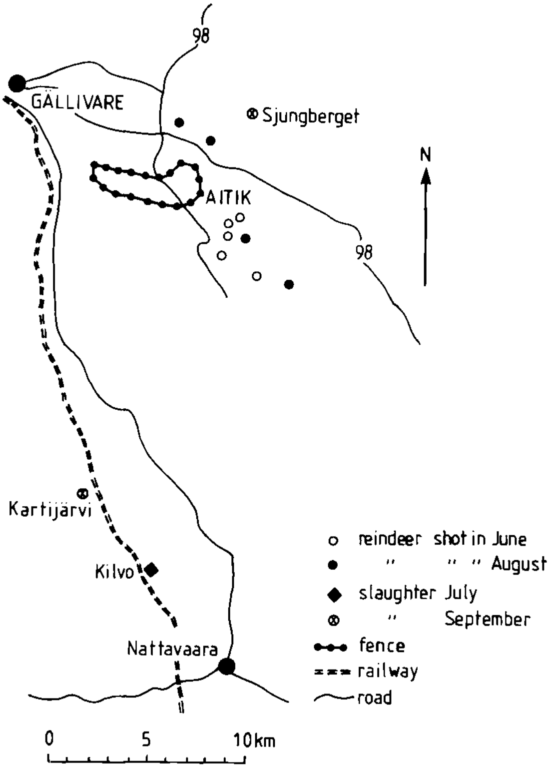

Figure 2. The sampling sites of reindeer around Aitik.

c) Sampling of organ material
Organ tissue samples were collected from the 15 reindeer which had also contributed rumen samples *(Aitik I)*.

Organ tissue samples were also collected from 29 reindeer *(Aitik II)* at routine slaughter in the autumn. Of these, 9 were slaughtered at Sjungberget, north of the mine, and 20 at Kartijärvi south of the mining area (cf. Fig. 2).

It should be pointed out that the degree of contact with the vicinity of the mine of the Aitik II reindeer has escaped determination. However, according to the local herdsmen most of the Ratukka-reindeer regularly utilize summer pastures round Aitik.

Reference samples from 20 reindeer were collected in connection with regular slaughter at Åberget (Fig. 1) in mid-December. A herd that had previously grazed within the reference area was then rounded up during its migration to the winter pastures.

The organ tissue samples consisted of liver and kidneys. The left metacarpal bone (for estimation of nutritional state) and the left mandibular bone (for age determination) were sampled as well. The Aitik material was examined at the SVA (the National Veterinary Institute), whereas corresponding investigations of the reference material was carried out at the slaughter site by members of the sampling staff.

The organ material was transferred to the SVA, where it was stored at -20° C until chemical analysis was performed.

Methods

a) Chemical analysis
Pretreatment of samples. - Combustion of *organ material* (5 g liver and kidney, respectively) was performed by automatic wet digestion. An oxidizing mixture (15 ml) of nitric/perchloric acids = 7:3 (vol.:vol.) was added to the samples in boro-silicate glass tubes, in an electrically heated block of aluminium. During the automatic wet digestion time and temperatures are controlled by a microprocessor (Autostep,

Digestor: Model 40, Tecator AB, Höganäs, Sweden) according to a standard ashing program (Frank 1976, 1983).

The air dried *plant samples* were cut to small pieces. One gram of each sample was wet digested according to the standard procedure.

Analysis. - The residue after wet ashing was evaporated to dryness and the dry residue dissolved in an ionic buffer solution for analysis using a direct current plasma-tomic emission spectrometer (SpectraSpan IIIA, Applied Research Laboratories Inc., Sunland, USA). The analysis comprised simultaneous determination of the concentration of i.a. lead, cadmium, copper, and zinc (Frank & Petersson, 1983).

Analytical results for plant material are given as mg/kg air dry weight, which means about 7 - 9 per cent water content; organ material results are given as mg/kg wet weight.

Mercury in the livers from the Aitik I and Aitik II materials was determined using neutron activation analyses (IVL, Institutet för vatten- och luftvårdsforskning, Stockholm, Sweden).

Statistical analysis were performed by using standard programs (Statgraphics) for i.a. calculation of linear regression.

b) Quantitative botanical analysis of rumen content

One litre of stirred rumen content was washed through a set of six sieves (mesh size ranging between 4000 - 125 μ m). Particles smaller than 125 μ m were discarded. The plant fragments were separated by aid of a grid and examined in a microscope.

The area frequency of plant groups was converted to frequency by weight using weight constants specific for plant groups and particle sizes (Eriksson et al., 1981).

Results and discussion

The summer diet of reindeer in the Aitik area

Figure 3 illustrates that dwarf shrubs contribute as much as 21 - 76 per cent to the summer diet of reindeer. In June *Vaccinium myrtillus* dominates, in July and August no species dominance was observed. The dwarf shrubs compartment then contains mainly *Vaccinium spp.*, *Calluna vulgaris*, *Empetrum nigrum*, *Andromeda polifolia* and others.

Leaves from *Betula spp.* and *Salix spp.* were found in the rumens during the entire summer. In August there was a noticeable increase from 15 per cent by weight to 53 per cent. In June *Salix* leaves dominated, in July *Betula nana* and in August *Betula spp.*

Herbs occurred only in minor quantities (less than 1 per cent by weight).

Graminoids quantitatively played a major role in June only, when 12 per cent by weight

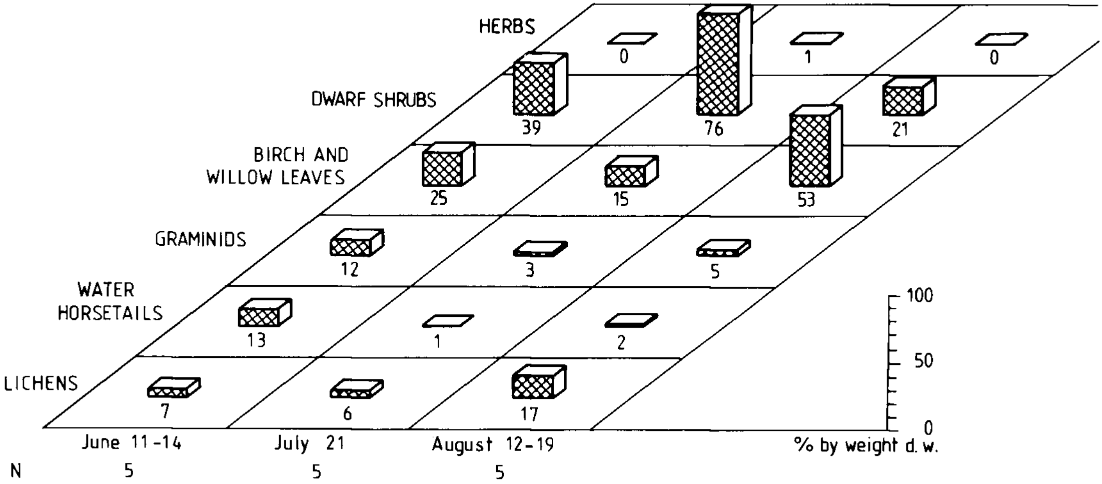

Figure 3. The forage selection of Aitik reindeer during summer. (Plant groups per cent by weight, d.w., + 80° C, 24 h.)

Table 2. Minimum and maximum values of copper and zinc concentrations in forage plants of reindeer in Aitik (n = 18) and the reference area (n = 5) in June, July, August 1982, and in July 1985. Values in mg per kg DM.

	month/82	Cu-Aitik	month/82	Cu-ref	Zn-Aitik	Zn-ref
Vaccinium myrtillus	8	6.5-16	8	6.7-14	21-47	19-42
Betula nana	6	7.5-52	8	2.3-3.8	109-282	128-206
Betula nana	7	4.1-25			91-232	
Salix glauca	8	3.0-25	8	5.1-7.4	39-410	151-567
S. phylicifolia	6	4.9-19	8	5.3-7.0	47-364	119-478
	8	2.7-12			8.8-230	
Deschampsia flexuosa	7	2.2-9.1	8	1.1-1.9	18-35	15-25
Eriophorum vaginatum	7	2.8-15	8	1.7-4.8	38-66	44-65
Equisetum fluviatile	7	2.2-17	8	0.95-3.0	32-72	39-97
Cladina rangiferina	6	4.8-184			16-29	
	8	3.9-170	8	1.0-1.6	13-30	15-22
	month/85		month/85			
Bryoria fremontii	7	4.9-54			32-61	
Br. spp.			7	2.0-2.2		30-32
Br. fuscescens	7	6.8-132			49-86	

were registered. Among grasses *Deschampsia flexuosa* was common.

Equisetum fluviatile was frequent in June only, when it amounted to 13 per cent by weight. The high concentration of sodium (500 - 600 mg Na/kg D.M. and values even as high as 2530 mg/kg D.M. was determined in the reference area) should be of great importance to reindeer as a major sodium source. The sodium concentration in other vascular plants as well as in lichens were mainly between 100 and 200 mg/kg D.M.

Lichens occurred in the diet on all three sampling occasions. A marked increase was noted from 6 per cent in July to 17 per cent in August.

The plant species preference shown by the Aitik reindeer corresponded fairly well to the observations of Skuncke (1968) and Warenberg (1977) on domestic reindeer in Sweden, and those of Helle (1981) on wild Finnish forest reindeer *(Rangifer tarandus fennicus).*

Plant material

Figure 5 shows the copper concentrations in *Cladina rangiferina* from the mining area.

The concentrations for copper, zinc, lead and cadmium are shown in Tables 2 and 3. They show the lowest and highest metal concentrations found in reindeer forage plants in the Aitik and the reference areas, respectively, as well as the date of sampling.

Considering the presence of gradients in the material from the Aitik area, which may be

Table 3. Minimum and maximum (lowest and highest) values of lead and cadmium concentrations in forage plants of reindeer in Aitik (n = 18) and the reference region (n = 5) in June, July, August 1982, and July 1985. Values in mg per kg DM.

	month/82	Pb-Aitik	month/82	Pb-ref	Cd-Aitik	Cd-ref
Vaccinium myrtillus	8	0.05-0.65	8	0.02-0.47	0.08-0.43	0.18-0.28
Betula nana	6	0.59-4.2	8	0.72-1.2	0.02-0.52	0.14-0.39
Betula nana	7	0.02-1.2			0.28-0.60	
Salix glauca	8	0.12-1.1	8	0.16-0.75	0.39-1.4	0.89-1.8
S. phylicifolia	6	0.02-0.34	8	0.47-0.74	0.28-1.3	0.80-2.0
	8	0.02-0.34			0.18-1.5	
Deschampsia flexuosa	7	0.21-1.0	8	0.29-0.73	0.02-0.24	≤0.02
Eriophorum vaginatum	7	0.02-0.72	8	0.47-1.2	0.02-0.22	≤0.02
Equisetum fluviatile	7	0.02-1.5	8	0.64-1.5	0.57-0.76	0.24-0.60
Cladina rangiferina	6	2.7-6.7			0.10-0.30	
	8	2.6-7.1	8	3.3-4.2	0.08-0.28	0.07-0.18
	month/85		month/85			
Bryoria fremontii	7	2.9-15			0.02-0.41	
Br. spp.			7	2.2-5.9		0.18-0.27
Br. fuscescens	7	8.2-30			0.22-0.58	

more or less obvious, calculations of mean or median values have not been considered realistic.

Metals are transferred to and accumulated in lichens by airborn dust or dissolved in rain water (Monitor, 1987). According to Tuominen and Jaakola (1973), lichens also are able to take up and accumulate metals from the substratum via living or dead basal parts of thalli.

Metals are usually accumulated in lichens as ions adsorbed to cell walls (Monitor, 1987).

Zinc and cadmium, on the other hand, are carried within cells, and, - as far as it is known - are the only metals with distinctly harmful effects on lichens monitor, 1987).

Beyond accumulation of metal containing dust on outer surfaces (leaves etc.) metals are accumulated also by root uptake in *Betula nana*, *Salix spp.*, *Deschampsia flexuosa*, *Eriophorum vaginatum*, *Equisetum fluviatile* and *Vaccinium myrtillus*.

Copper: The highest copper concentrations found in *Cladina rangiferina* and *Bryoria spp.* from the reference area are low (1.6, and 2.2 mg Cu/kg) compared to the copper concentrations in *Cladina rangiferina*, *Bryoria fuscescens* and *Br. fremontii* from Aitik with the highest values of 170, 132 and 54 mg/kg, respectively (cf. Table 2).

Within a circle round the mine with a radius of about 8 kilometres the dust downfall has caused conspicuously elevated contents of copper in *Cladina rangiferina* and *Bryoria spp.* as compared to the reference area (cf. Fig. 4 and Table 2). The latter concentrations are in agreement with the values registered by Holm

Table 4. Heavy metals in reindeer lichen (*Cladina* sp.) from the Rogen area (1961-1975) μg/g dry weight (Holm 1981).

Fe	Zn	Mn	Pb	Cu	Ni	Cd
160 ± 20	18 ± 2	10 ± 3	9 ± 3	1.8 ± 3	0.70 ± 0.10	0.10 ± 0.02

(1981) in *Cladina* sp. at Rogen, county of Jämtland (cf. Table 4).

The mining company, within its own measuring program, is continuosly monitoring the dust downfall and its copper concentration at 9 measuring stations around Aitik (Göransson, 1983).

For these 9 downfall measuring stations the copper concentration of *Cladina rangiferina* was estimated by weighting measuring values from three adjacent plant sampling plots. Weights were inversely proportional to the square of the distance from the mine centre. A stepwise regression analysis between measuring values for copper in *Cl. rangiferina* and 24 monthly mean values was carried out. The downfall for the year 1982-1983 was proportional to the copper concentration of *Cl. rangiferina* (r^2 = 0.91) (cf. Fig. 6). How much of the downfall from the time before measuring that had contributed to the copper content of *Cl. rangiferina* is, however, not known.

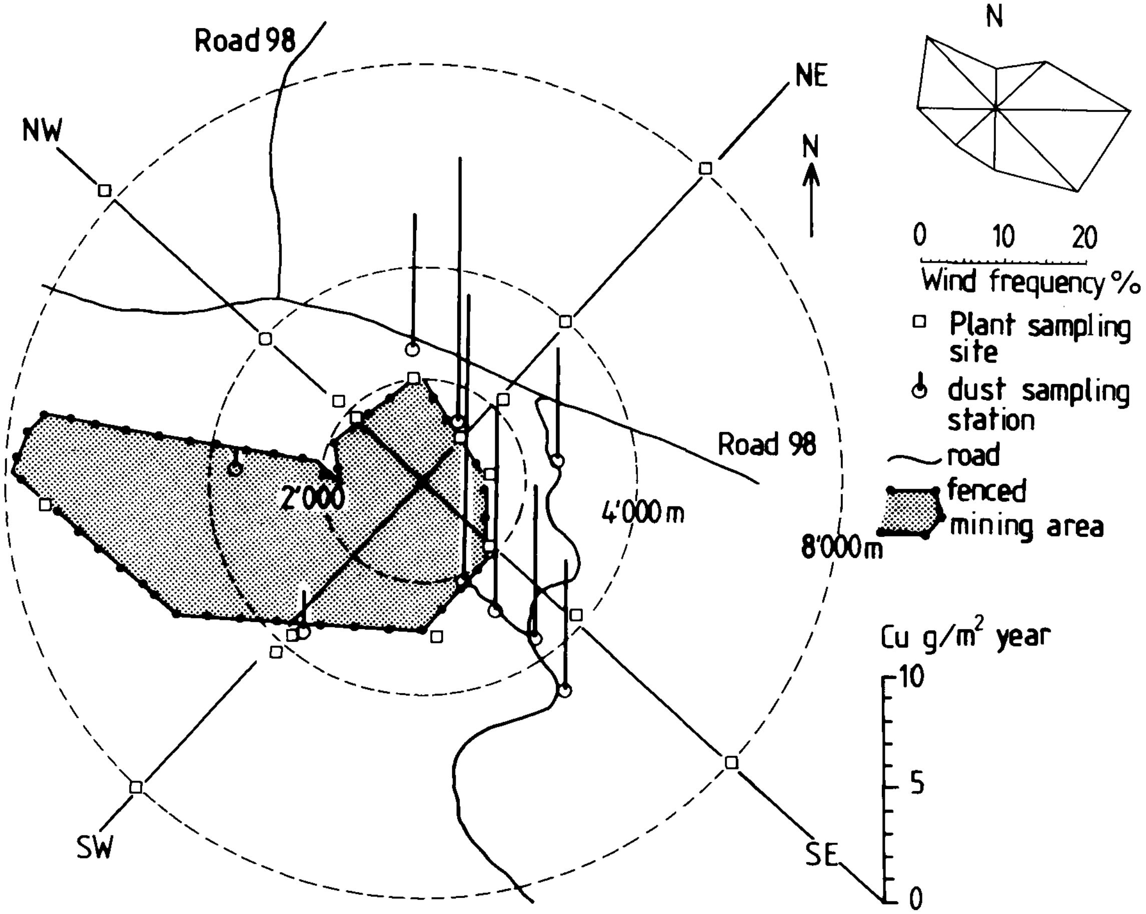

Figure 4. Fallout of dust-carried copper around Aitik, 1982 - 1983. (Wind frequency registered at Gällivare airport, close to the plant sampling site: NW 8'000 m.)

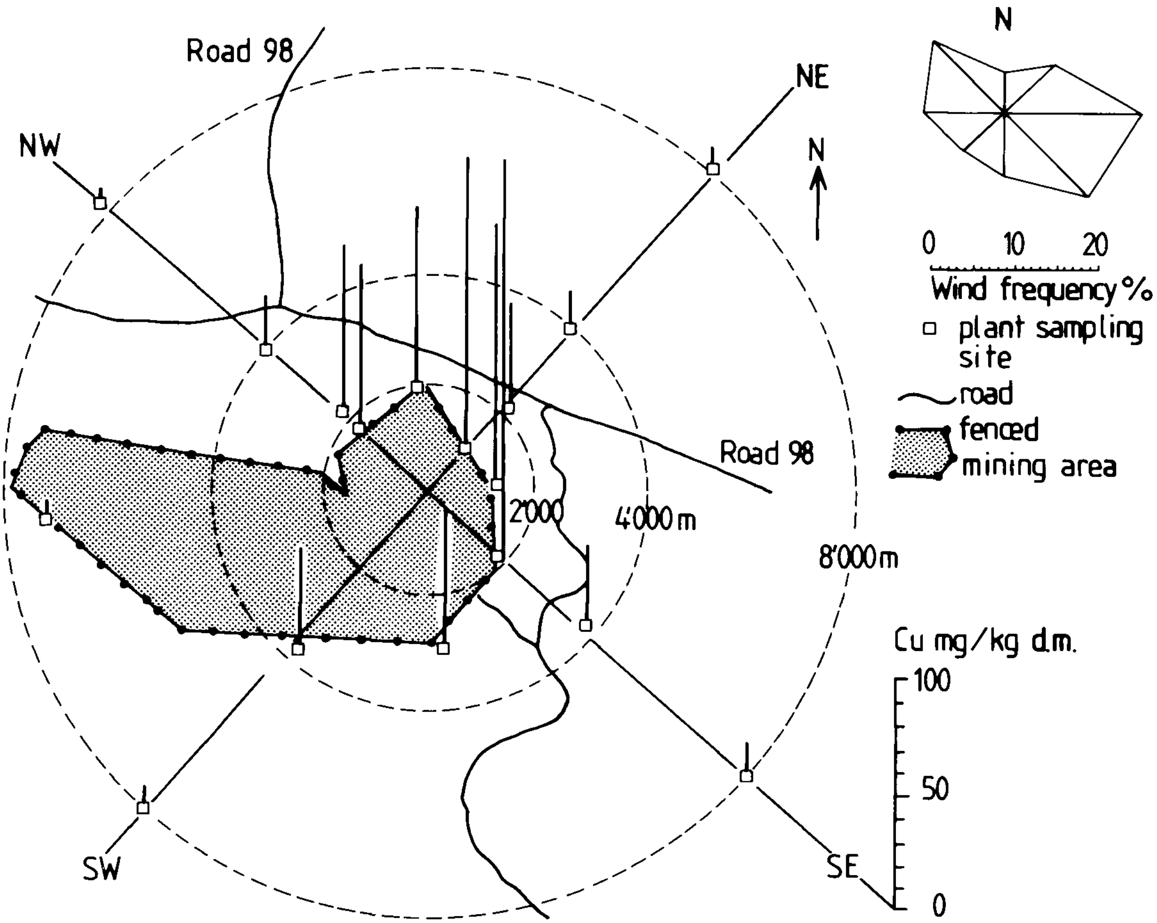

Fig. 5. Copper concentrations in *Cladina rangiferina* growing in the Aitik-area.

Figures 4 and 5 show the influence of dominating winds on downfall and copper concentration in *Cl. rangiferina* in the Aitik area. As expected, most of the copper in the lichens of the investigated area originates from the emission caused by the mining activities.

The highest concentrations of copper in *Cl. rangiferina* and *Bryoria spp.* have been established E and SE of the mine centre in dominating wind directions, show in Fig. 5, which together make 30 per cent of the relative wind frequency (SMHI, 1982). The highest values measured in *Cladina rangiferina* were 184 and 170 mg/kg (cf. Table 2 and Fig. 5), values which are much lower than the highest concentration (370 mg/kg) reported by Rühling (1979). The lowest value reported by Rühling (8 mg/kg) was in a distance of 12 kms West of the mining centre and is higher than the lowests in our survey (3.9 and 4.8 mg/kg).

Metal containing dust accumulates in snow during the winter. After the snow-melting period release and subsequent uptake of metals was negligible in *Cl. rangiferina* as shown by its copper concentrations in June and August. According to Table 2 minimum and maximum values were only insignificantly higher in the June material.

The highest *copper* contents of the reference area in *Salix glauca* and *S. phylicifolia* are 7.4 and 7.0 mg Cu/kg, respectively, whereas the corresponding plants from Aitik contained 25, 19 (June) and 12 mg Cu/kg (August), respectively, as shown in Table 2.

The copper concentrations in *Salix glauca* and *S. phylicifolia* of the reference area are of the same level and are about three times higher than those in *Cladina rangiferina,* indicating copper uptake from the ground of vascular plants. Compared to the lichens the differences in copper concentration between the *Salix spp.* of the reference and the Aitik area are not as great.

The differences in copper concentration in *Betula nana* between the reference area (2.3 - 3.8 mg/kg) and Aitik are conspicuous. The highest concentration of 52 (June) and 25 (July) mg/kg were found near the centre of the mining area.

Of the grass species examined, *Deschampsia flexuosa* from the reference area has low copper concentrations (1.1 - 1.9 mg/kg). The highest value from the mining area is 9 mg/kg.

Larger variations in concentration are shown by *Eriophorum vaginatum* (cf. Table 2). The copper concentration from the reference area is 1.7-4.8 mg/kg and the highest level from Aitik was 15 mg/kg.

A similar pattern is shown in *Equisetum fluviatile* with lower copper values from the reference area than from the Aitik area (2.2 — 17 mg/kg).

The range between minimum and maximum copper values is much larger in Aitik than in the reference area and varies with different plant species. The range is very wide for lichens but much more narrow for other plants.

In the reference area there is a tendency for the copper concentrations of the reindeer forage plants to be low. The only exception was shown by *Vaccinium myrtillus* with a slightly higher concentration of 14 mg/kg. This value is of the same magnitude as the highest concentration in Aitik (16 mg/kg) and is explained by the high degree of soil mineralization in the reference area.

Zinc: Zinc concentrations in *Cladina rangiferina* from Aitik (13 — 30 mg/kg) do not differ remarkably from those of the reference area (15 — 22 mg/kg, cf. Table 2) but they are about 2 — 3 times higher in *Bryoria spp.* from Aitik (61 and 86 mg/kg, respectively, as the maximum values), than from the reference area with zinc concentrations of 32 mg/kg as the highest values. In *Cladina rangiferina* from Aitik concentrations of 25 — 56 mg/kg were found by Rühling (1979) close to the values found in our investigation.

The zinc concentrations of the vascular plants are of the same magnitude in both areas. It is possible that there is a certain species specific accumulation of zinc in *Salix glauca* and *S. phylicifolia.* In the reference area on the border of the ore province zinc concentrations are higher (567 and 478 mg/kg, respectively) than in Aitik, when comparing the highest concentrations (410, 364, 230 mg/kg).

Differences in *Vaccinium myrtillus, Betula nana, Graminidae,* and *Equisetum fluviatile* are negligible as shown in Table 2.

Lead: A study of the highest lead values found does not give any indication for a general tendency for lead accumulation. If, however, separate lead concentrations are studied in detail a less uniform picture emerges.

The lead concentration in *Cladina rangiferina* from the reference area was 3.3 - 4.2 mg/kg as shown in Table 3. In Aitik, where the highest concentrations were 7.1 and 6.7 mg/kg, respectively, 11 of 17 measuring plots yielded lead concentrations exceeding the highest ones from the reference area.

For *Bryoria spp.* higher lead concentrations can be recorded for *Bryoria fuscescens* than for *Br. fremontii.* In the latter species the lead concentrations exceeded the highest value of 5.9 mg/kg from the reference area at 7 measuring plots only, whereby the highest value round the mine was 15 mg/kg. In *Br. fuscescens* all values were higher (8.2 - 30 mg/kg) than the highest ones of the reference area (cf. Table 3).

There is, however, a different picture to be seen when studying the lead uptake by vascular plants. In the latter the lowest lead values of the plants from the reference area are often higher than those from, e.g. *Beula nana, Salix glauca,* *S. phylicifolia*, *Deschampsia flexuosa*, *Eriophorum vaginatum*, and *Equisetum fluviatile* from Aitik. Thus, there are indications that the soils of the reference area are richer in minerals than those of Aitik, the latter mainly carrying cupreous minerals.

The higher lead concentration of the Aitik-lichens compared to those of the reference areas, may be explained both by anthropogenic sources in the ares, such as automobile transports etc. and by the lead concentration of the dust, the latter explanation finding support in the efficiency of *Bryoria fuscescens* in dust enrichment.

The results indicate that a certain deposition of lead occurs in the neighbourhood of the mine, but the mineralization and the lead uptake is larger in the vascular plants of the reference area than in those of Aitik.

Cadmium: In *Cladina rangiferina* of the reference area the highest cadmium concentration was 0.18 mg/kg. In Aitik 0.28 and 0.30 mg/kg were found to be the highest values. Differences are greater in the efficiently dust filtering *Bryoria spp.* In *Br. fremontii* and *Br. fuscescens* 0.41 and 0.58 mg Cd mg/kg, respectively, were observed as the highest concentrations in Aitik, whereas the cadmium concentration of the reference area did not exceed 0.27 mg/kg. Thus, cadmium levels increased towards the mining centre, probably as a result of increased dust downfall.

In similarity to lead it can be noted as a remarkable observation, that the lowest cadmium concentrations in *Salix glauca* and *S.phylicifolia* were higher in plants from the reference area (0.89 and 0.80 mg/kg, respectively) than in those from Aitik (0.39, 0.28, and 0.18 mg/kg). This phenomenon can be interpreted, partly as an indication of species specificity, partly as an expression for the higher degree of mineralization of the soils of the reference area.

The cadmium uptake of the other vascular plants was largely of the same magnitude in the two areas examined, possibly somewhat larger in the reference area.

Even for cadmium the same phenomenon as for lead can be observed, namely that the downfall at the mine implies a certain cadmium burden, but the greater mineralization in the soils of the reference area seems to bring about an increased cadmium uptake by vascular plants.

A constant characteristic of the metal concentrations (copper, zinc, lead, and cadmium) in sampled *Bryoria fuscescens* and *Br. fremontii* from Aitik was that the former had 138-282 per cent higher metal concentrations than the latter. *Br. fuscescens* was collected on Norway spruce *(Picea abies)* whereas *Br. fremontii* was collected on Scots pine *(Pinus sylvestris)*. One

Table 5. Regional means ($\bar{X}$), medians ($\tilde{X}$) and ranges (min - max) of lead, copper, zink and mercury in liver and kidney of reindeer (mg per kg wet weight)

Region	N	Lead			Copper			Zink			Mercury		
LIVER		$\bar{X}$	$\tilde{X}$	min-max	$\bar{X}$	$\tilde{X}$	min-max	$\bar{X}$	$\tilde{X}$	min-max	$\bar{X}$	$\tilde{X}$	min-max
Aitik I	15	0.27	0.13	0 -0.99	21	16	3.1-65	31	29	24-46	0.07	0.004	0.02-0.19
Aitik II	29	0.26	0.25	0.14-0.44	26	19	3.3-131	27	25	15-51	0.05	0.004	0.02-0.11
Ref.	20	0.81	0.75	0.40-1.66	29	21	7.7-72	32	31	24-45			
KIDNEY													
Aitik I	15	0.19	0.17	0.10-0.44	5.4	5.3	4.2-6.7	23	24	19-29	not measured		
Aitik II	29	0.28	0.26	0.13-0.48	5.0	4.8	3.4-7.4	23	24	20-28	”		
Ref.	20	0.42	0.44	0.22-0.70	4.0	4.0	3.1-4.8	24	25	19-29	”		

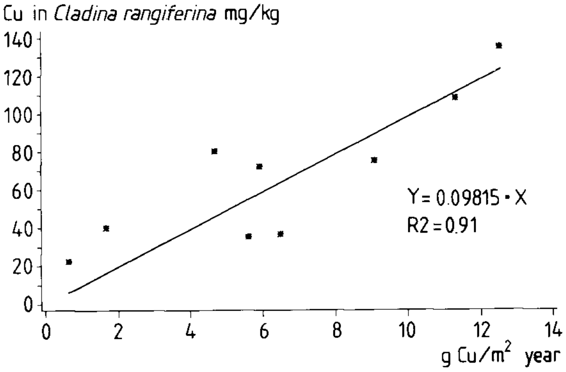

Figure 6. Dry deposition of copper at nine monitoring stations compared to copper concentrations in *Cladina rangiferina* (weighted mean values).

might suggest that the canopy of Norway spruce funnels wet downfall towards the parts of the tree where arboreal lichens grow more efficiently than does the canopy of Scots pine.

Organ material

Results of analysis of reindeer organs from Aitik I and II and from the reference area are shown in Table 5 and are further illustrated by Figures 7 & 8. There was a wide range in several elements, and therefore both mean and median values are given.

Copper: Mean values (medians within brackets) for copper concentrations from Aitik I, Aitik II, and the reference area are 21 (16), 26 (19), and 29 (21) mg Cu/kg, respectively. Range was considerable and largely of the same magnitude in all groups, excepting the highest copper concentration in liver of 131 mg/kg, which was found in the group from Aitik II. The value is considered moderately elevated. In a material from Norway higher concentrations were observed, 3.8 per cent of the reindeer examined having copper levels of more than 150 mg/kg liver (Frøslie *et al.* 1987).

The copper concentrations in liver varied considerably, an observation which coincides with earlier data on copper in the livers of wild ruminants (Bonniwell 1986). The concentrations found in the present material were in several instances critically low, seen from the nutritional point of view. As upper limit 10 mg Cu/kg wet weight is regarded for copper deficiency in domestic ruminants, especially in sheep. Serious deficiency in considered at levels lower than 3 - 5 mg/kg (Blood *et al.* 1989, Frøslie *et al.* 1987, Schwan *et al.* 1987).

If the same criteria are applied to reindeer, copper levels are inadequate in 27 percent of the Aitik I, in 31 per cent of the Aitik II, but in 5 per cent only of the reference material. No serious deficiency was found in our material, whereas in the Norwegian investigation 43 per cent of the material was reported to be deficient *(Frøslie et al.* 1987). The copper supply of the reindeer in the present investigation seems to be better than that in the Norwegian one.

The renal copper levels are within normal values in all groups. The mean concentrations (medians within brackets) were 5.4 (5.3), 5.0 (4.8), and 4.0 (4.0) mg Cu/kg for Aitik I, Aitik II, and the reference area, respectively. It was interesting to note that the copper concentration in the livers was lowest in Aitik I and highest in the reference reindeer, where as in the kidneys the case was reversed. This fact is true both for mean values and medians (cf. Fig. 7).

The following thoughts may contribute to a possible explanation. The two grazing areas in question have different geo-chemical backgrounds. Different elements may interact in reindeer organs. Higher intake of copper, but also of molybdenum and tungsten, in the reference area, can be thought to influence copper metabolism and the excretion of copper in pastures otherwise rich in copper. High levels of tungsten were found in some vascular plants from the reference area as illustrated by *Equisetum fluviatile* (5.8 - 50 mg W/kg, *Betula nana* (2.8 - 4.0 mg W/kg) and *Salix phylicifolia* (4.2 - 5.0 mg W/kg). Both molybdenum and tungsten are known to influence the copper metabolism of ruminants, especially that of sheep (Blood et al. 1989). The copper state of the reindeer in the reference area is the highest, although neither high nor low extremes are present, and it is possible that this fact is due to interaction with molybdenum and/or tungsten.

Zinc: The range in zinc concentration in liver has not been found to be as wide as that for copper. Only in Aitik II there are reindeer, at a rate of 21 per cent, with zinc levels lower than 20 mg/kg. The median values (27 - 31 mg Zn/kg) are of the same magnitude as that found in the investigation in Norway (28 - 48 mg/kg), but the range in the latter material is much wider. The highest zinc value in the Swedish material was 51 mg/kg compared to 120 mg/kg in the material from Norway (Frøslie *et al.* 1987).

The *zinc* levels in kidney are largely the same in three groups.

Lead: The mean (and median) value in livers is 0.27 (0.13) in Aitik I, 0.27 (0.25) in Aitik II, and 0.81 (0.75) mg/kg in the reference group. Corresponding values for kidney are 0.19 (0.17), 0.28 (0.26), and 0.42 (0.44) mg/kg (cf. Table 5). The result is a clear indication and it is shown in Fig. 7, that the reindeer in Aitik I are the least lead burdened, and those of the reference area the most heavily burdened. The higher lead burden and the better rate in copper supply might be explained by the higher rate of mineralization of the soil of the reference area.

The lead burden of reindeer in Norway showed a wide regional variation (Froslie *et al.* 1984). Mean values from 0.19 (Hattfjelldal, mid Norway) to 1.08 mg/kg (Dovre, south Norway, with maximum value of 1.8 mg Pb/kg) were obtained, whereas in our investigation the highest value observed was 1.66 mg/kg.

Mercury: Analysis have been made in livers from Aitik I and Aitik II only. The median value was low in both groups. The exposure to mercury is considered to be low. The highest mercury concentrations observed (0.19 and 0.11 mg/kg, respectively) are comparable to the highest values observed in Norway (0.24, Dovre, south Norway, and 0.18, Karasjok and 0.10 mg Hg/kg, Sortland, north Norway, Frøslie *et al.* 1984).

Table 6. Cadmium concentrations in liver and kidney from the reindeer in Aitik I, Aitik II and the reference area. Means $\overline{X}$, standaerd deviations (S.D.), and ranges (min - max), mg Cd per kg wet weight.

			LIVER			KIDNEY	
Age, years	N	$\overline{X}$	S.D.	min-max	$\overline{X}$	S.D.	min-max
AITIK I							
1 - 2	6	0.15	0.07	0.05-0.25	0.45	0.25	0.22-0.93
3 - 4	6	0.15	0.05	0.09-0.21	1.33	1.58	0.29-4.42
5 - 8	3	0.31	0.08	0.22-0.38	2.99	2.18	0.67-4.99
AITIK II							
2.5	3	0.17	0.07	0.09-0.23	0.71	0.45	0.31-1.19
3 - 4.5	20	0.22	0.07	0.14-0.42	1.29	0.74	0.50-3.42
5 - 8	6	0.44	0.33	0.21-1.09	3.94	3.06	1.23-8.47
REFERENCE							
1.5 - 2.5	7	0.44	0.15	0.22-0.62	1.44	0.62	0.49-2.22
4.5	2	0.70	0.04	0.68-0.73	4.38	0.54	4.00-4.77
5.5 - 7.5	11	1.00	0.39	0.58-1.89	10.2	6.28	2.52-19.0

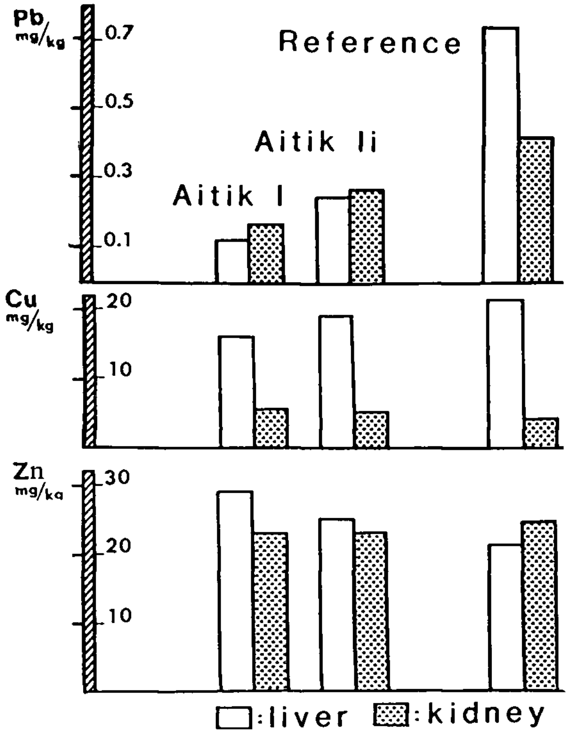

Figure 7. Lead, copper, and zinc concentrations in the liver and kidney of the reindeer from Aitik I, Aitik II and reference areas.

Cadmium: With a view to the fact that cadmium accumulation in liver and kidney is age dependent the groups have been treated according to age for the preliminary study. The result of the statistical treatment (cf. Table 6) illustrates this fact when cadmium levels in liver and kidney are concerned.

A heavier cadmium burden of the reindeer of the reference area than of those from Aitik is statistically significant in both liver and kidney for both age groups (P 0.01 for kidney in the younger age group; in the other age groups P is <0.001).

As mentioned above the accumulation of cadmium in liver and kidneys is age dependent. Therefore, one can not express the cadmium burden of an animal species without considering the age of the individual. The longer an animal has lived in a certain environment, the higher the cadmium levels in the organs become. Cadmium accumulates in the liver, but mainly in the kidneys. The correlation between cadmium concentration and age can be approximately define in the form of a linear regression and be expressed by the equation: $Y = A \cdot X + B$, where Y is the cadmium concentration of the organ and X is the age of the animal. A and B are constants, A (slope of the regression line) is characteristic for a certain region and/or population, and should be used together with B, the intercept of the regression line.

The constants A and B calculated for age dependent cadmium accumulation in kidney and liver for the three groups are shown in Table 7.

Table 7. Calculated values of A (slope) and B (intercept) of regression lines expressing the cadmium burden of populations as a function of Cd-concentration in the respective organ (kidney resp. liver) and the age of the animal. All values in mg Cd per kg wet weight.

Population	Kidney		Liver	
	A	B	A	B
Aitik I	0.54	-0.52	0.031	0.077
Aitik II	0.90	-1.79	0.055	0.044
Reference	1.93	-2.71	0.112	0.239

Figure 8 illustrates the relation between age and cadmium accumulation in kidney in the groups examined from Aitik I, Aitik II, and the reference area. Where the slope is the largest the same goes for the cadmium burden. The latter is largest in the reference area, as is the uptake of copper and lead, the explanation being the high degree of soil mineralization of the reference area.

Similar calculations were reported in an investigation of Norwegian wild as well as domestic reindeer (Frøslie et al. 1986). The regression coefficients (slopes) represent three regions in Norway with values of 1.8 in the South, 1.5 in the middle, and 0.25 in the

North. In comparison with the values from Norway, the ones from Sweden calculated from nearby areas, seem to reveal a higher degree of local variations. However, comparison of slopes gives only a rough idea of not fully comparable relative values.

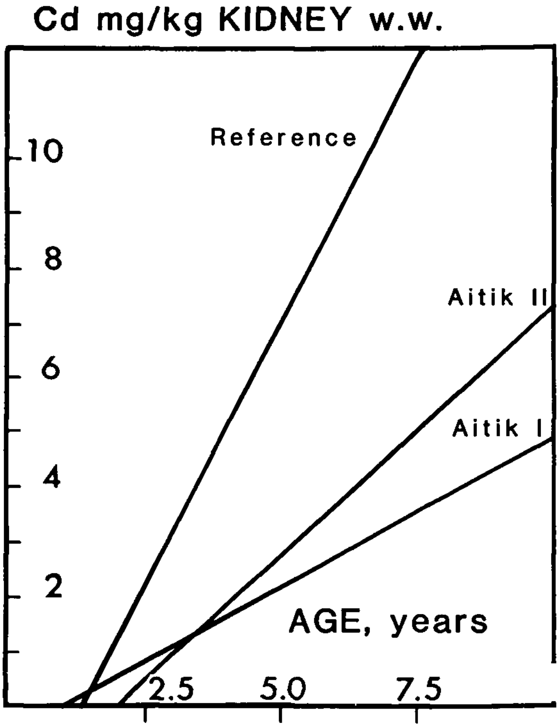

Figure 8. Age related cadmium accumulation in the kidney of reindeer from Aitik I, Aitik II and reference areas.

The intercepts, shown in Fig. 8 and the values given in Table 7, but not given in the Norwegian investigation, show a great variation from positive to negative values depending on individual variations in the investigated groups. As the regression line in total expresses the relationship between age and cadmium concentration of the kidney, neither A nor B must be neglected. Consequently, only the slopes do not give the true values, on the other hand taken together with the intercept result in unrealistic values.

The material has been treated also according to another statistical model, which is less prone to objection and allows comparison of the cadmium burdens of different regions. A quotient is formed by dividing the cadmium concentration of the respective organ with the estimated age of the animal. From these quotients mean and median values are calculated as shown in Table 8. No weighting for age distribution has been made, as the size of the population is limited and the age distribution is different in the three groups.

Table 8. Means $\overline{X}$, $\overline{Z}$ and medians ($\tilde{X}$, $\tilde{Z}$) of the quotients of Cd-concentration in the organs (kidney resp. liver) and the age of animals expressing the cadmium burden of the investigated populations. All values in mg Cd per kg wet weight.

Population	Kidney		Liver	
	$\overline{X}$	$\tilde{X}$	$\overline{Z}$	$\tilde{Z}$
Aitik I	0.285	0.234	0.051	0.069
Aitik II	0.369	0.311	0.056	0.067
Reference	1.297	1.053	0.157	0.196

In comparison to the values calculated as in Table 8 the calculation as in Table 7 yields more correct values, negative intercepts according to the first calculation mode are unlikely to occur. Age determination by way of visual estimation and not by closer examination of cut sections of the teeth means a somewhat uncertain procedure. Medians are preferable means and show the average yearly cadmium uptake in the respective organ in the actual population and the respective region in question.

The calculation illustrate the same feature, namely, that the cadmium burdens like the uptake of other trace elements by animals and vascular plants were heaviest in the reference area.

Summary

Activities at the open pit copper mine at Aitik, county of Norrbotten, causes fallout of considerable amounts of metal-containing dust in the neighbourhood of the mining area. Mapping of metal contamination was made round the mine and within a reference area by analysing important reindeer forage plants as well as liver and kidneys from reindeer.

The highest metal contents were demonstrated in lichens, which accumulate *i.a.* metals by airborne deposition and with precipitation. Elevated concentrations of copper could be registered within an area with the mine as its centre and with the radius of 8 kilometers. Outside that range background levels were generally obtained. For zinc, lead, and cadmium higher values than normal background levels were not found other than in close vicinity of the mine. Dominating winds contributed to an increased contamination NE - SE of the mine.

Near the centre of the mining area copper concentration even of the vascular plants was higher, probably due to the metal-containing dust. A clear trend towards elevated metal concentration in the vascular plants of the reference area could also be registered, even though no notable presence of airborne dust could be observed. This phenomenon is thought to be due to the fact that the reference area is situated on the border to an ore province. The finding even of a species specific metal accumulation has been made during the study.

Analysis of reindeer organs revealed largely the same offering of metals as did the analysis of the forage plant material. Copper, lead, and cadmium levels were higher in the reindeer of the reference area than in those of the mining area. In comparison with the animals from the reference area the differences in metal concentrations were smaller between reindeer from Aitik I and Aitik II. The latter, though, presented signs of the stronger influence of metals, which in turn, may be due to the possibility that they may have been grazing in other - unknown - areas with a heavy metal burden, or to the fact that they were slaughtered in September and had consequently the time to consume considerable amount of lichens after slaughtering of the Aitik I reindeer had occured.

Reindeer migrate and utilize widely spread pastures. A local source of metal emission, consisting in the present investigation of copper mainly, does not seem to imply any health hazard worth mentioning.

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Life history of the reindeer sinus worm, *Linguatula arctica* (Pentastomida), a prevalent parasite in reindeer calves

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Expanded abstract:

Introduction

Registrations of a pentastomid species from the nasal cavity of caribou and reindeer *Rangifer tarandus* (L.) have earlier been reported a few times (e.g Murie 1926; Voblikova 1961; Skjenneberg 1965). Postlarval part of the life cycle of this pentastomid, *Linguatula arctica* (Riley, Haugerud and Nilssen 1987), has been studied in slaughtered and naturally dead semidomesticated reindeer in northern Norway and wild reindeer shot in South-Norway.

Results and discussion

Three hypotheses of life cycle have been tested. A direct transmission to reindeer hosts with monoxenous development is the most probable. Infective eggs are then transmitted during grazing to calves, the main infected age group (Haugerud 1988a; Haugerud *et al.*, in prep.).

Endlarval stage and preadults are found in the sinuses of calves from September to November with subsequent growth and development to patency registrated from April (Haugerud 1988b and in prep.).

Climate is supposed to be of profound importance for the life cycle. The egg is assumed not to tolerate frost, and relatively short time for larval development is the main reason to hypothesize a direct life cycle in *L. arctica.*

Abundant parasites are generally thought to have much impact on host populations. When assessing potential damage in reindeer calves, it is essential to look at the total parasitic effect on infracommunity level. Regarding *L. arctica* which is claimed to have insignificant impact (Rehbinder and Nordkvist 1982), one should especially evaluate the total impact caused by all the parasite species in the respiratory system (see Halvorsen 1986).

Postscript

The poster was a synthesis of the present knowledge of *L. arctica,* mainly based on own studies (reference above and Riley *et al.* 1987) In addition we have also used information found in Murie (1926), Voblikova (1961), Christensson et al. (1974), Rehbinder and Nordkvist (1982) and S.Skjenneberg (pers.comm.).

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Ultrastructure of *Besnoitia* cysts from reindeer *(Rangifer tarandus tarandus* L)

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Abstract: The ultrastructure pf *Besnoitia* cysts in reindeer is described. The observations made on *Besnoitia* cysts and merozoites indicate a form distinct enough to be placed in a new species - *Besnoitia tarandi.*

Key words: parasitology

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Introduction

The presence of *Besnoitia* cysts in reindeer is a common finding (Hawden & Palmer 1922, Nikolaevskii 1961, Nordkvist 1966, Choquette et al 1967, Skjenneberg & Slagsvold 1968, Rehbinder *et al.* 1981). Little, however, is known about the morphology of the parasite in reindeer.

The aim of the present investigation was to study the ultrastructure of the *Besnoitia* cysts and the cyst content of merozoites from reindeer.

Material and methods

Fascias and periost from metatarsal and metacarpal bones, having palpable cysts, were collected from reindeer in connection with the slaughter of the animals the 9th of March 1988 (Mausjaure, Lappland, Sweden). The specimens were cut into pieces of approximately 1 mm^3 and fixed according to Karnowsky at a temperature around 4°C for 4-8 hours and at room temperature for 48 hours.

Before embedding, the material was postfixed in 1% OsO_4solution buffered with 0.1 M phosphate buffer. After embedding in Epon, 1 mm thick sections were cut and stained with toluidine blue for light microscopy.

Ultrathin sections were prepared on an LKB ultratome, picked up on formvar coated and uncoated copper grids, stained with uranyl acetate and lead citrate and examined in a Philips electron microscope 420, at 60 kv, at magnifications varying between 1 000 and 60 000.

Results

By light microscopy the *Besnoitia* cysts are subspherical and measuring 0,18 - 0,22 x 0,28 - 0,32 mm. The cyst wall appears to be composed of two layers, a parasitophorous vacuole of a hypertrophied multinucleated cell and a surrounding homogenous extracellular capsule. The parasitophorous vacuole contains thousands of banana shaped merozoites.

The outer cell membrane of the parasitophorous vacuole, in the light microscope, has numerous pseudopods appearing almost as microvesicles bordering the extracellular capsule. The nuclei are large and pale, some containing dark nucleoli. The extracellular capsule is mostly of a homogenous character but has scattered and clustered elongated nuclei (Fig 1).

Ultrastructurally the extracellular cyst wall consists of an electron lucid material with fibrillar structures and fibrocytes morphologically similar to the keratinocytes of the cornea.

The plasma membrane of the host cell has numerous microvilli or pseudopods protruding into the electron lucid material of the extracellular cyst wall (Fig 2).

The plasma membrane of the parasitophorous vacuole had numerous protrusions extending into the vacuole. The vacuole contains the merozoites and a ground substance which shows an obvious condensation along the plasmamembrane (Fig 3).

The nuclei of the multinucleated cell have a low electron density pattern with an evenly dispersed chromatin, while the nucleoli are com-

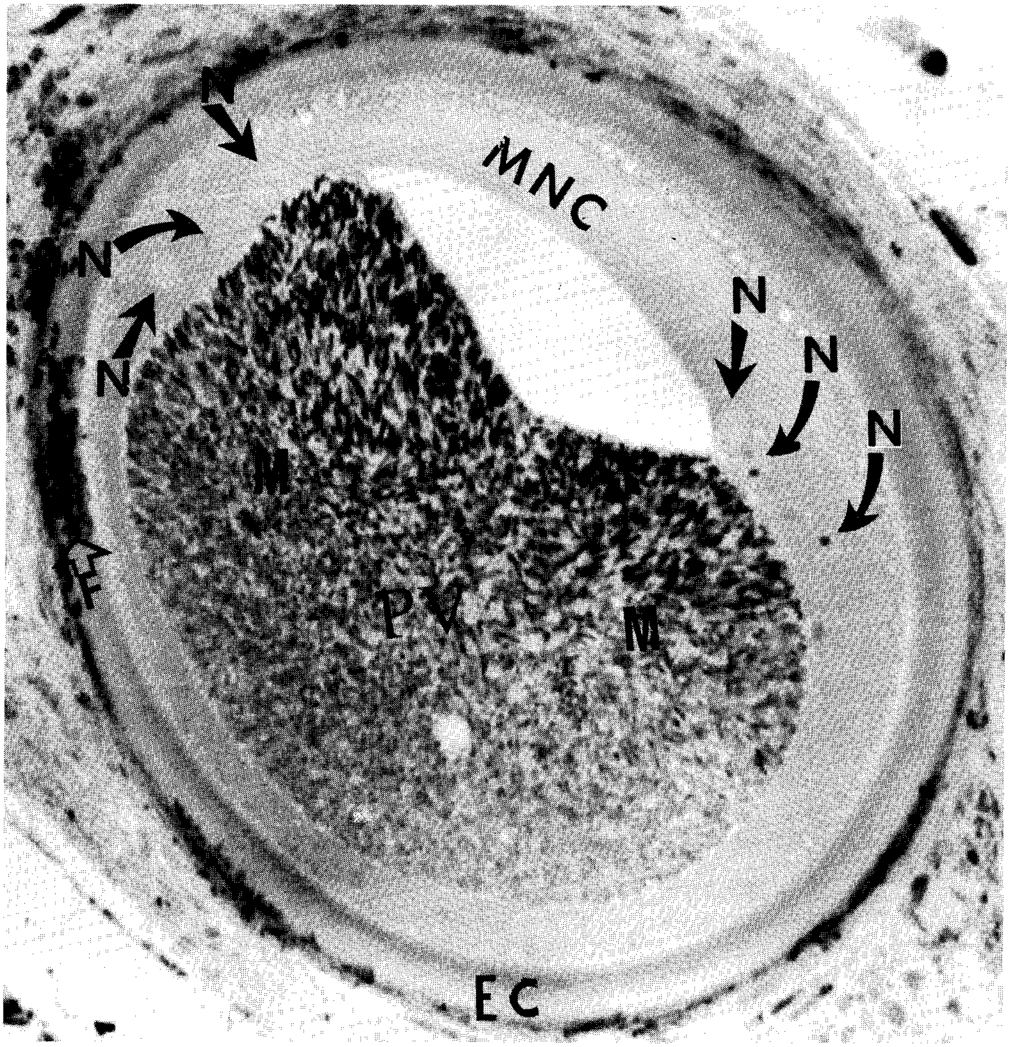

Fig. 1. *Besnoitia* cyst. Note extracellular capsule of a homogenous charcter (EC.) fibrocytes (F) several nuclei (N) of the multinucleated cell (MNC) and parasitophorus vacuole (PV) filled with merozoites (M). Light microscopy x 800.

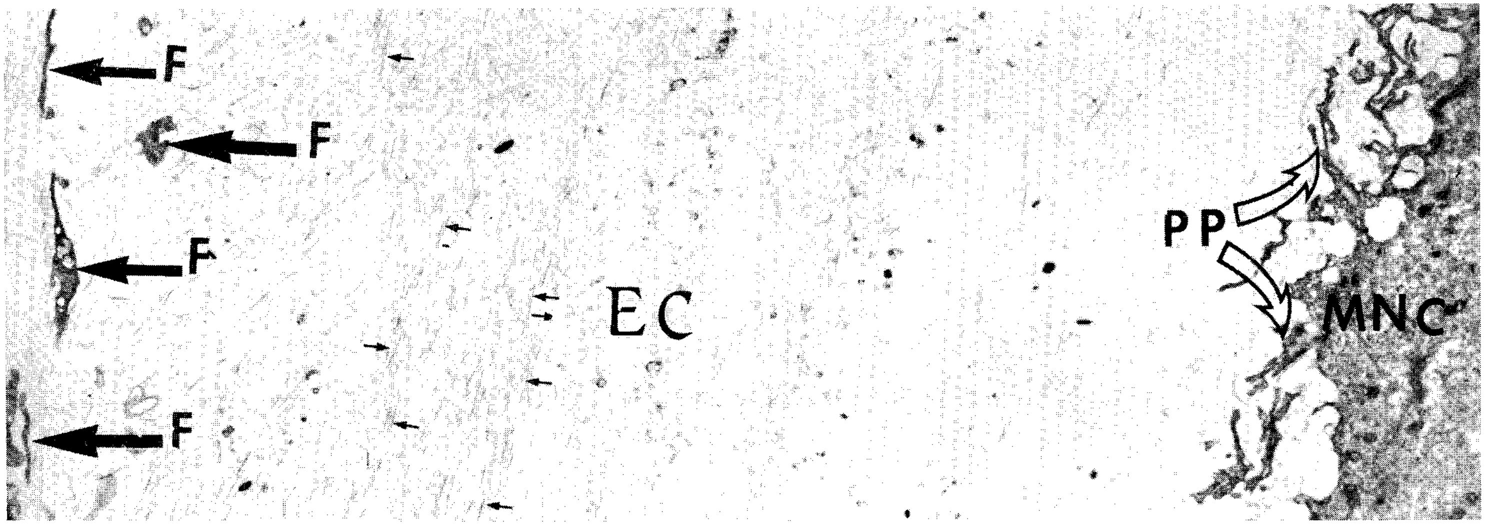

Fig. 2. Extracellular wall. Note electron lucid matrix with filbrillar structures (arrows), fibrocytes morphologically similar to the kerationcytes of the cornea (F) and numerous microvilli or pseudopods (P.P) of the multinucleated cell (MNC) x 5400.

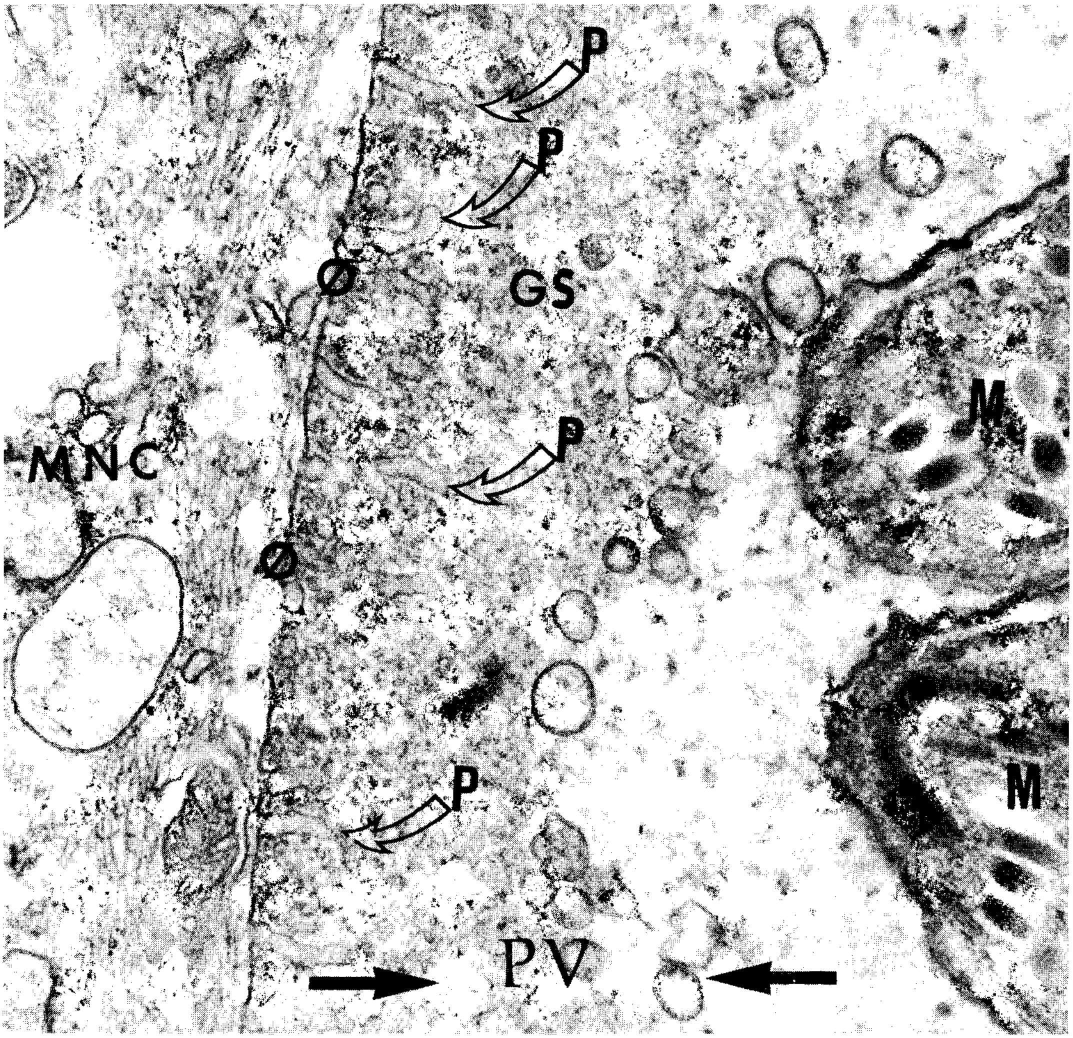

Fig. 3. The plasma membrane (Ø) of the multinucleated cell (MNC) forming a parasitophorus vacuole (PV) containing merozoites (M). Note numerous protrusions (P) and a condensation of the ground substance (GS) at the plasma membrane x 55000.

pact and markedly electron dense. The cytoplasma contains a considerable amount of mitochondria and dilated rough endoplasmic reticulum (Fig 4).

Ultrastructurally, merozsites are found inside a large parasitophorous vacuole of a multinucleated cell.

The spindle shaped merozoites are lying in an electronlucid material. They are pointed at both ends and measuring 6.5 - 11.0 μm x 1.0 - 1.5 μm (mean 8.7 x 1.2 μm). The merozoites have a typical coccidian pellicle. They contain in the anterior end a polar ring, the conoid 22 microtubules, 1-6 rhoptries and numerous elongated micronemes. The nucleus is relatively large and usually located at the beginning of or in the posterior half of the merozoite. The position of the mitochondrion varies from the region of the micronemes to the posterior end of the merozoite (Figs 5 & 6).

In the anterior part of the merozoite one or two vacuoles 1.0 x 0.5 μm are present . These vacuoles have a not very well defined wall and some contain a rounded clump of an electron dense material (Fig 7).

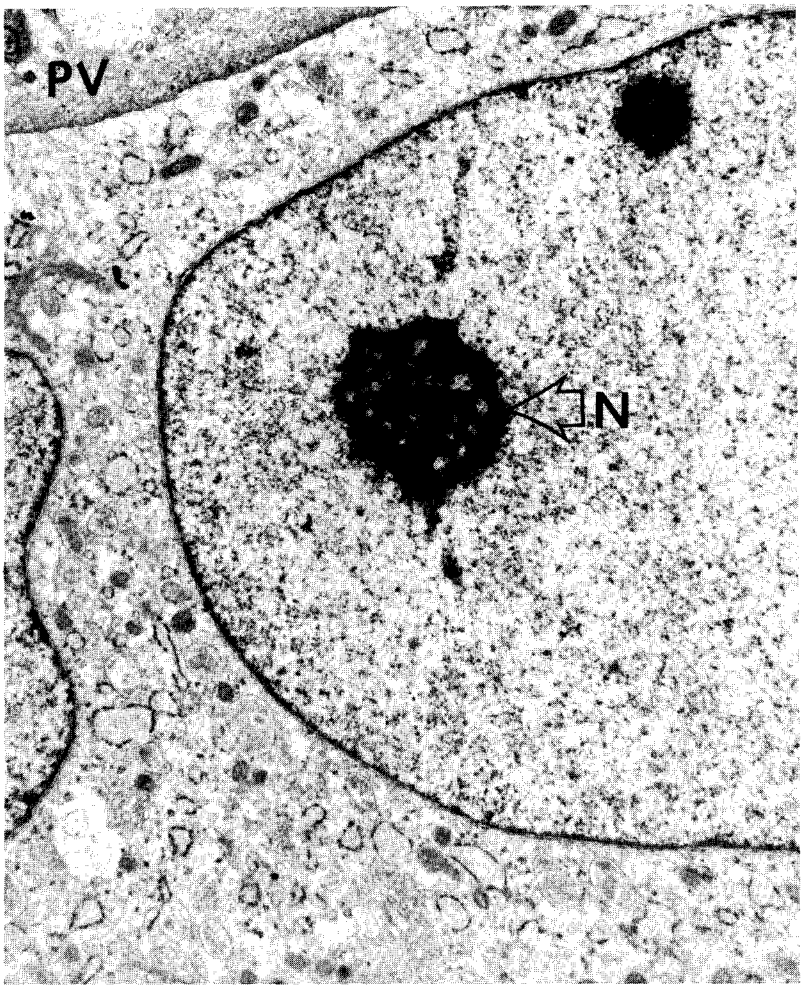

Fig. 4. Multinucleated cell. Note the electron dense nucleous (open arrow N) and the evenly dispersed chromatin of the nucleus. Note also numerous mitochondria and dilated rough endoplasmic reticulum. Pv=parasitophorus vacuole x 9000.

Discussion

The ultrastructure of the *Besnoitia* cysts and merozoites from reindeer show great similaritres with *B. jellisoni* (Sheffield 1968, Senaud 1969, Scholtyseck *et al.* 1973, Scholtyseck *et al.* 1974) and *B. besnoiti* (Senaud *et al.* 1986). *Besnotia* cysts of reindeer are smaller and the merozoites are longer and more slender than those of *B. jellisoni* and *B. besnoiti* (Senaud 1969, Scholtyseck 1973, Widauer 1983). The number of rhoptries in the merozoites of *Besnoitia* cysts from reindeer (1-6 in number) differs from those reported in *B. jellisoni* (3-5 in number, Scholtyseck *et al.* 1973) or *B. besnoiti* up to 12 in number, Senaud 1969). *B. besnoiti* merozoites possess two preconoidal rings (Widauer 1983, Göbel *et al.* 1985) while *B. jellisoni* has no preconoidal ring (Scholtyseck *et al.* 1970) and it is also lacking in the merozoits from *Besnoitia* cysts of reindeer.

Also differing the merozoits found in *Besnoitia* cysts of reindeer from merozoits of *B. jellisoni* and *B. besnoiti* is the presence of vacuoles with a not very well defined wall and containing rounded clumps of an electron dense material.

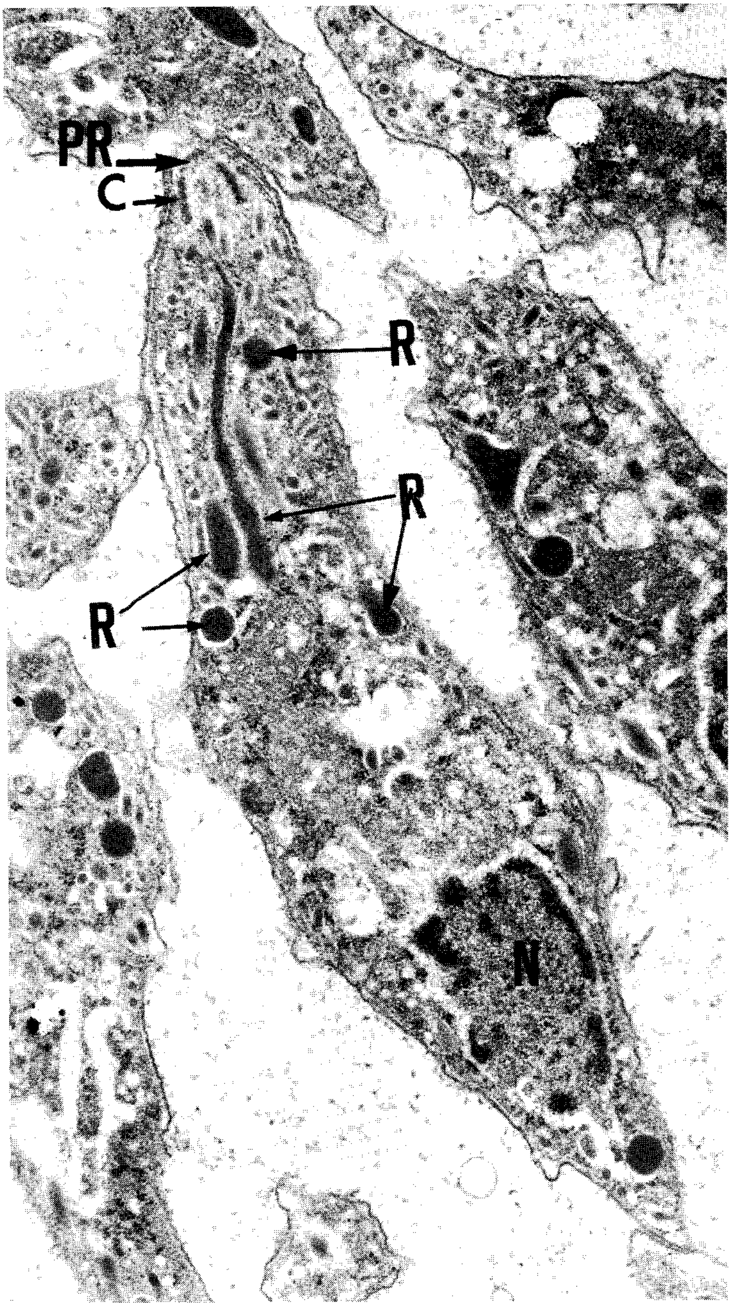

Fig. 5. Merozoites. Note polar ring (PR) conoid (C), rhoptries (R) and a relatevely large nucleus x 24000.

The authors have not found any reports on such vacuoles in previous studies.

The observations presented on *Besnoitia* cysts and merozoits from reindeer indicate a form distinct enough to be placed in a new species - *Besnoitia tarandi.*

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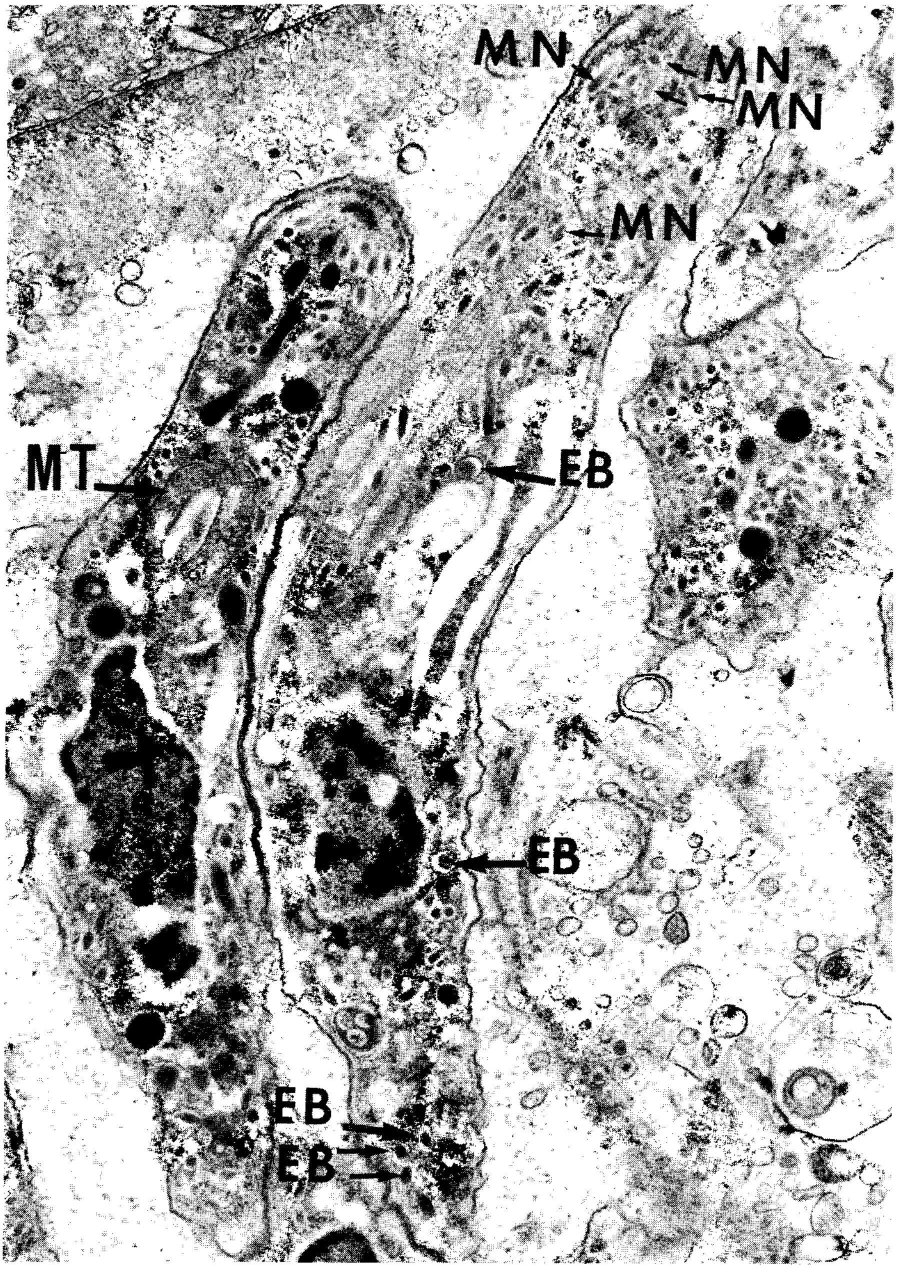

Fig. 6. Merozoites. Note elongated micronemes (MN), enigmatic bodies (EB), and mitochondrion (MT) x 24000.

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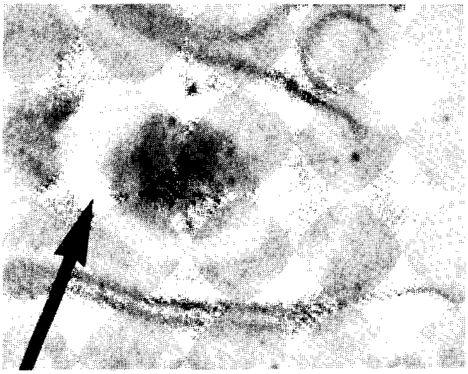

Fig. 7. Vacuole (arrow) without well defined wall containing rounded clumps of elctron dense material x 90000.

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Reproductive investment by females in semi-domesticated reindeer

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Abstract: This paper discusses maternal investment in a herd of semi-domesticated reindeer in Kaamanen, Finnish Lapland (69°N 27°E). Male-producing cows weighed 2% more at the previous conception then the female-producing cows did. The body weight of cow accounted for more of the variation of birth sex ratio than the age or the parity. The lightest cows ($<$61 kg) produced a significant excess (62%) of female calves. Both the medium-sized and the largest cows gave birth to a slight, nonsignificant excess of males. In terms of weight change from one conception to the next, rearing a male to weaning was more expensive to cows than rearing a female. The frequency of reproductive failures did not, however, depend significantly upon the sex of the previous calf. The survival and growth of male and female calves related in an approximately similar fashion to maternal weight.

Key words: Sex ratio, maternal investment

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Introduction

Theoretical treatment of parental investment has evoked a hypothesis which predicts that parents should invest more heavily in the sex among which reproductive success varies more widely (Trivers, 1972; Maynard Smith, 1980; Meikle *et al.*, 1984). this sex is commonly suggested to be the male. Trivers and Willard (1973) have predicted that parents can improve their fitness by controlling the sex ratio of their offspring. They have hypothesized that in polygynous breeding system mothers in good condition should produce more male offspring whilst those in poorer condition should produce more female offspring. Parents can accomplish preferential investment also by investing relatively more in individual males than in individual females (Reiter *et al.,* 1978; Trillmich, 1986), or vice versa (Hoogland, 1981; Caley and Nudds, 1987). In several polygynous mammals, maternal investment before weaning is greater for males than for females (Reiter *et al.*, 1978; Clutton-Brock *et al.*, 1981; Kovacs and Lavigne, 1986; Lee and Moss, 1986; Trillmich, 1986). In polygyny males are more likely than females to disperse as juveniles (Greenwood, 1980; Dobson, 1982). Post-weaning resource competition between mother and female offspring in natal groups may conterbalance heavier investment given in males (Clutton-Brock *et al.*, 1981) or even make females the more expensive sex (Hoogland, 1981; Caley and Nudds, 1987).

Reindeer exhibits a very pronounced sexual limorphism in size. In wild herds, adult bulls veigh twice as much as adult cows (Skogland, 989). This indicates an intense male-male ompetition for mates and, accordingly, a high egree of polygyny (see Trivers, 1972; Clutton-rock et al., 1980). The variance of lifetime reeding success should therefore be diffe-ential for males and females. We may expect hat dominant, large-bodied females produce ore male offspring than subordinate, more ood-limited females do. Provided that female eindeer invest more heavily in male than in fe-ale offspring, the sex of the offspring raised hould influence the weight change of mother etween two consecutive autumns. The barren-ess in the subsequent year could also be more ommon after weaning a male than weaning a emale calf (Clutton-Brock *et al.*, 1981; Wolff; 988).

This short review draws together the most ssential issues of papers dealing with sex ratio nd maternal investment within the herd of emi-domesticated reindeer in Kaamanen, Fin-ish Lapland (Kojola, 1989a; 1989b; Kojola and loranta, 1989). Herein we also consider data n sex ratio and available information of maternal investment revealed in other studies of reindeer and caribou.

Material and methods

The data were collected in 1970-1987. The number of reproductive females varied annually between 29-93. Reindeer were permitted to move freely within an enclosed pasture of 70 km^2. From December to June, reindeer were supplementarily fed. During other seasons they met their energy demands by grazing natural vegetation. Reindeer were weighed in autumn, usually in November. Before the calving period (May) reindeer were gathered to give birth to their calves in a 10 hectare enclosure. During calving, newborns were daily sought out, sexed and weighed. Most calves (50% of females, 85% of males) were slaughtered in autumn. Data comprise of 1087 reproductions. Maternal body weight was known in 849 cases. In 1985-1986, reindeer were weighed also in the end of April and in the middle of June.

Results

In 1970-1987, sex ratio was 51.2% males at birth and 50.5% males one month after weaning. The cows which produce male calves weighed 2% more in November the preceding autumn than the cows which gave birth to female calves (means of 71.7 and 70.4 kg, respectively). This difference was statistically significant (t=2.46, p=0.012, df=849; Kojola and Eloranta, 1989). Weights for females females ageing 2-4 years did not differ with the sex of the subsequent offspring (Fig. 1). As regards parity, weights were different for females carrying their fourth or fifth offspring (Fig. 1).

Fig. 1. Post-breeding weights of cows as functions of maternal age (left) and parity (right) are shown separately according to sex of the subsequent progeny. (Kojola and Eloranta, 1989). Statistical tests are given in the text.

The sex of the calf accounted for more of the variation in the maternal body weight than maternal age (F=5.4, df=1.880, p=0.020) or the parity (F=4.4, df=1.713, p=0.036) (hierarchi-

Table 1. Progeny sex ratio for mothers of different weight categories. P values are from binomial tests.

Maternal body weight (kg)	Males (%)	n	p
< 61	38.5	83	0.048
61-65	45.9	135	0.655
66-70	53.5	214	0.648
71-75	53.1	213	0.696
76-80	57.2	138	0.229
> 80	52.0	100	0.764
Totals	51.2	883	0.812

cal analyses of variance in which weight, age and parity were treated as independent variables; Kojola and Eloranta, 1989). Cows weighing equal or less than 60 kg (at which there was a sharp increase in fertility; see Eloranta and Nieminen, 1986) produced a significant excess of females (Table 1). Both the medium-sized and the largest females produced a slight, nonsignificant excess of male calves (Table 1). An analysis of sex-ratio variation for mothers within different combinations of parity showed that three-year old first-breeders (mean weight 66.7 kg) produced significantly more males than the two-year old first-breeders (mean weight 61.9 kg) did 62.7%, n=69 and 45.1%, n=122, respectively, chi-square test, $p=0.041$). Among other categories of parity, sex ratio (or the maternal weights) did not differ with the age (Kojola and Eloranta, 1989).

Measured as a weight change from one conception to the next, rearing male to weaning resulted in greater energetic demands on cow than rearing a female (difference in proportional weight change was 2%; an analysis of variance; cow weight and age were treates as covariated; $F=5.7$, $df=3{,}527$ $p=0.018$; Kojola and Eloranta, 1989). The sex ratio which preceded barrenness did not, however, deviate significantly from 1:1 (56.1% males; n=82, chi-square test; $p > 0.10$). Female offspring up to the age of 4 years tended to remain close to their mother (Kojola and Nieminen, 1988; Kojola 1989c). The number of female offspring present (range 0-3) did not affect maternal weight change between consecutive years (Kojola, 1989b). During the first post-weaning winter female calves share snow craters with their mother twich as often as did male calves (Kojola, 1989a). The weight change of mother did not however depend on the sex of the calf (Kojola, 1989a).

The mortality rate of male and female calves before weaning depended in appoximately similar fashion on maternal body weight (sex ratio of died calves did not deviate from 1:1 or from the sex ratio produced within different categories of body weight (class spaces of 5 kg) or age; chi- square tests, p values > 0.10). Maternal body weight accounted for 21% of variation in autumn weights both for male and female calves (linear regression models; p values <0.001).

Discussion

There is much recent evidence for mammals giving support to the Trivers and Willard's (1973) "maternal condition hypothesis" which predicts that superior females produce more females than weak females do (Clutton-Brock *et al.*, 1981; Burley, 1982; Meikle *et al.*, 1984; Austad and Sunquist, 1986, 1986; Huck *et al.*, 1986, Rutberg, 1986; Wright *et al.*, 1988). In many mammalian populations, however, results are contradicting: well-fed females overproduce daughters (Simpson and Simpson, 1982; Silk, 1983; Verme, 1983; Skogland, 1986; Silk, 1988). In mammals, males usually equal or outnumber females at birth (Parkes, 1926; Clutton-Brock and Iason, 1986). This seems to be the case in *Rangifer tarandus*, too (Kelsall, 1968; Espmark, 1971; Nowosad, 1975; Kojola and Eloranta, 1989). Results revealed for reindeer and caribou are not invariably supportive to the model of Trivers and Willard (1973). In a study by Varo (1964) of semi-domesticated reindeer, first-breeding, small females produce more female calves than the older ones. In the herd studied by us, the sex ratio of calves born to the first-breeders did not deviate from unity or from the sex ratio of calves born to older females (Kojola and Eloranta, 1989). In caribou (*R.t. pearyi* and *R. t. groenlandicus),* young females carry more often female fetuses than the older ones (Thomas, 1988). In ungulates, female social rank usually increases with the age (Rutberg, 1981; Townsend and Bailey, 1981; Hall, 1983). In wild reindeer, however, more female are born in rich than in poor habitat (Skogland, 1986). It is fair to notice, as has been pointed out by Clutton-Brock and Iason (1986), that sex-ratio trends are not likely to be explained by one adaptive theory. Results revealed for wild reindeer coincide well with Fisher's (1930) argument that parents should overproduce the more cheaper sex: on poor range, highter mortality rate of male calves tends to decrease costs associated with producing males (Skogland, 1986). On a variety of primate populations, sex-ratio trends are likely to be explained by the resource competition model, which implies that overt female-female competition for access to locally limited resources in natal groups makes maternal social rank more important for survival and breeding success of female offspring than for those of male offspring (Silk, 1983; 1988; see also McFarland Symington 1987 for a species in which males are the more sedentary sex). Well-fed white-tailed deer *(Odocoileus virginianus)* females produce more female fawns than do females that are nutritionally deprived (Verme, 1969). On the other hand, the proportion of male fawns decreases with the increasing litter size (Verme, 1983). Since the litter size is likely to affect the intensity of reproductive effort white-tailed does are likely to produce one male fawn whenever not able to successfully rear two fawns (see Williams, 1979). Caley and Nudds (1987) have challenged this idea and suggested that the increased female-female competition for food in poor habitat makes the females the more expensive sex and hence brings about a male-bias for offspring (see Fisher, 1930 for theoretical background).

Body weight of cow is a measure which is closely correlated with social rank (Kojola, 1989a). Access to food is favored by high social rank. Therefore we may expect large-bodied females to have higher-than-average capacity to invest in reproduction. In this paper we consider maternal post-breeding weights as an indicator of mother's quality. This measure is likely to predict maternal ability to allocate resources to progeny during gestation as well as postnatally. In two unprovisioned winter herds in Kaamanen, large-bodied, high-ranking females were able to maintain their body weight proportionately better than lower-ranking females (Kojola, 1989a).

Our results are not unambigiously supportive to the Trivers and Willard's (1973) "maternal condition hypothesis". The very smallest cows overproduced females, as is initially predicted by the model, but the sex ratio produced by the very largest cows did not deviate from unity or from the sex ratio of offspring born to the middle-sized cows.

Measured as the weight change of mother, rearing a male offspring to weaning was more costly than rearing a female offspring. This did not occur at a cost to mother's reproductive success in the subsequent year, however. This result deviates form that revealed for red deer on Rhum, Scotland, where hinds more often fail to reproduce after a male than after a female calf (Clutton-Brock et al., 1981; see also Wolff (1988) for bison *(Bison bison)* in Montana).

Reindeer give birth to their calves soon after a period of increased resource competition and before the burst of vegetation. Therefore females which show the lowest competitive ability might reach best reproductive success by investing predominantly in the sex that needs less maternal resources for survival or being reproductive in adulthood. Helle et al. (1987) have shown that on poor winter ranges the very largest as well as the very smallest male calves lose their fat depots sooner than do the medium-sized calves. Such normalizing selection may weaken the association between maternal investment and male reproductive success is not necessarily much enhanced by exceptionally heavy maternal investment (Kojola, 1989b). In the reindeer herding district of Finland, winter ranges have been poor during this entire century (Helle, 1982). This provides one potential explanation for the marginality of the difference in maternal investment given for male vs. female offspring.

Females invested more heavily in male than female offspring during gestation and during the first life weeks of the calf. Male calves weigh 6% more than female calves at birth (Eloranta and Nieminen, 1986). When giving birth to a male, cows lose more body weight than when giving birth to a female (10.3 ± 0.8% (SE) with a female, 12.8 ± 0.6% with a male offspring; expressed as proportional weight change from the end of April to the middle of June; $F=4.2$, $df=1, 112$, $P<0.05$; data for 1985-1986; Kojola 1989b). Male calves are permitted to suckle more than female calves during the first month postnatally (Kojola, 1989b). From June to November, cows investing in males were able to recover from the heavier weight loss they suffered during calving (Kojola, unpublished). Herbivores of tundra and northern taiga have to meet the demands of short growth period and strict seasonality of resources. These selection pressures result in birth synchrony (Berglund, 1975; Skogland 1989). There is evidence that body condition influences the timing of conception (Skogland 1989). Therefore cows that produce male calves should be able to recover from their heavier investment before next breeding season.

Acknowledgements

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Laboratory and field trials of killed *Brucella suis* type 4 vaccine in reindeer

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Abstract: Reindeer vaccinated with killed *Brucella suis* type 4 vaccine in adjuvant and non-vaccinated sero-negative controls were challenge-exposed in separate experiments with live *B. suis* type 4 organisms at 2, 14, 26 and 43 months post- vaccination. Vaccination induced protection against infection in all laboratory trials. A portion of reindeer in two herds and the majority of reindeer in a third herd were vaccinated with killed *B. suis* type 4 vaccine in adjuvant. Serologic titers were monitored in vaccinated and non-vaccinated animals. Post-vaccination titers were detected in 100% of the animals as long as 24 months in the first herd; in 72% of vaccinated animals as long as 48 months in the second herd; and in 30% of animals vaccinated as adults in the third herd. A difference in natural exposure rates may have affected the duration of serotiters in the three herds.

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Growth and relationship of live weight to body measurements in semi-domesticated reindeer (*Rangifer tarandus tarandus* L.)

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Abstract: Estimation of live weight from measurements of body dimensions is useful in many management activities with domestic animals. In present study live weight was measured from 2932 female and 1037 male semi-domesticated reindeer *(Rangifer tarandus tarandus* L.) during different seasons in 1969-85. The age of reindeer varied between 1 day and 14 yrs. Back length (along back from second spinous process to base of tail) and chest girth (just behind front legs) were taken also from 1490 female and 510 male reindeer. The growth of reindeer from birth to adulthood was cumulative consisting of a rapid weight accretion during summers followed by a weight loss or stasis during winters. The mathematical analyses of the growth based on exponential solutions gave average values for growth of female and male reindeer. Body weight of females increased until the age of 4.5 yrs and that of males until the age of 5.5 yrs. During winter and spring body weight of hinds decreased 10 to 15 kg and that of stags 30 to 50 kg in different age groups. Significant linear regressions were found between live weight and back length (r=0.809 and 0.892), live weight and chest girth (r=0.860 and 0.872) and live weight and combined body measure (back length + chest girth) (r=0.877 and 0.941) and live weight and body volume (r=0.905 and 0.954, respectively) in female and male reindeer. Exponential regressions gave, however, the best estimations of live weight with combined body measure.

Key words: reindeer husbandry, management

Rangifer, Special Issue No. 3, 1990: 353-361

Introduction

Rates of reproduction are usually related to body size, and growth and development are also functions of adult body size (see Blueweiss et al. 1978). According to Clutton-Brock et al. (1982) red deer *(Cervus elaphus)* and reindeer *(Rangifer tarandus)* are species that form the largest breeding parties and also show the greatest degree of size dimorphism: in reindeer, average male weights in autumn are 1.6 times female weight. Sexual weight dimorphism is not, however, consistent since at the same female weight Norwegian reindeer may reach a dimorphism of 2.2 - 2.8, while Canadian tundra caribou reach only 1.2 - 1.6 (see Geist 1988).

Relationship among body weight, size and morphological traits have been described for numerous large animals, but most data are based on dead animals. Body measurements and rations are useful taxonomic criteria and are used in *Rangifer* systematics (Banfield 1961, Nieminen & Helle 1980). Interrelationships between live weight and live measurements have been investigated in several studies with domestic animals (see Ruohomäki 1975). The most common measurements taken have been heart girth, width of chest, depth of chest, height at withers, height of back and natural length. Estimation of live weight from body measurements has been useful in many management activities with domestic animals. According to Ringberg et al. (1981) length measurements were considered, however, to be impractical for the prediction of carcass weight in reindeer.

The growth of the reindeer from birth to adulthood is cumulative consisting of an rapid weight accretion during summers followed by a weight loss or stasis during winters. The growth rate of the reindeer is, thus, a complex of events. Mathematical analyses on the dynamics of the growth based on logarithmic or exponential solutions have been carried out on the reindeer by Krebs & Cowan (1962) and on the caribou by McEwan (1968). The growth rate of the reindeer is handled mathematically also with the aid of polynomial functions fitted to the average values obtained from several populations (see Timisjärvi et al. 1982).

This paper describes growth and average growth curves and relationships of live weight to body measurements in semi-domesticated reindeer in northern Finland. Regressions between live weight and body measurements are examined to determine the best predictive equation for weight in situations where weighing of reindeer is not practical.

Material and methods

Live weight was measured from 2932 female and 1037 male reindeer in Kaamanen Reindeer Research Station and in different reindeer hearding cooperatives in Finland during different seasons in 1969-85. Reindeer were freely grazing. The age of reindeer varied from 1 day to 14 yrs. The calves ranging in age from 1 day to 20 days were weighed with a steelyard to the nearest 0.1 kg. The older calves and adults were weighed using a spring balance to the nearest 0.5 kg. Body measurements were taken on the same day of live weight determination. All the measurements were performed mainly by the same person. Back length (from second spinous process to base of tail) and chest girth (just behind front legs) were taken from 1490 female and 510 male reindeer (Fig. 1). Body measurements were measured to the nearest millimetre with a steel metric rule. The combined body measures (back length + chest girth) and body volumes were calculated $\left(V = \frac{\textit{back length x chest girth}^2}{4\pi}\right)$

The exponential equations were used for estimation the growth in reindeer. Exponential and linear regressions between body measurements and body weight were calculated.

Results

The mean birth weight was 5.0 kg for female and 5.3 kg for male calves. The birth weight doubled within 4 weeks, and then again within 6 weeks. At the age of 5 to 6 months the mean body weight of female calves showed a range from 40 to 45 kg. The mean body weight of male calves ranged from 45 to 50 kg. The growth ceased during winter. The growth proceeded during the next spring and summer. The hinds reached the adult body weight at the age of 3 to 4 yrs and the stags at the age of 5 to 7 yrs. During winter and spring the body weight of hinds decreased on an average 10 to 15 kg in different age-groups.

The decrease of body weight in stags was higher (30 to 50 kg). The actual measurements

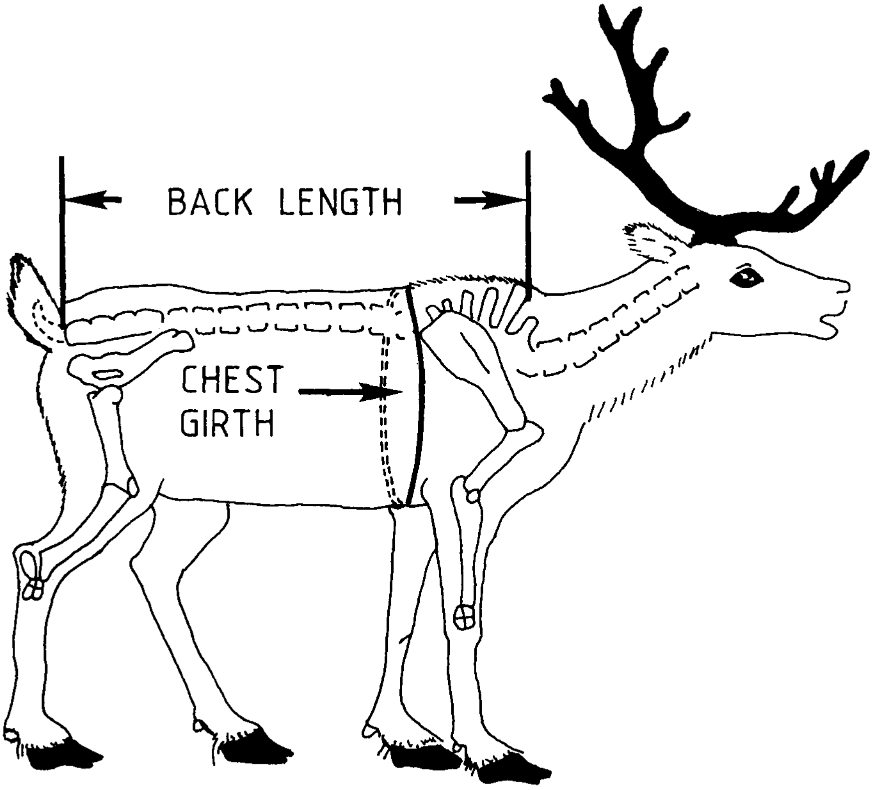

Fig. 1. Body measurements used in the study.

of body weight for female and male reindeer are presented in Figs 2 and 3. Figs 4 to 6 represent mathematical growth curves in female reindeer during different seasons and Figs 7 to 9 in male reindeer, respectively.

The combined body measure (back length + chest girth) showed a range from 131 to 215 cm in young reindeer females (age <3 yrs) and from 141 to 218 cm in young reindeer males. The values for adult hinds (age >3 yrs) and stags were from 170 to 220 cm and from 180 to 238 cm, respectively. There were significant linear regressions between back length and body weight ($r=0.809$, $n=1490$, $P<0.001$ and $r=0.892$, $n=510$, $P<0.001$), between chest girth and body weight ($r=0.860$, $n=1490$, $P<0.001$ and $r=0.872$, $n=510$, $P<0.001$) and between combined body measure and body weight in female and male reindeer. Significant linear regression were also found between body weight and body volume in female and male reindeer ($r=0.905$, $n=1490$, $P<0.001$ and $r=0.954$, $n=510$, $P<0.001$, respectively) (Figs 10 and 11).

Exponential regressions between body weight and combined body measure in female and male reindeer are presented in Figs 12 and 13. Comparisons of linear and exponential regressions are given in Table 1. Exponential regressions gave better correlations than linear regressions in this study. Estimations of live weight from combined body measure for female and male reindeer are given in Table 2.

Discussion

Growth is a complex set of metabolic events, which are environmentally and genetically controlled. Rates of prenatal, preweaning and postweaning growth of reindeer are influenced, for example by temperature, snow depth, humidity, air movement and radiation. These in turn affect the amount of food and water intake, en-

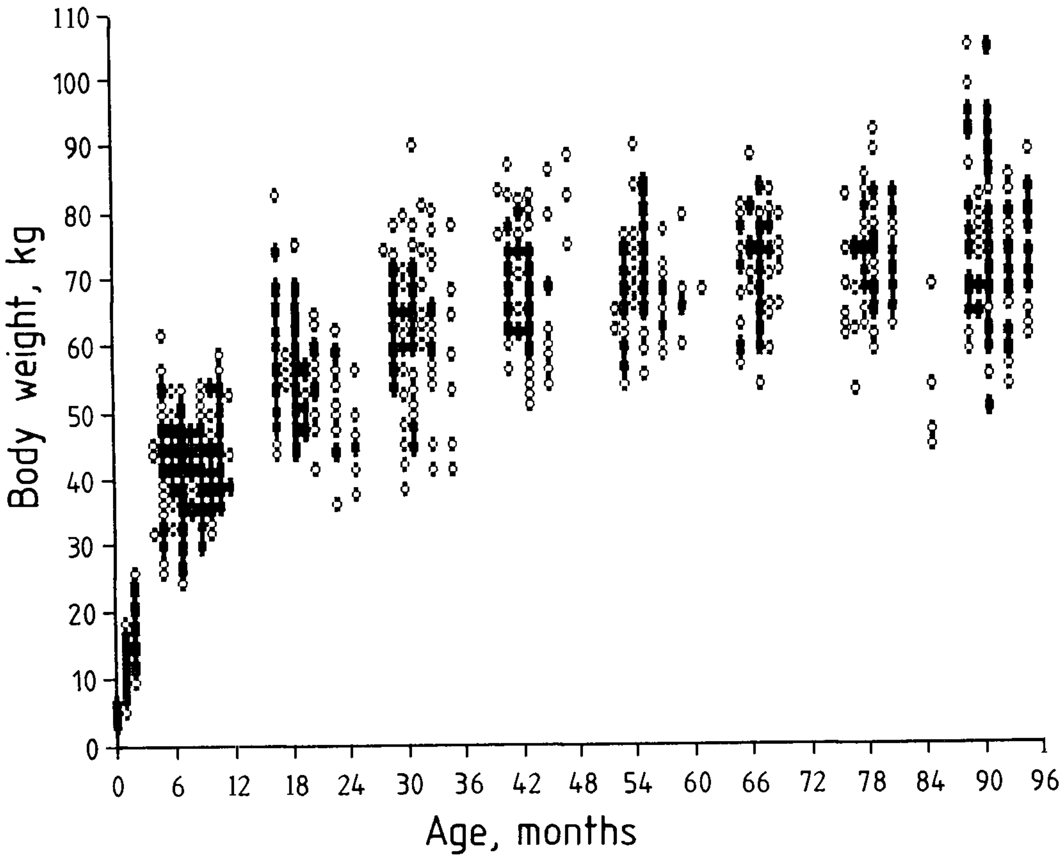

Fig. 2. Body weights of female reindeer (n=2932) in different age groups during different seasons 1969-85.

ergy available in ingested forage, the heat production and net energy available for productivity and body composition. According to Anderson (1981) there are in theory three phases of postnatal growth: 1) from birth to near the end of weaning, when growth is accelerating, 2) from weaning to sexual maturity, when growth is slowing rapidly, and 3) during sexual maturity, when growth may be slightly negative.

Brown (1961) published the first growth-in-body-weight curve of black-tailed deer *(Odocoileus hemionus columbianus)*, based on sequential weighings of one female and male deer from 12 to 54 months of age. These curves reflected seasonal changes in weight and continuing growth until maturity. Wood et al. (1962) noted later the complexity of growth among deer subspecies and employed four curves to describe the course of growth : 1) prepubertal growth, 2) actual weight changes through an animal cycle, 3) maximum annual weight reached, and 4) minimum annual weight reached. According to Timisjärvi et al. (1982) the growth in the reindeer was also phasic and complex with the greatest growth rate in the neonatal period. The growth was stopped by winter and proceeded the next spring but now at a lower rate. The polynomial growth curves used gave average values for growth and growth rate. In present study the mathematical analyses of the growth based on exponential solutions gave average values for growth of female and male reindeer.

Sexual dimorphism is well known among ruminants. According to Fock (1966) the breadth measurements and particularly length-breadth indicies were important for distinguishing the sexes. Because also reindeer are sexu-

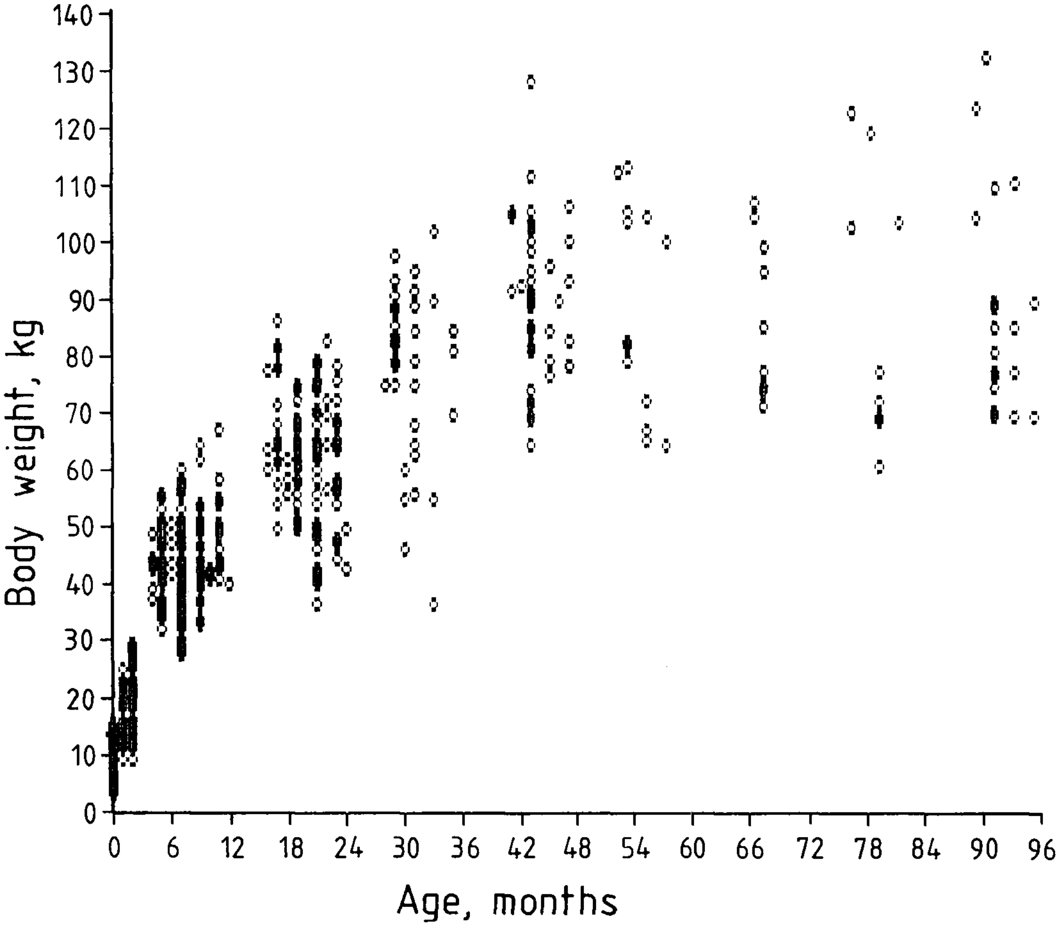

Fig. 3. Body weights of male reindeer (n=1037) in different age groups during different seasons 1969-85.

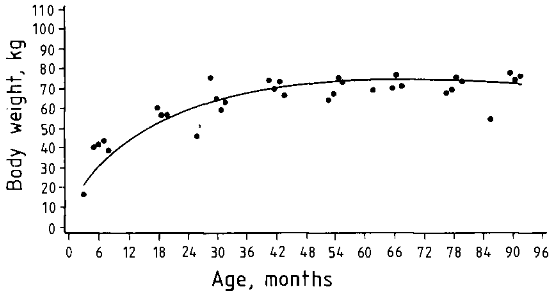

Fig. 4. The body weight of the female reindeer (n=1522) as plotted against the age of the reindeer. The weight curve is a weighed exponential equation ($y=11.35 \times ^{0.584}e^{-0.009X}$, $R_2=95.43$) based on actual mean values measured during summers and autumns in 1969-85.

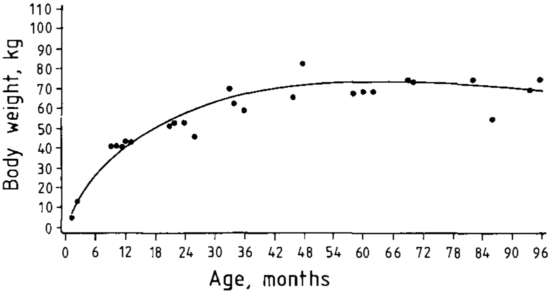

Fig. 5. The body weight of the female reindeer (n=1424) as plotted against the age of the reindeer. The weight curve is a weighed exponential equation ($y=8.41\ x^{0.688}e^{-0.011X}$, $R_2=97.78$) based on actual mean values measured during winters and springs in 1969-85.

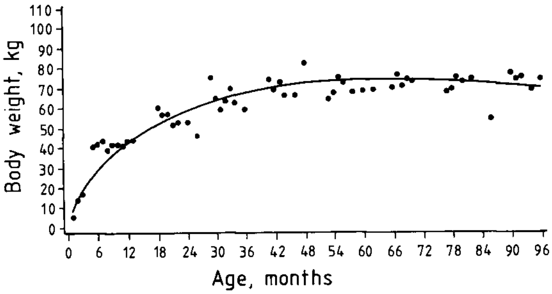

Fig. 6. The body weight of the female reindeer (n=2932) as plotted against the age of the reindeer. The weight curve is a weighed exponential equation ($y=9.65\ x^{0.644}e^{-0.009X}$, $R_2=97.03$) based on actual mean values measured during different seasons in 1969-85.

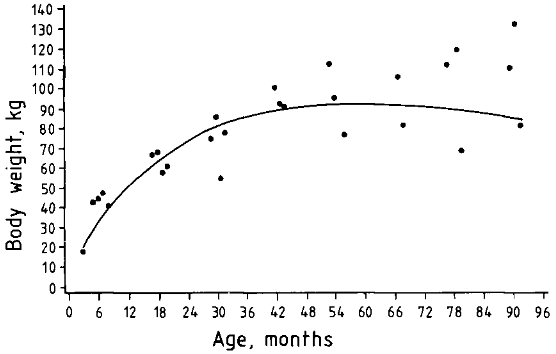

Fig. 7. The body weight of the male reindeer (n=832) as plotted against the age of the reindeer. The wieghed curve is a weight exponential equation ($y=9.25\ x^{0.748}e^{-0.013X}$, $R_2=94.54$) based on actual mean values measured during summers and autumns in 1969-85.

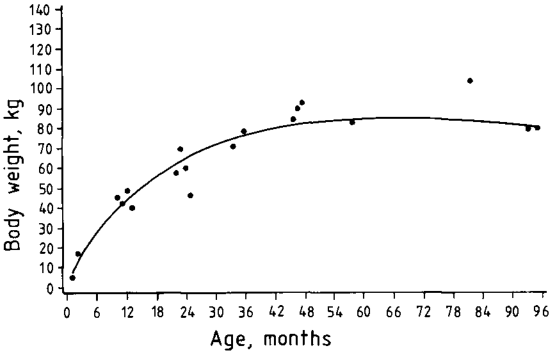

Fig. 8. The body weight of the male reindeer (n=921) as plotted against the age of the reindeer. The weight curve is a weighed exponential equation ($y=8.29\ x^{0.731}\ e^{-0.011X}$, $R_2=96.50$) based on actual mean values measured during winters and springs in 1969-85.

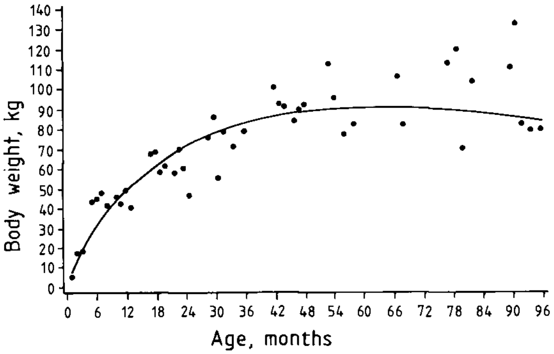

Fig. 9. The body weight of the male reindeer (n=1037) as plotted against the age of the reindeer. The weight curve is a weight exponential equation ($y=8.95\ X^{0.739}e^{-0.012X}$, $R_2=95.44$) based on actual mean values measured during different seasons in 1969-85.

ally dimorphic and sexes differ in their body proportions, females and males were analyzed separately in present study. In both sexes postpubertal weight fluctuated seasonally during each year of life. Weight was gained in summer and early autumn and lost during late autumn and winter. Bandy *et al.* (1970) found that mule deer male declined in weight during winter twice as fast as did females but generally reached the point of inflection about twenty days later and at higher body weight. Present results show that during winter and spring body weight of adult semi-domesticated reindeer females decreased about 10 to 15 kg and that of males about 30 to 50 kg in different age groups. The winter body weight loss of 41 - 55% in Svalbard reindeer *(R. t. platyrhynchus* Vrolik) is caused by a nearly complete loss of fat, 28-40 % loss of lean tissue and 16 - 50% weight decrease of the digestive tract (Reimers & Ringberg 1983).

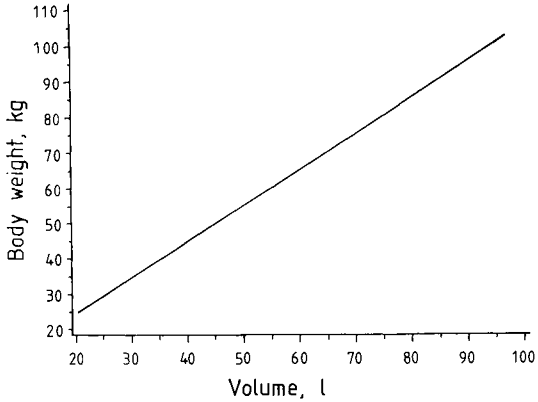

Fig. 10. The linear regression between body weight and body volume in female reindeer ($y=4.09 + 1.02\ x$, $R_2=81.89$, $n=1490$).

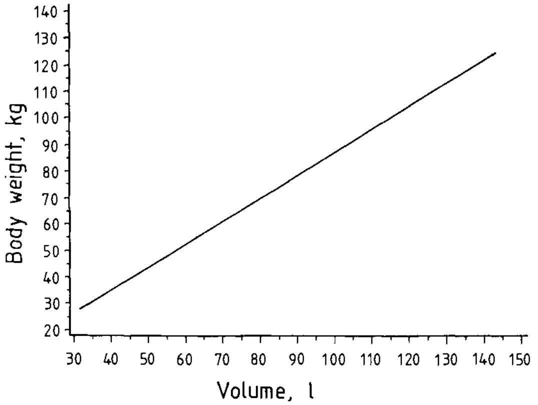

Fig. 11. The linear regression between body weight and body volume in male reindeer ($y=0.33 + 0.87\ x$, $R_2 91.04$, $n=510$)

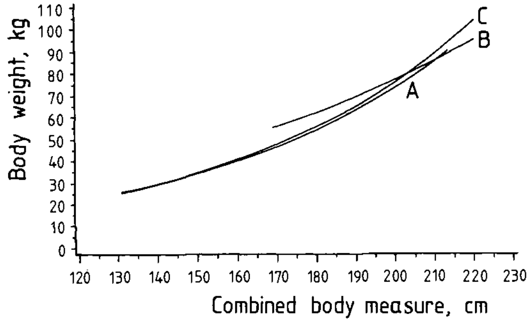

Fig. 12. The exponential regressions between body weight and combined body measure (back length + chest girth) in young (age < 3 yrs), adult (age > 3 yrs.) (B) and all (n=1490) female reindeer (C) in study. Equations are: (A) $y=3.45\ e^{0.015X}$, (B) $y=9.27\ e^{0.011X}$, (C) $y=3.27\ e^{0.016X}$.

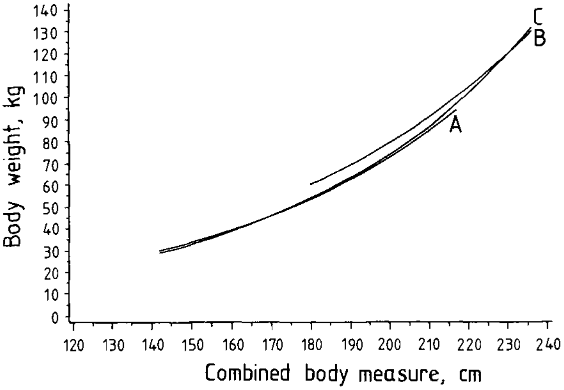

Fig. 13. The exponential regressions between body weight and combined body measure (back length + chest girth) in young (age <3 yrs) (A), adult (age > 3 yrs) (B) and all (n=510) male reindeer (C) in study. Equations are: (A) $y=3.44\ e^{0.015X}$, (B) $y=5.11\ e^{0.014X}$, (C) $y=3.06\ e^{0.016X}$.

According to Seip and Bunnell (1984) chest girth provided the best predictive equation for body weight in Stone's sheep *(Ovis dalli stonei)*, but hind foot length and horn length were also useful estimators. From live measurements in young beef cattle the best estimators were width of chest, chest girth and natural length (Ruohomäki 1975). Significant linear regressions were found in the present study between live weight and back length, live weight and chest girth. The best linear regressions were found between live weight and combined body measure and live weight and body volume. Exponential regressions gave, however, the best estimations of live weight with combined body measure.

The basic requirement for the measurements is that they are biologically reasonable and according to Weber (1957) the following sources of error are possible: 1) differencies between animals, 2) differencies between persons who perform the measuring, 3) differencies between animals and persons and 4) errors in the measurements by one person. It is observed

Table 1. Comparison of linear and exponential regression between body weight and combined body measure (back length + chest girth) in female and male reindeer.

Sex and age	n	Linear regression	r	Exponential regression	r
Females					
<3 years	856	$y= -81.9+0.758x$	0.914	$y=3.45e^{0.015x}$	0.958
>3 years	623	$y= -75.8+0.763x$	0.697	$y=9.27e^{0.011x}$	0.983
Total	1490	$y= -78.6+0.761x$	0.877	$y=3.27e^{0.016x}$	0.931
Males					
<3 years	433	$y= -87.6+0.794x$	0.924	$y=3.44e^{0.015x}$	0.959
>3 years	69	$y=-161.1+1.208x$	0.932	$y=5.11e^{0.014x}$	0.969
Total	510	$y=-111.9+0.940x$	0.941	$y=3.06e^{0.016x}$	0.939

that usually no errors occur provided when the head and feet of the animal remain in one position. The greatest difficulties and inaccuracies under the practical circumstances are caused by the movements of the animal. In the present study the measurements were performed mainly by the same person. Thus it can be supposed that there appears a minimum of measurement errors in this material.

In conclusion, the growth in semi-domesticated reindeer is phasic and complex with the greatest growth rate in the neonatal period. The growth is stopped by winter and proceeds the next spring. Body weight of females increases usually until the age of 4.5 yrs and that of males until the age of 5.5 yrs. The mathematical analyses of the growth based on exponential solutions gave average values for growth of female and male reindeer. In present study exponential regressions gave the best estimations of live weight with combined body measure.

Table 2. Estimated body weights from combined body measures (back length + chest girth) based on exponential regressions in female ($y=3.27e^{0.016x}$) and male ($y=3.06\ e^{0.016X}$) reindeer.

Combined body measure (cm)	Body weight (kg) Females	Males
180	55.6	54.5
181	56.5	55.4
182	57.4	56.3
183	58.3	57.2
184	59.2	58.1
185	60.1	59.1
186	61.1	60.0
187	62.1	61.0
188	63.0	62.0
189	64.0	63.0
190	65.1	64.0
191	66.1	65.0
192	67.1	66.1
193	68.2	67.2
194	69.3	68.2
195	70.4	69.3
196	71.5	70.5
197	72.6	71.6
198	72.8	72.7
199	75.0	73.9
200	76.2	75.1
201	77.4	76.3
202	78.6	77.6
203	79.8	78.8
204	81.1	80.1
205	82.4	81.4
206	83.7	82.7
207	85.0	84.0
208	86.4	85.4
209	87.7	86.8
210	89.1	88.2

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Ultrastructure of granulated cells in the bile duct of reindeer

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Abstract: The presence and ultrastructural characteristics of mast cells and globule leucocytes in bile ducts of the reindeer have not been previosly documentated. Tissue blocks of *ductus bepaticus communis* from six reindeer were processed by commonly used methods for TEM and examined with a JEOL JEM 100 S electron microscope. The present material originates from reindeer without clinical signs of parasites. However, several types of granulated cells were identifiable. The granules of connective tissue and subepithelial mast cells were small and mostly diffusely electron dense but also fine granular matrices were shown. The globules of intraepithelial globule leucocytes were fewer in number and distinctly larger than the granules of the mast cell. In addition there were noted intraepithelial granulated cells appearing similar to the neuroendocrinic cells reported in bovine bile ducts.

Key words: anatomy, bile ducts, mast cells, globule leucocytes

Rangifer, Special Issue No. 3, 1990: 363-367

Introduction

The presence of numerous mast cells and globule leucocytes in tissues of animals and man has been associated with parasitic infections (Befus and Bienenstock 1982). The function of these cells is, however, far from clear (Befus et al. 1986).

It has been established that the properties of mast cells depend on the animal species and even on the tissue location (Barrett and Metcalf 1984). Since no reports on mast cells and globule leucocytes in bile ducts of the reindeer are available, this study seemed appropriate.

Material and methods

The tissue samples originated from six reindeer slaughtered in the winter at the Reindeer Research Station at Kaamanen, in Lapland of Finland. Small tissue blocks of common bile duct wall were taken and as soon as possible transferred into cold 2.5 % glutaraldehyde in 0.1 M phosphate buffer and fixed for 24 hours. Then the blocks were processed by commonly used methods for TEM and examined with a JEOL JEM 100 S electron microscope.

Results and discussion

Mast cells and globule leucocytes were identified according to the characteristics described for these cells in general (Rahko 1971). Connective tissue mast cells were rare in the tissue samples (Figs. 1 to 3). On the other hand, the subepithelial mast cells occured frequently. The numerous intracytoplasmatic granules of the mast cells were usually electron dense with rounded profiles.

The intraepithelial globule leucocyctes were easily distinguished from the subepithelial mast cells (Figs. 4 to 6). The globules of the globule leucocytes were few in number and distincly larger than the granules of the mast cell. The nucleus of the globule leucocyte was often deeply indented by the large globules. All the globules were usually electron dense while some cells possessed globules with apparently dissolving matrices (Figs. 7 and 8). The mast cells, on the contrary, displayed mostly electron dense granula but also fine-granular matrices in a few granula.

In addition to these granulated cell, there were intraepithelial cells with numerous small electron-lucent intracytoplasmatic granules (Fig. 9). The intraepithelial location and ultrastructural appearance of these cells was similar to the neuroendocrinic cells present in bile ducts of cattle (Morales 1983) and in intestine of some other species of animals (Dellman and Brown 1976).

The present material originates from reindeer without clinical signs of parasites. However, numerous globule leucocytes and subepithelial mast cells were identified in the wall of the common bile duct. Mast cells located both in subepithelial and connective tissues while globule leucocyte displayed a strictly intraepithelial occurrence. To contribute to the clarifying of functional significance of the mast cells and globule leucocytes future studies by the present authors will be concentrated on these cell types in other mucosal tissues of reindeer.

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Fig. 1. A transverse section of the wall of the common bile duct. x 2.400.

Fig. 2. Ultrastructure of granules of a connective tissue mast cell. x 4.800.

Fig. 3. Detail of exceptionally small mast cell granules. x 24.000.

Fig. 4. A subepithelial mast cell. The granules appear homogenic. x 3.600.

Fig. 5. Ultrastructural appearance of a subepithelial mast cell and a globule leucocyte (GL). x 2.400.


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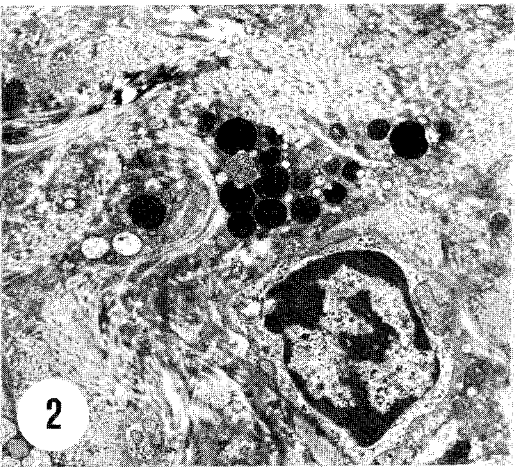
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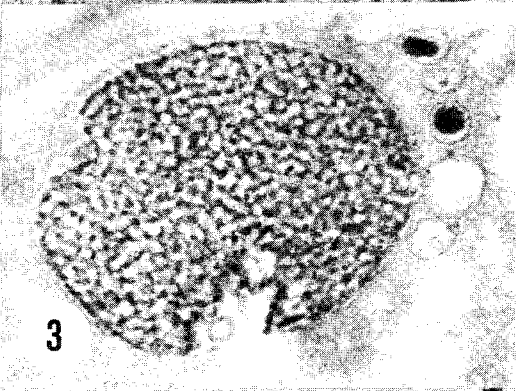
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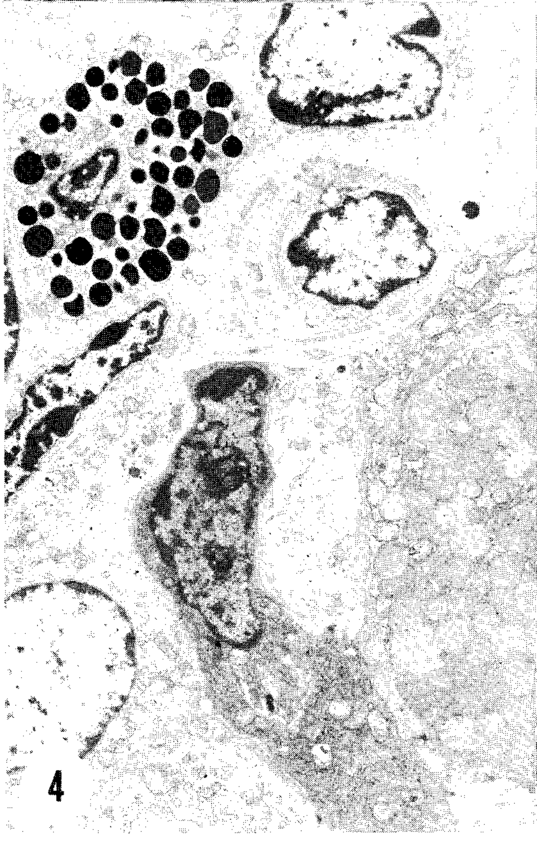
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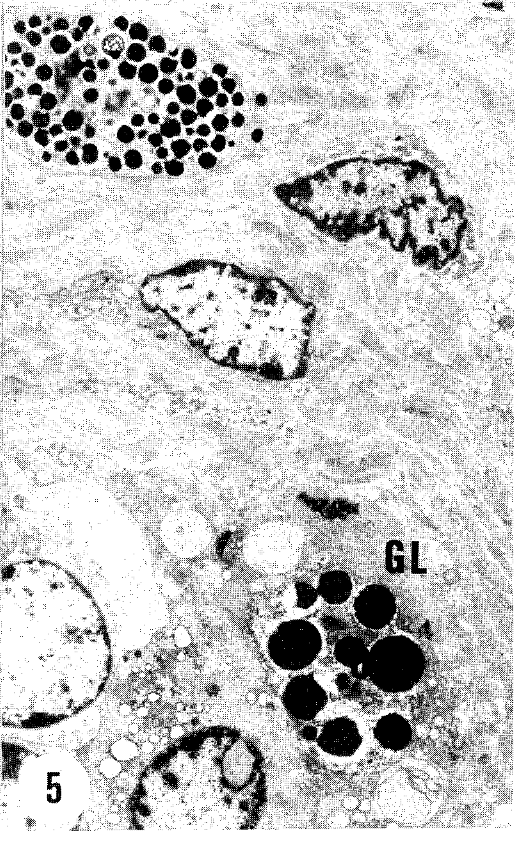
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Fig. 6. Typical location of a globule leucocyte (GL). x 2.400.

Fig. 7. Typical appearance of the nucleus and globules of a globule leucocyte. x 4.800.

Fig. 8. Ultrastructure of different organelles in a globule leucocyte. x 24.000.

Fig. 9. A detail of an apparently endocrinic cell with small basally locating granules. x 7.200.


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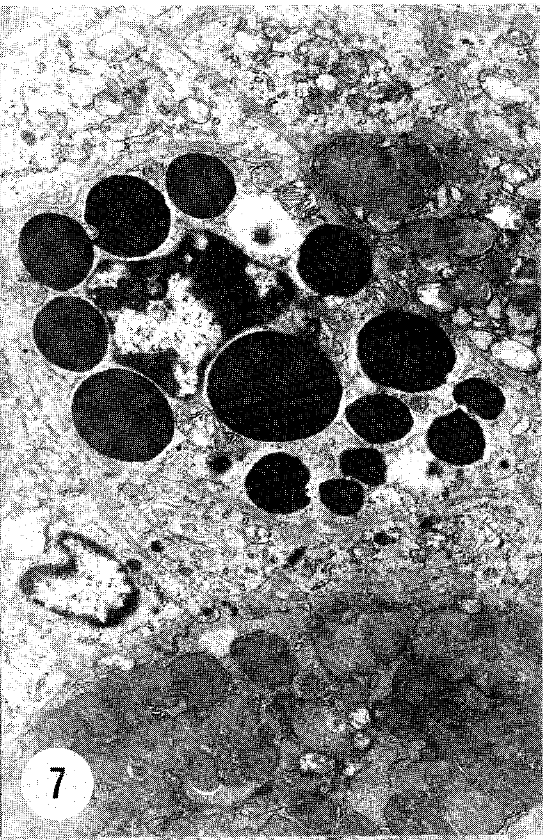
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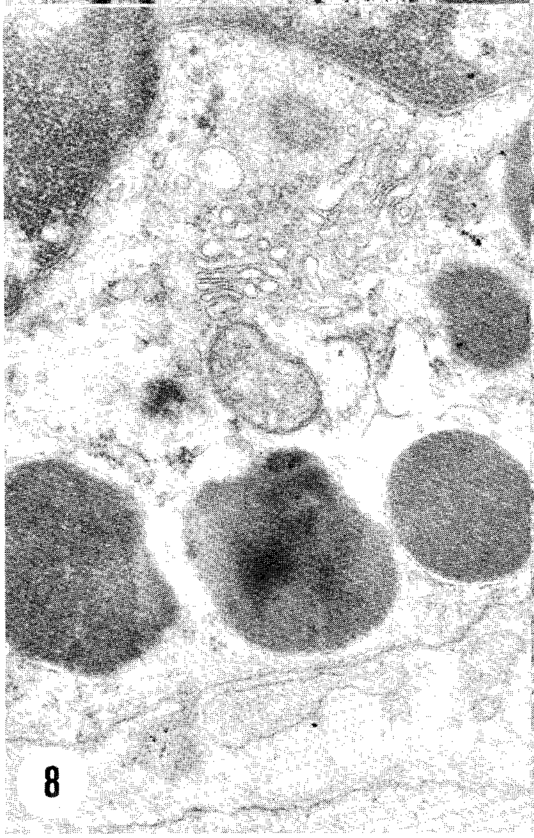
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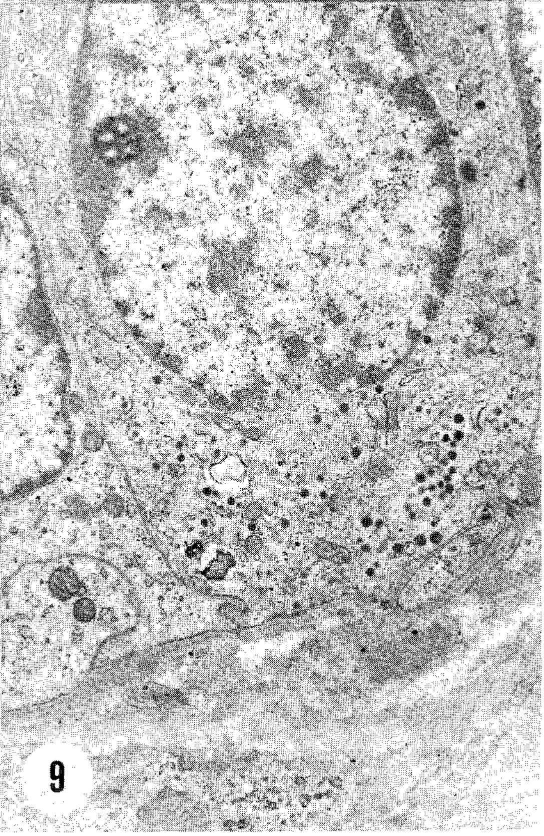
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The major histocompatibility complex of reindeer

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Abstract: The major histocompatibility complex (MHC) is a system of closely linked genes showing an extremely high degree of polymorphism. These genes are major elements in the government of specific immune reactions. Consequently they may represent a genetic marker system well suited to investigate variability in selective pressure from disease agents on different populations. On this background we have started investigation of the MHC complex in reindeer *(Rangifer tarandus* L). The MHC complex consist of polymorphic regions as well as regions conserved during evolution which should allow the use of cross-species reagents. We have shown that human MHC gene probes hybridize with genomic DNA from reindeer, and thus can be used as a tool in reindeer MHC research. By RFLP (restriction fragment length polymorphism) analysis using these probes we have also been able to show polymorphism in MHC related genes from reindeer.

Key words: *Rangifer*, MHC, RFLP

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Introduction

The Major Histocompatibility Complex (MHC) is a family of related, highly polymorphic and closely linked genes occupying one chromosomal region. These genes encode different classes of cell-surface glycoproteins. The glycoproteins are involved in cell - cell interactions and functions as major elements in the government of specific immune reactions.

Class I proteins occur on the surface of nearly all cell types and function as restricting elements in the process of eliminating virus infected and foreign cells. Class II proteins are expressed on specialized cells involved in regulation of the humoral and cellular response against foreign antigens. The number of genes for class I and class II polypeptides shows variation both between and within species. Moreover individual MHC genes contains regions conserved during evolution as well as highly polymorphic domain. The degree of polymorphism varies with the species, the population and the locus.

The conserved regions makes reagents such as antibodies and DNA- probes developed for typing of MHC genes in one particular species, potentially useful for MHC typing in other species as well.

The properties and peculiarities of the Major Histocompatibility Complex in different species are reviewed in Klein (1986) and Klein & Figueroa (1986).

The polymorphism of MHC genes in a given species might reflect the diversity of respective environmental pathogens. MHC may thus represent a genetic marker system well suited to investigate variability in selective pressure from disease agents on different populations.

On this background we have started investigation of the MHC in reindeer. Reindeer mainly live under natural environmental conditions. In Scandinavia numerous different populations exist both as semi-domestic and wild animals. The amount of differentiation and the evolution of the different populations are unknown. Studies on the pattern of genetic variability of the MHC of reindeer (tentatively called RaLA - Rangifer Leucocyte Antigens) might provide information regarding evolution of the different reindeer populations.

Here we describe the results of using a human class II ß MHC gene probe in restriction fragment length polymorphism (RFLP) studies on reindeer genomic DNA.

Materials and methods

Genomic DNA was isolated from 26 semi-domestic reindeer from Norway. Some of the animals were related (dam/offspring).

The DNA was digested with restriction endonucleases at 37°C over night. The digests were separated in 0.7 % agarose gels and blotted onto Gene Screen Plus filters (NEN - Du Pont) by alkaline capillary transfer. Hybridization (at 42°C with formamide) and washing was performed according to the filter producers manual.

Cloned DNA from a human class II gene was used as probe: The DQ ß probe was isolated as the 672bp Ava I fragment from the cDNA clone pII-ß-1 (Larhammar et al. 1982). The fragment was isolated by preparative agarose gel electrophoresis followed by extraction with GeneClean (BIO 101) and radiolabelled with α (-^{32} p) dCTP by multiprime DNA labelling (Amersham).

Results and discussion

The tested probe from the human MHC class II gene did hybridize to reindeer DNA showing that this DNA contains MHC class II related gene sequences.

14 different RFLP-phenotypes were revealed among the tested animals. Fig. 1 shows some of these phenotypes. This indicates the existence of at least 4 different variants of DQß related genes in reindeer. Offspring always had bands in common with their mothers. The family material was however to small to allow assignment of distinct bands belonging to specific alleles.

RFLP studies with human MHC gene probes have revealed highly polymorphic MHC gene loci in other animals such as cattle, sheep, horses, pigs, squirrels etc. (Vaiman & Chardon, 1986; Wettstein & States, 1986 a,b; Sigurdardôttir, Lundén & Andersson, 1988). For some of these animals the RFLP patterns were shown to be associated with serologically determined MHC types (Vaiman & Chardon, 1986). Our RFLP results from reindeer conform with the results from other animals and strongly indicates the existence of MHC genes in reindeer.

Confirmation of this can be achieved in different ways. One is to isolate the tentative RaLA gene fragments, perform sequencing and compare the results with known MHC gene sequence data. Further mapping of genes in a RaLA complex can be done by chromosome walking. Another method for confirmation involves studies of cell reactions in mixed lymphocyte cell cultures. Genes in the Major Histocompatibility Complex are related to disease resistance and susceptibility. The high amount of variation revealed in reindeer MHC genes suggests these genes as useful disease related genetic markers in studies of reindeer populations.

Lately there has been a lot of speculation con-

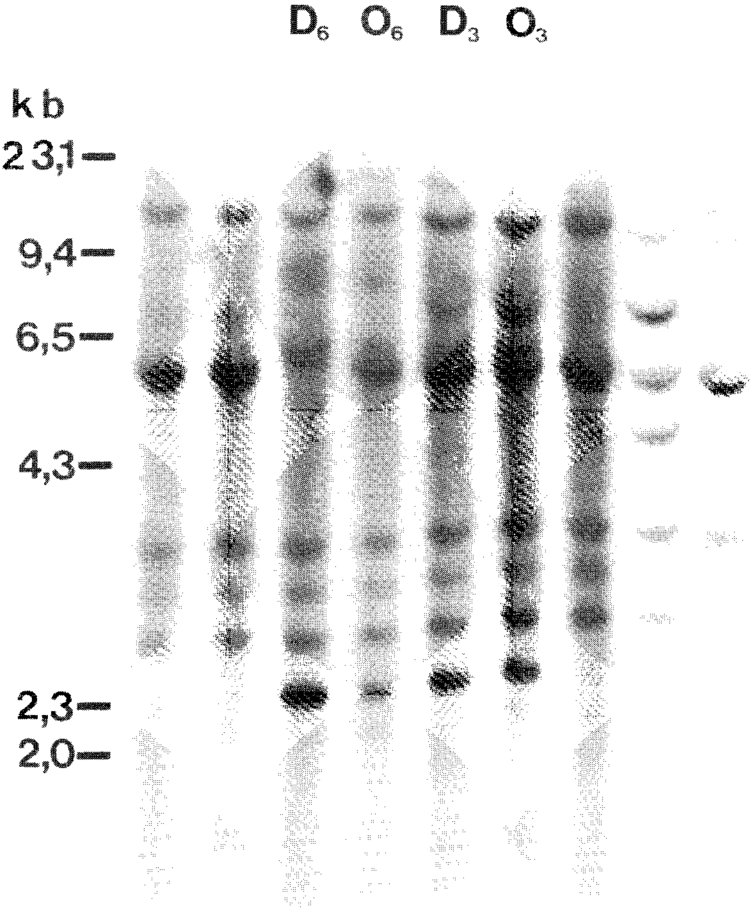

Fig. 1. EcoRI digested DNA from reindeer hybridized to a human DQ ß probe. D:dam. O:offspring

cerning the evolution of the high degree of polymorphism in the MHC. There is a large genetic distance between different alleles and a large number of alleles within most of the investigated species. Generally it has been assumed that these differences accumulated after speciation. Recent reports indicate that a large part of the MHC polymorphism pre-dates speciation and is passed from species to species (McConnell *et al.* 1988, Figueroa, Günther & Klein, 1988; Lawlor *et al.* 1988). Reinder populations live under natural environmental conditions. Investigations of reindeer MHC therefore have considerable interest in the light of MHC evolution as well.

Further analysis of tentative MHC genes in reindeer including more family material and animals from differens populations are under way.

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In ROCKBORN et al, pages 373 - 384, all the figure captions are placed under wrong figures and the figures ,consequently,have got wrong numbers .

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The demonstration of a herpesvirus, related to bovine herpesvirus 1, in reindeer with ulcerative and necrotizing lesions of the upper alimentary tract and nose

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Abstract: In 11 male reindeer, all esposed to transportation stress, signs of conjunctivitis and later on ulcerative and necrotizing lesions of the mucosa of the nostrils and mouth were recorded. Blood and secretions from the nose were sampled. Antibodies to bovine herpesvirus 1 (BHV-1) were detected in 2 animals. No animal had antibodies to bovine viral diarrhoea virus (BVDV). Virus isolation was negative.

The sampling was repeated 2 weeks later and complemented with biopsies from the mouth lesions, fixed in formalin. At this occasion 3 animals were seropositive to BHV-1 and in biopsies from 2 of these intranuclear herpesvirus-like particles were found by means of electron microscopy. Four animals, 3 of them seropositive, were treated with cortison during 8 days. The size of the ulcers in the mouth increased in all animals. A herpesvirus was isolated from 3 of them at 10 different occasions. The ultrastructural investigation of the virus suspension demonstrated the presence of typical herpesvirus particles. On day 11 all 4 animals suffered from a severe diarrhoea and anorexia. On day 12 one animal died and on day 13 post challenge with cortison two additional animals died. The remaining animal was slaughtered on day 13. Bacteriological investigation revealed growth of *Fusobacterium necrophorum* from the spleen and oral wounds of all 4 animals.

The animals were obviously subjected to an infection with a herpesvirus colsely related to BHV-1. Virus could be liberated by cortison treatment. It is possible that infections with the found herpesvirus, and the lesions caused by it, may be the background to earlier recorded severe outbreaks of necrobacillosis of the alimentary tract in reindeer herds.

Keywords: *Fusobacterium necrophorum.*

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Introduction

A disease producing ulcerations in the upper respiratory and oral mucosa (njunne-vikke or njunne-dawda) of reindeer *(Rangifer tarandus* L.) was reported already by Horne (1898) and Turi (1910). Its possible connection with outbreaks of oral and generalized necrobacillosis has been suggested by Horne (1898), Quigstad (1941) and Skjenneberg and Slagsvold (1968). A similar disease, also reported to be commonly complicated by oral necrobacillosis, is described from the USSR by Nikolaevskii (1961). Serological evidence of the presence of neutralizing antibodies to bovine herpesviurs 1 (BHV-1) in reindeer has been reported by Elazhary *et al.* (1981) and by Dieterich (1981), but none of them reported on connected pathological lesions. In 1982 Ek-Kommonen *et al.* reported on the finding of neutralizing antibodies to BHV-1 in Finnish reindeer. The virus was later on isolated and characterized as a herpesvirus antigenically realted to but different from BHV-1 (Ek-Kommonen *et al.*, 1986). The relationship between the reindeer herpesvirus and a herpesvirus isolated from red deer *(Cervus elaphus* L.), which also crossreacts with BHV-1 (Inglis *et al.*, 1983; Rönsholt *et al.*, 1987), is not yet established. Ek-kommonen *et al.* (1982, 1986) did not find any clinical signs of disease in the investigated animals, althoug in the latter investigation the animals were treated with dexamethasone in order to facilitate the isolation of the virus.

In 1985, Rehbinder *et al.* reported on a suspected virus infection of the oral mucuosa in Swedish reindeer exhibiting vesicular and ulcerative lesions. Material for serlolgical investigation was not obtained from autopsied animals but blood samples were obtained from animals at feeding sites where the necropsied animals had died. In some of these blood samples antibodies to BHV-1 were found.

The objective of the present paper is to report on the demonstraion of a herpesvirus, ralted to BHV-1, in reindeer with ulcreative and necrotizing lesions of the upper alimentary tract and nose and exhibiting generalized necrobacillosis.

Material and methods

Case history and clinical specimens

A number of 13 reindeer (11 males, 2 females) were moved from a grazing herd, by means of a 200 km lorry ride, into a corral where they were given hay and concentrates. The two females were let out but the males were kept in the corral. Three weeks after the transport some of the males showed sings of dullness, purulent conjunctivitis (5 animals) and "wet belly disease" (3 animals). The clinical signs were considered to be caused by the alomst grinded hay from which numerous dust particles were found in the conjunctival sacs but also producing the "wet belly disease" (Nordkvist, 1967).

One week later the animals had almost recovered from the initial clinical symptoms but now 6 of the animals had a purulent discharge from the nose. Rounded erosions, 5 mm in diameter were found in the oral muscosa of the lips. Rectal temperatures varied from 39.8 - 40.0°C. Serum samples, mouth and nose swabs (Culturette^R) were collected. Seventeen days later the sampling was repeated. From 6 animals with erosions of the oral mucosa biopsies were obtained by means of a "Stiefel" biopsy needle with a diameter of 4 mm. The tissues were directly fixed in 10% formalin. Approximately 3 weeks later 4 of the animals (No 84, 86, 88 and 90) were isolated and challenged daily with cortison (0.1 mg dexamethason/kg bwt.) according to Dennett et al. (1976). From the 5th day of cortison treatment and onwards serum and swab samples were taken each day, to day 10, on all 4 animals. Additional sampling was performed on some of the animals day 12 and 13.

One of the animals died on the 12th day of cortison challenge and two more animals died one day later, and the remaining reindeer was slaughtered on the same day. In connection with the deaths, samples from each animal were taken for:

1. Virological investigation: Blood, nasal mucosa, mouth erosions, conjunctival mucosa, prepuce and fecal samples.
2. Bacteriological investigation: Secretions from mouth and nose by means of Culturette and swabs of the spleen.
3. For histopathology and electronomicroscopy: Pieces from nose, eyelids, oral mucosa, trachea and lungs were fixed in 10% formaldehyde.

Cell cultures and virus references strains used

Primary bovine embryonic turbinate (BT) and primary embryonic dermis (ED) cell were used for isolation and propagation of viruses and serum neutralisation tests (SN). The cell cultures were maintained in Eagle's MEM and supplemented with 1% fetal calf serum.

A Swedish BHV-1 strain isolated from cattle and labeled 96, and one Swedish BHV-1-like isolate from reindeer designated 41, were used in the SN tests.

Virus isolation

If not processed immediately specimens were kept frozen at - 70° C. Swab material was suspended in 0.5 ml of PBS, pH 7.4, and clarified by low speed centrifugation before inocultion into tubes with BT and/or ED cells. Organs were perpared as 10% suspensions (w/v) in PBS. Penicillin and streptomycin were added to the suspensions. BHV-1 isolation: 0.2 ml of the suspension was inoculated into tube cultures, 2 tubes per suspension. After absorbtion for 1 hour at 37° C, the tubes were rinsed with Eagle's MEM and new medium was added and the tubes further incubated at 37° C. The tubes were checked each day for the presence of CPE for appoximately 7 days. If negative after 7 days, 0.1 ml of the cell culture harvest was passaged into new tubes, 2 tubes per material.

Immunofluorescence test for detection of bovine viral diarrhoea virus (BVDV): An indirect immunofluorenscence technique was used to detect BVDV in inoculated BT cells. Two tube cultures per material were inoculated with organ or swab suspensions, incubated for 7 days at 37°C and checked for CPE daily. The tubes were freeze-thawed, the medium pooled and clarified by low speed centrifugation. Each pool was inoculated into 2 Leighton tubes with outgrown BT cells. After 4 days of incubation at 37°C the slides were air dried, fixed with acetone and incubated with a 1:50 dilution of a monoclonal antibody (VD-1) directed to a structure of BVDV with a molecular weight of 20,000 (Juntti et al., 1987). A commercially available fluorenscein isothiocyanate-labelled rabbit anti-mouse Ig (Dakopatts, Denmark) was used at a dilution of 1:50.

SN-test

Antibody to BHV-1 was detected by a SN-test performed in a microtiter system (Reid et al., 1986). The mixture of serum and virus was incubated for 24 hours at 4 ° C as described by Bitsch (1973).

Histopathological investigation

Tissues were fixed in 10% formalin, embedded in paraffin, cut 5μ and stained with haematoxylin-eosin and periodic-acid-schiff.

Electron microscopical investigations

Selectes areas were cut from paraffin blocks, put in "Histo- clear" (National Diagnostics) for 24 hours, at room temperature, hydrated in graded ethanol series 90% - 70% - 50% - 30% for 10 min each at room temperature, postfixed in Karnowsky solution for 60 - 120 min at 4° C and in 1% osmium tetroxide in 0.1 M phosphate buffer for 60 min at 4°C, dehydrated in ethanol series 30% - 50% - 70% - 90% absolute alcohole for 10 min each at 4°C, put in prophytanoxide/Epon 1/1 over night at room temperature and embedded in Epon.

After embedding thick sections were cut and stained with toludine blue for light microscopy and thin sections were prepared with a LKB ultrotome and picked up on uncoated copper grids, stained with uranyl acetate and lead citrate and examined in a Philips electron microscope 420 at 60 Kw.

To examine the virus particles ten bottles of TB cells were infected with the reindeer isolate 41. When the cell monolayer showed 80-100% CPE, the cells were freezethawed once and the harvest centrifuged at low speed for 30 min. The supernatant was centrifuged in a Kontron ultracentrifuge rotor TST 28.38 at 100,000 x g for 1 h. The pellet was suspended in 200 μl of PBS, pH 7.4. Viruspreparations were negatively stained by mixing with an equal volyme 2% ammonium molybdate. The samples were applied to 2 % amylacetate coated collodium film supported on 400 mesh copper grids.

Bacteriology
The material obtained was subjected to routine bacteriology. For the isolation of *Fusobacterium necroforum* Fastidious Anaerobe Agar was used. Suspected colonies were inoculated in chopped meat medium for 48 h at 37° C. Standard biochemical test, gaschromatography and microscopy were performed.

Results

Clinical investigations
During the period when four of the animals were challenged with dexamethason the lesions of the oral mucosa, in these animals, increased considerably (Fig. 1). At the end of the challen-

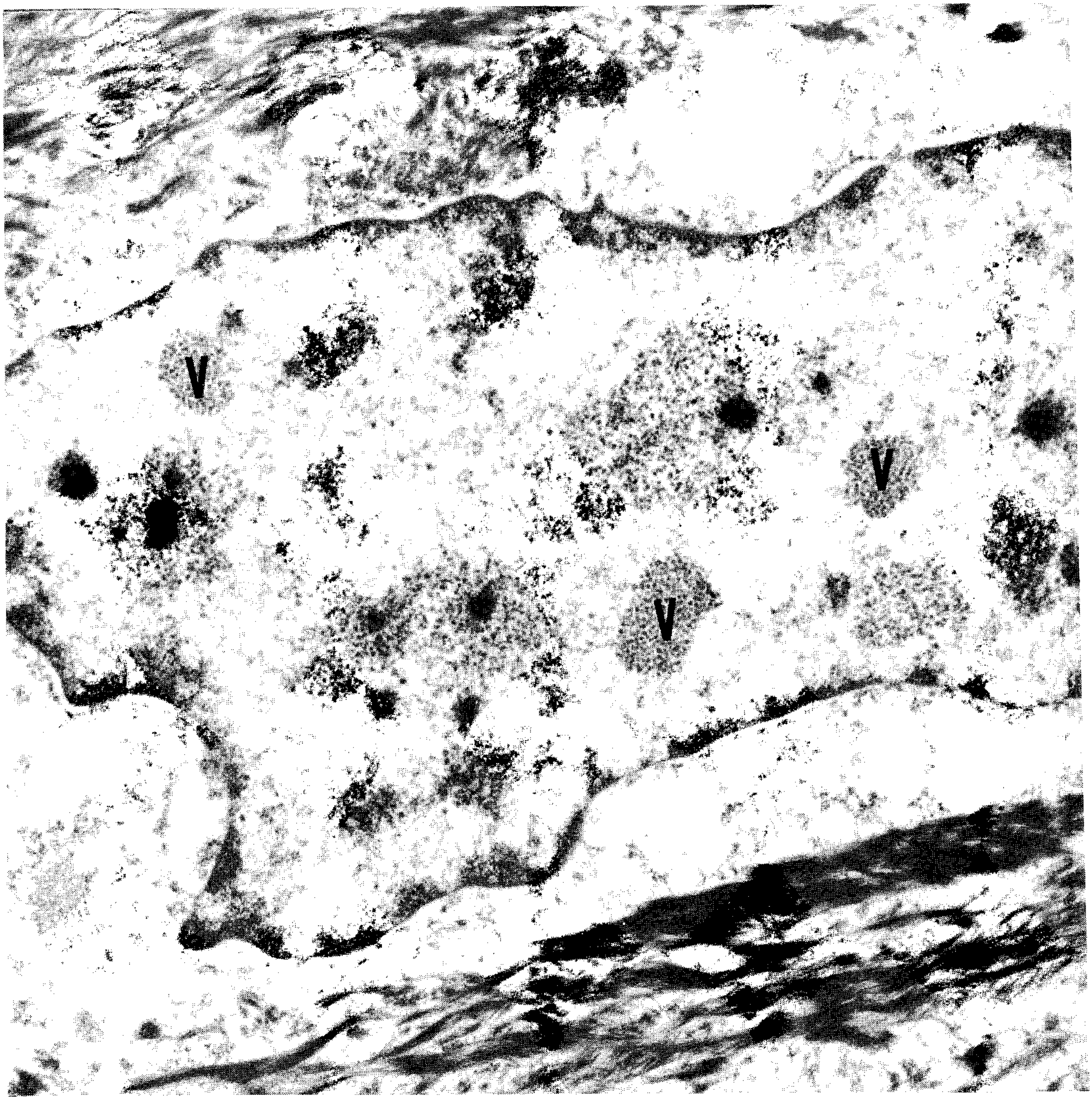

Fig. 1 Ulcers in the oral mucosa of the lip of a reindeer. The ulcers increased in size during the dexamethason treatment.

Fig. 2 Epithelial cell from the oral mucosa. Note structures similar to viral inclusions (V) and scattered virus like particles in the nucleus. Biopsy material x 19200.

ge period all four developed a watery diarrhoea and stopped consuming hay but were still eating lichens. At the same time they presented a serous discharge from the nose and mouth and to a minor extent from the eyes.

Pathological investigations

At the histological investigation of the biopsy material, the oral mucosa of all 4 animals, showed focal vesticle formation, inter- and intracellular oedema, swollen nuclei with degenerative changes and indistinct intranuclear and distinct cytoplasmic inclusion bodies. Areas with sloughed necrotic epthelium and ulcerations were also present. The ulcers were covered with colonies of fungi and bacteria and demarcated by heavy neutrophilic infiltrations. Similar colonies were occcasionally found at varying depths in the lamina propria and submucosa. The nucleoli of the epithelial cells at several instances appeared swollen. Electron microscopy revealed intranuclear structures similar to viral inclusions and scattered virus-like particles with an approximate diameter of 100 nm (Fig. 2) in material from two animals.

At necropsy a catarrhal enteritis, rumen indigestion and enlarged pulpy spleens were found. In the mucosa of the nose and oral cavity, mainly in the rostral parts, erosions and ulcers of the mucosa 5 x 10 mm - 50 x 20 mm were found. Erosions and ulcers were not found anywhere else in the alimentary systeme. The tracheas showed a moderate to severe hyperemia.

The histopathological investigation of the material from the necropised animals revealed in the oral mucosa almost the same, but more pronounced changes than found in the biopsy material. The surface epithelium was to a large extent lost and necrotic lesions pronounced. Ulcers were demarcated by heavy infiltrates surrounding bacterial colonies, some of them typical for *Fusobacterium necrophorum*. Bacterial colonies surrounded by neutrophilic infiltrates were also found in the lamina propria and submucosa. The mucosa of the nostrils showed less pronounced changes but the epithelium appeared swollen with loss of surface cells. Ulcerations, when present, were smaller and with less inflammatory response.

The nasal mucosa showed a prominent loss of surface epithelium with swollen tilted basal cells. The epithelium of the submucous glands and ducts was partly disintergrated. Goblet cells were numerous. The mucosa of the trachea showed prominent changes. The vessels and capillaries were dilated. The epithelium was characterized by a heavy destruction, loss of large parts of the epithelial lining, the remaining cells being short and whithout cilia. The surface was covered by cell detritus masses and blood.

The conjunctivae showed an uneven loss of the surface eptihelium. Most epithelial cells were swollen some few were shrunken. The Meibom glands presented epithelial degeneration and were partly filled with detritus masses. Most mucous membranes investigated revealed limited subepithelial infiltrates by mononuclear cells, mainly lymphocytes, except for areas with ulcerations in which generally a heavy purulent inflammatory process was present.

Affected epithelial cells were enlarged with a swollen nucleus in which commonly was present structures similar to swollen nucleoli. Intracytoplasmic inclusion bodies were common. Electron microscopy again revealed intranuclear structures similar to viral inclusion bodies and scattered virus like particles. (Fig. 3).

Serological investigations

Two out of the 11 reindeer had antibodies to the BHV-1 strain 96 when sera of the first sampling was tested, and 3 at a second sampling. None of the animals has antibody titers to BVDV and this was not further investigated.

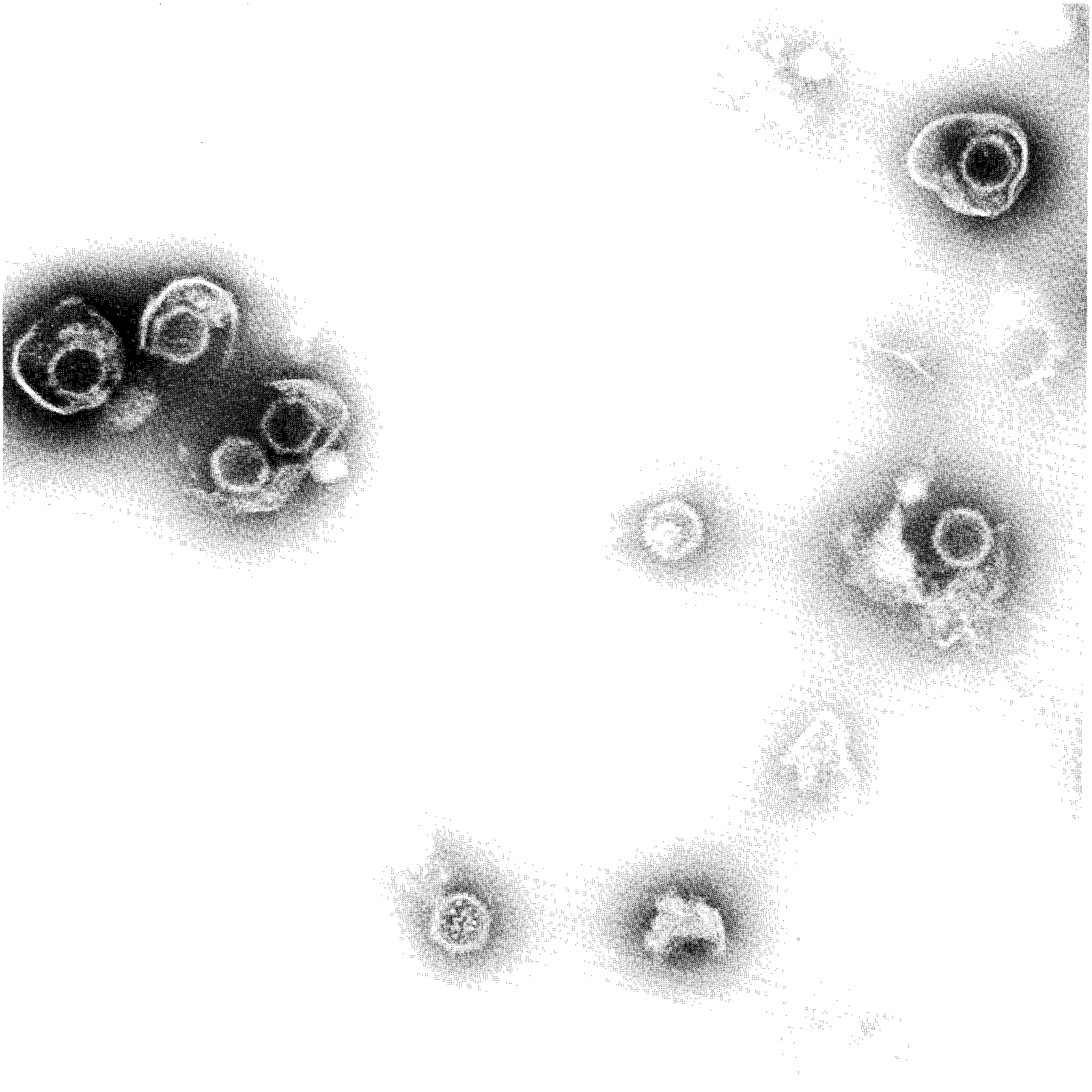

Fig. 3. Epithelial cell from the oral mucosa. Note virus like particles (arrows) and unspecific inclusion body (U.I) Necropsy material x 12500.

These three animals and one additional seronegative animal were isolated, challenged with cortison and repeatedly sampled as described in Material and Methods. The serum samples were tested for the presence of antibodies to BHV-1 isolates 96 and 41. The amount of antibodies detected increased in 3 of the animals and the antibody level was dependent on the virus isolate used in the SN-test (Table 1).

Virus isolation

From the two initial samplings of swabs neither BVDV or BHV-1 were isolated. No further

Table 1. Neutralizing (SN-) antibody titers in serum from reindeer to BHV-1 isolate 96 from cattle and BHV-1 isolate 41 from reindeer.

Day of sampling[a]	SN-titer and reindeer No BHV-1 96				BHV-1 41			
	84	86	88	90	84	86	88	90
-38	<1[b]	<1	22	4	11	8	90	22
-21	<1	4	8	6	11	11	64	16
5	<1	<1	4	<1	6	8	32	16
6	<1	<1	6	2	8	8	32	11
7	<1	<1	4	4	11	6	45	11
8	<1	<1	6	4	8	8	45	16
9	6	<1	16	8	16	16	178	45
10	22	<1	45	11	90	11	>256	32
12[c]	NT[e]	2	NT	NT	NT	8	NT	NT
13[d]	22	—	45	11	90	—	>256	64

[a] The reindeer were challenged with cortison Day 0.

[b] Reciprocal of serum dilution.

[c] Reindeer No 86 died.

[d] Reindeer Nos 84 and 88 died; No 90 was slaughtered.

[e] NT=not tested.

Table 2. Recovery of BHV-1-like isolates from reindeer after cortison treatment

Day of sampling post challenge with cortiston	Swab or organ material sampled and labeling of animals[a] Nose				Mouth erosion			
	84	86	88	90	84	86	88	90
5	—[b]	—	—	—	—	—	—	NT[c]
6	—	—	—	—	—	—	—	NT
7	—	—	—	—	—	—	—	NT
8	+	—	+	—	—	—	—	NT
9	+	—	+	+	+	—	—	NT
10	—	—	+	—	—	—	—	NT
13	+	—	+	+	—	—	—	NT

[a] Sporadically, samples were taken from the conjunctiva (86, 90) prepuce (88, 90), and faeces (84, 86, 90); all these materials were investigated with negative results.

[b] -=virus not isolated; +=a BHV-1-like virus isolated.

[c] NT=not tested.

attempts to isolate BVDV were made. On day 8 post challenge BVD-1-like viruses were isolated from nose swabs of 2 of the reindeer. On day 9 virus was also isolated from a mouth erosion of animal No 84. From 3 of the 4 animals BHV-1-like viruses were isolated on 10 different occasions (Table 2). The isolates were identified as colsely related to BVH-1 by SN-test with a polyclonal hyperimmune rabbit anti-BVH-1 seurm. The isolate designated 41 was used in the SN-tests.

At electron microscopy typical herpesvirus particles were found (Fig. 3 & 4).

Bacteriological investigation

Spleens and material from the oral mocosa of all the animals produced a moderate to rich growth of *Fusobacterium necrophorum* in a mixed culture.

Discussion

In 1985, Rehbinder *et al.* reported on a suspec-

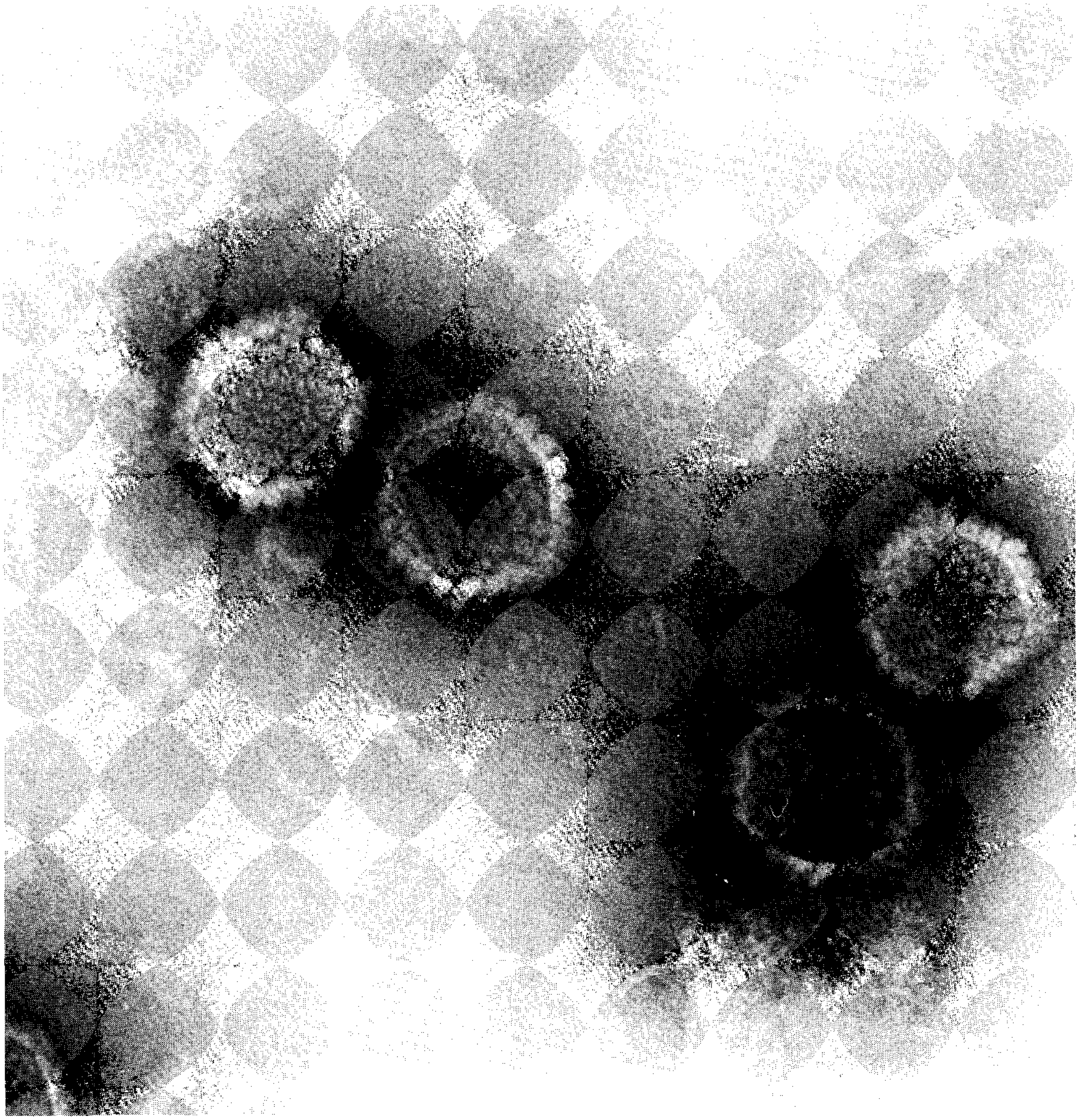

Fig. 4 Virus suspension. Typical herpes virus particles. Note envelope and capsid. Negative stain x 260000.

ted virusinfection of the oral mucosa in reindeer causing vesicular and ulcerative lesions. In some instances *F. necrophorum* contributed to the death of the animals. Antibodies to a virus related to BHV-1 were found in blood samples obtained from clinically healthy animals from the flocks from which the necropsied animals emanated. Antibodies to BVDV/MD-virus were not present. The importance of the exposure to the BHV-1 related virus was not established.

In reindeer, serological evidence of an exposure to BHV-1 was earlier reported by Elazhary (1979, 1981) and Dieterich (1981). In 1982 Ek-Kommonen *et al.* reported on a virus related to BHV-1 and in 1986 Ek-Kommonen *et al.* described a herpesvirus antigenically related but different from BHV-1. No clinical signs of disease were found to be connected with the presence of the virus. In red deer (*Cervus elaphus* L.) latent herpesvirus infectons with a cervidae herpesvirus type 1 (CHV-1) appears to be widely spread (Lawman *et al.*, 1978; Nettleton *et*

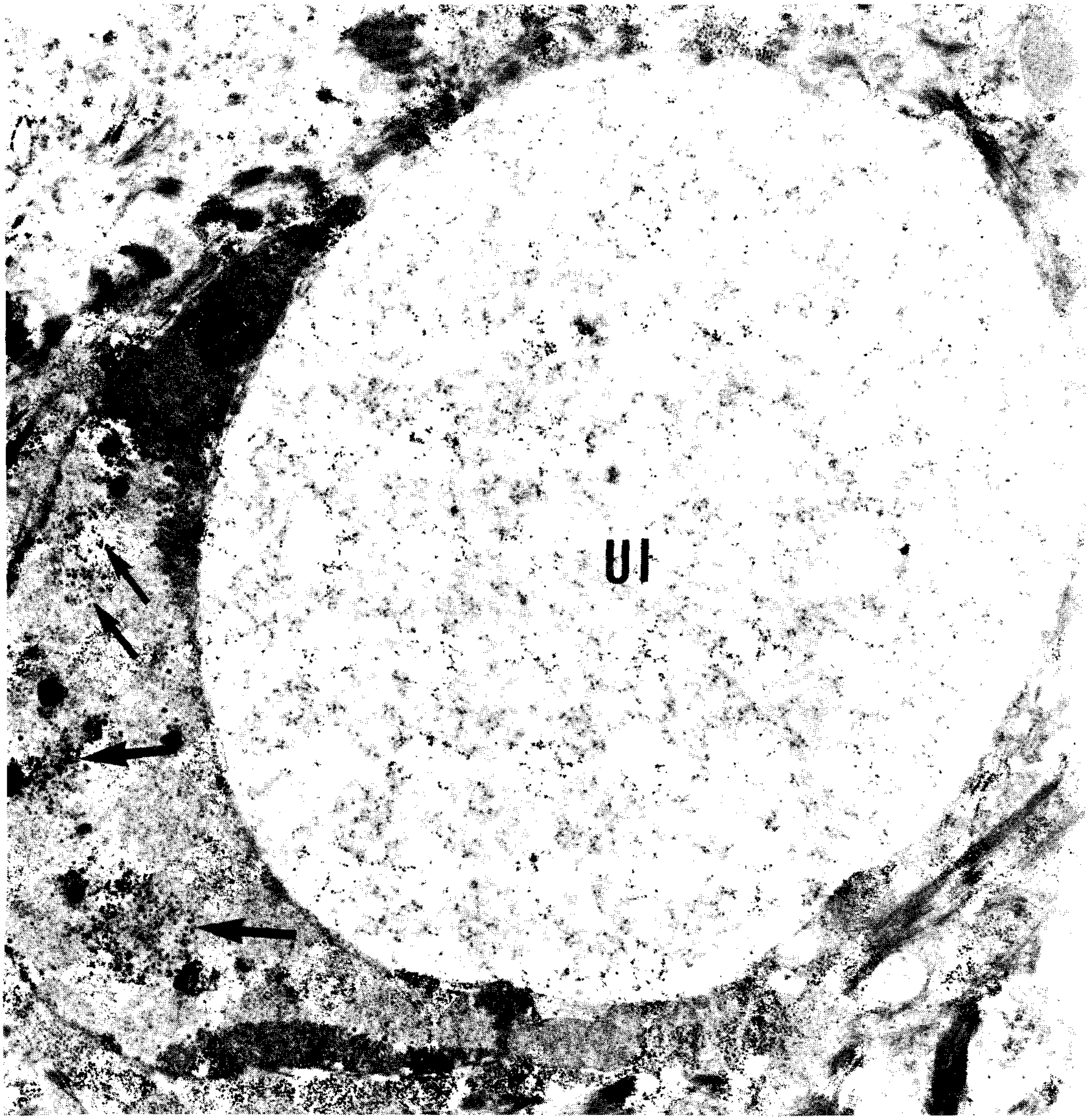

Fig. 5. Virus suspension. Typical herpes virus particles. Note hexagonal shape. Negative stain x 260000.

al., 1986; Kokles *et al.*, 1988) and some times connected with disease.

The main clinical and pathological lesions reported are associated with ocular lesions and affection of the upper respiratory tract and oral mucosa (Inglis *et al.*, 983; Reid *et al.*, 1986; Argyle, 1986; Rönsholt *et al.*, 1987). Although it is prevalently occurring in red deer populations, the CHV-1 does not appear to be a major cause of disease. Almost all outbreaks of CHV-1 related disease seem to have occurred at times of stress (Nettleton *et al.*, 1986). The present investigation shows that, in reindeer, clinical signs of disease affecting the eyes and the mucous membranes of the mouth and nose were observed after a row of stressfull events such as handling, transport and changes to a less suitable fodder. In these animals, by means of electron microscopy and virus isolation, an infecton with a herpesvirus was proven. The intranucler presence of virus particles, partly forming intranuclear inclusion bodies, has to be considered typical to herpesviridae. The intracytoplasmic inclusion bodies have to be considered the result of an unspecific degenerative change (Diaz *et al.*, 1989).

The virus was antigenically realted to but different from BHV-1 as seen by the results presented in Table 1. It seems likely that the herpes virus isolated in this investigation is the same or closely related to the herpesvirus isolated from Finnish reindeer by Ek-Kommonen *et al.* (1986). The relationship between those two virus isolates and CHV-1 will be genetically determined. The clinical manifestations of CHV-1 in red deer and the herpes virus of this investigation infecting reindeer appeares very similar and connected with stressful events.

A herpes virus infection as a possible cause to the disease producing ulcers in the upper respiratory and oral mucosa as reported by Horne (1898) Turi (1910) and Nikolaevskii (1961) seems obvious. The death of the dexamethason treated animals in generalized necrobacillosis, with the entrance port most probably being the oral ulcers, judged from histopathology and bacteriology, indicates a connection between herpesvirus infections and outbreaks of necrobacillosis as suggested by Horne (1989), Quigstad (1941) and Skjenneberg and Slagsvold (1968). Principally any lesion in the oral mucosa whether caused by trauma, viral or bacteriological agents or parasites give way to *F. neophorum bacteria* to enter the submucousal tissues and to establish their presence (Rehbinder & Nordkvist, 1983). Similar leisons as observed in connection with the presently described herpes virus infection is reported in cattle and sheep in association wiht BVDV infection. Antibodies to BVDV have been found in reindeer (Elazarhy, 1979; Dieterich, 1981; Rehbinder, unpublished observations). The importance of this agent to reindeer is not known. Red deer are known to have antibodies to BVDV-virus (Nettleton *et al.*, 1980; Derek *et al.*, 1988) and the virus has been isolated in red deer (Nettleton *et al.*, 1980) roe deer (Romvary, 1965) and fallow deer (Díaz *et al.*, in press). In red deer (Anon, 1981) and fallow deer Díaz *et al.*, in press) the virus is reported to produce lesions similar to those seen in cattle. In this investigation and the investigation by Rehbinder *et al.* (1985) antibodies to BVDV were not found.

Kerato-conjunctivitis, oral and cutaneous lesions associated with poxvirus infection in reindeer were reported by Barker *et al.* (1980). This outbreak was confined to a zoo and as poxviridae are easy to diagnose by means of electron microscopy or tissue culture and no further reports are available, the outbreak has to be considered incidental. Kerato-conjunctivitis in reindeer, neither associated with outbreaks of necrobacillosis nor ulcerative lesions of the mouth and upper respiratory tract, but of a multifactorial genesis (trauma, bacterial infections and UV- irradiation), is common among woodland reindeer (Rehbinder, 1978). The disease ought to be easily distinguished from the presently decribed ailment.

In addition, malignant catarrhal fever gives rise to ocular and mucosal lesions. Reindeer kept in close contact with sheep may be affected (Beatson, 1985, Röken, personal communication, 1988). Typical vascular lesions are present, but were not observed in this investigation. As presented in this investigation, the BHV-1-like virus isolated from reindeer has the capacity to cause disease and, most probably, give way to infections with other microorganism, especially *F. necrophorum*.

Conclusions

Reindeer were obviously subjected to an infection by a herpesvirus colsely related to IBR-virus. The relationship will later be genetically determined. Virus could easily be liberated by cortison treatment. It is possible that infections with the found herpes virus, and the lesions caused by it, may be the background to earlier recorded outbreaks of necrobacillosis of the alimentary tract in reindeer herds.

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Transferrin variation and evolution of Canadian barren-ground caribou

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Abstract: Blood samples were obtained from 95 barren-ground caribou *(Rangifer tarandus groenlandicus)* of the Beverly herd in Northwest Territories, Canada. Polyacrylamid gel electrophoresis was used to score for genetic variation in the locus coding for transferrin. The pattern of allele frequency distribution are compared with previously reported values of Eurasian tundra reindeer *(R.t. tarandus)*, Alaska caribou *(R.t. granti)*, Peary caribou *(R.t. pearyi)*, and Svalbard reindeer *(R.t. platyrhynchus)*. In the Beverly herd a total of 21 different transferrin alleles were detected. The amount of genetic variation was higher in the Canadian barren-ground caribou than what has been detected in other subspecies of reindeer/caribou. Highly genetical differences in the allele frequencies were detected between the Canadian barren-ground caribou and the other subspecies. The genetic identity analyses indicates approximately the same amount of genetic differentiation when the Canadian barren-ground caribou are compared with Alaska caribou as with the Peary caribou. The allele frequency pattern could be explained by a possible origin of the Canadian barren-ground caribou from an ancestral population which was genetical influenced by animals surviving the Weichselian glaciation in refugia both in high Arctic, in Beringia, and south of the ice sheet.

Keywords: *Rangifer*, reindeer, polymorphism

Rangifer, Special Issue No. 3, 1990: 385-389

Introduction

According to the basic taxonomic study by Banfield (1961), the reindeer/caribou should be divided into two groups: the tundra reindeer (Cyclicornis) and the forest reindeer (Compressicornis). The main distribution of the different subspecies within the tundra reindeer group is given in Fig. 1. Within this group of reindeer it has been reported a major dichotony in the transferrin allele distribution between Alaska caribou *(R.t. granti)* and Eurasian reindeer *(R.t. tarandus)* on the one hand and Peary caribou *(R.t pearyi)* and Svalbard reindeer *(R.t platyrhynchus)* on the other (Røed and Whitten, 1986; Røed *et al.*, 1986). The Canadian barren-ground caribou *(R.t groenlandicus)* also belongs to the tundra reindeer group and has its main distribution in the mainland of northern Canada (Fig. 1) We report here the result of an electrophoretic examination of the transferrin locus in Canadian barren-ground caribou sampled from the Beverly herd. The allele fre-

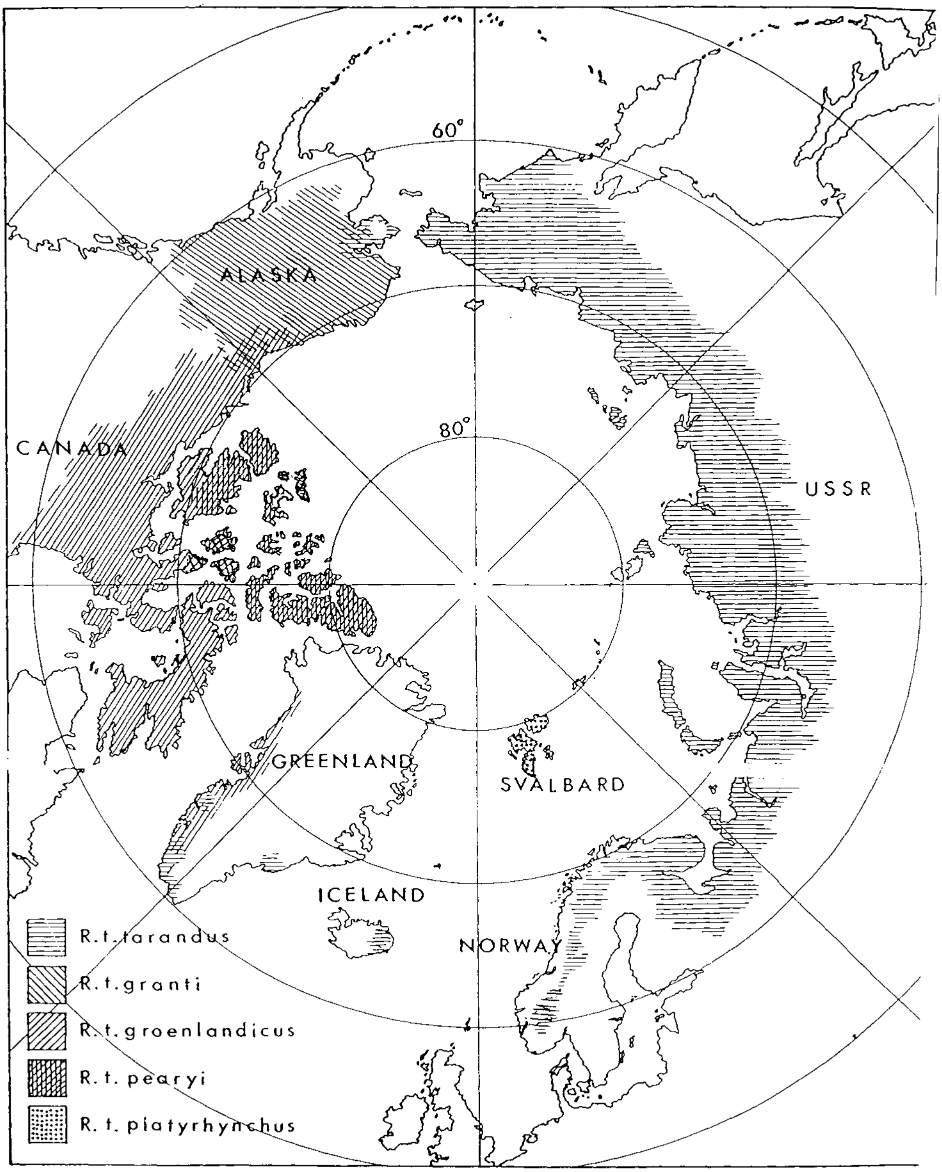

Fig. 1. Main distribution of different subspecies of tundra reindeer/caribou.

quency distribution is compared with those in other subspecies of the tundra reindeer and the results are discussed in relation to the origin of different subspecies of the genus.

Material and methods

Blood samples were obtained from 95 barren-ground caribou of the Beverly herd in Northwest Territories, Canada. The blood samples were taken into heparinized test tubes and centrifuged, after which the plasma fraction was removed and stored at -20°C until the electrophoretic analysis was performed. Plasma samples were subjected to vertical slab polyacrylamide gel electrophoresis as previously described by Røed (1985a). The transferrins were made visible by overnight staining with Coomassie Brilliant Blue R250 (Diezel *et al.*, 1972). Relative mobilities of transferrin bands were confirmed by re-running samples of approximately the same mobility side by side on the same gel. Reference plasma was from continental Norwegian wild and domestic reindeer, *R.t. tarandus*, (Røed, 1985a), from Svalbard reindeer, *R.t. platyrhynchus*, (Røed, 1985b), from Peary caribou, *R.t pearyi* (Røed *et al.*, 1986) and from Alaska caribou, *R.t. granti* (Røed and Whitten, 1986).

Results

The amount of genetic variation at the transferrin locus was high in the Canadian barrenground caribou. 21 separate alleles could be resolved in the present material. Compared with the reference plasma, three new alleles were detected. These have been designated according to their mobility relative to the reference alleles: two alleles with banding patterns anodal to Tf^{a} were arbitrarily given the designation Tf^{a-1} and Tf^{a-2} according to their increasing mobility, and one with bands slightly anodal to Tf^{M} (cathodal to Tf^{L}) was labeled Tf^{L2}. Accordingly, Tf^{L} is here renamed Tf^{L1}. Table 1 presents the allele frequencies in the sampled *R.t. groenlandicus* together with previously reported values for *R.t. pearyi* from the Canadian Arctic islands (Røed et al., 1986), *R.t. granti* from Alaska (Røed and Whitten, 1986), *R.t. tarandus* from Norway (Røed, 1985a), and *R.t. platyrhynchus* from Svalbard (Røed, 1985b). The presence of 21 different alleles in *R.t. groenlandicus* (95 individuals analysed) compared to 16 alleles in *R.t. pearyi* (86 individuals analysed), 18 alleles in *R.t granti* (112 individuals analysed) and 2 alleles in *R. t. platyrhynchus* (49 individuals analysed) indicated higher amount of genetic variation in the *R.t groenlandicus* than in the other subspecies of the tundra reindeer type.

The pattern of allele frequency distribution at the transferrin locus indicated considerable genetic heterogeneity among the different subspecies within the tundra reindeer group. The contingency chi-square test for homogeneity among subspecies was highly significant ($p < 0.001$). Highly significant differences ($p < 0.001$) in the transferrin locus were also detected when *R.t. groenlandicus* was compared one by one with the other subspecies. This is illustrated, among others, by the frequence of the Tf^{E1} allele which was the most common allele both in *R.t. granti* ($p=0.30$) and in *R.t. tarandus* ($p=0.31$). In *R.t. groenlandicus*, however, this allele was present with a frequence of only 0.11. Furthermore, $Tf^{G2}$was definitely the most common allele both in *R.t. pearyi* ($p=0.30$) and in *R.t. platyrhynchus* ($p=0.75$), while the frequence of this allele was considerable less in *R.t. groenlandicus* ($p=0.12$).

Coefficient of genetic identity, I (Nei, 1972), was calculated from the allele frequencies in Table 1. Table 2 gives the genetic identity between the different subspecies of the tundra reindeer type and illustrates that the genetic identity between subspecies was highly variable, ranging from 0.886 between *R.t. tarandus* and *R.t. granti*, to 0.000 between *R.t. platyrhynchus* and *R.t. tarandus*. The genetic identity between *R.t. groenlandicus* and the other subspecies shows that this subspecies is most genetic similar to *R.t. pearyi* and to *R.t. granti*, with approximately the same amount of genetic similarity to both subspecies.

Discussion

The results of the present study indicate that *R.t. groenlandicus* contains a high amount of genetic variation, and that considerable genetic divergence has occurred in comparison with other subspecies of the tundra reindeer group. The early evolution of reindeer and caribou is largely unknown. The genus has been traced back to about 440 000 B.C. in central Germany, and its existence in North America may well be equally long (Banfield 1961). The present finding of several more transferrin alleles in subspecies in North America than in the Eurasian reindeer could be of importance in this context. As much as sixteen transferrin alleles

Table 1. Transferrin allele frequencies of different subspecies of tundra reindeer/caribou

Allele	*R.t. groenlandicus*	*R.t. peary*a)	*R.t. granti*b)	*R.t. tarandus*c)	*R.t. platyrhynchus*d)
A-2	.005				
A-1	.005				
A	.032	.041	.027	.016	
B		.006	.013		
C1	.063	.058	.085	.270	
C2	.068	.099	.036	.038	
C3		.006			
D				-e)	
E1	.111	.023	.304	.307	
E2			.036	.006	
G1	.047		.054	.046	
G2	.116	.297	.049		.745
G3					.255
G4			.004		
H1	.011	.023	.013	.036	
H1b			.009		
H2	.153	.180	.147	.090	
I	.121	.163	.134	.130	
J	.037	.006	.013		
K1	.032		.013	.034	
K2	.016				
L1	.053	.041	.018		
L2	.011				
M	.042	.017	.040	.028	
N	.005	.006			
O1	.026	.023			
O2	.032		.004		
O3	.016				
P		.017			

a) From Røed *et al.* 1986
b) From Røed and Whitten, 1986
c) From Røed 1985a
d) From Røed 1985b
e) Frequency < 0.001

Table 2. Paired combinations of genetic identity between subspecies of tundra reindeer/caribou

Subspecies	1	2	3	4	5
1 R.t. groenlandicus	****				
2 R.t. pearyi	.838	****			
3 R.t. granti	.818	.512	****		
4 R.t. tarandus	.671	.360	.886	****	
5 R.t. platyrhynchus	.374	.688	.120	.000	****

were detected in subspecies in North America which were not detected in the Eurasian supspecies, while only two alleles present in the Eurasian reindeer were not detected in North American caribou. Such a pattern could indicate a larger evolutionary time of North American caribou and an origin of present Eurasian mainland reindeer from ancestral populations in North America (Røed and Whitten, 1986).

Concerning the origin of the different subspecies of reindeer and caribou, it has been hypothezised that continental tundra forms evolved in the Beringia refugium in Alaska-Yukon during the Wisconsin glaciation, the woodland caribou south of the ice sheet, and the Peary caribou in a refugium in the Canadian Arctic Archipelago or in northern Greenland (Banfield, 1961). A common genetic origin of Svalbard reindeer and Peary caribou has also been suggested from the similarity in the transferrin locus (Røed, 1985b, Røed *et al.*, 1986). As indicated by Røed and Whitten (1986), the genetic similarity between Alaska caribou and the Eurasian reindeer could be explained by a common ancestor of these subspecies in the Beringia refugium during the late Weichselian, and as the ice barriers retreated, this population may thus have colonized the Eurasian tundra region.

The present populations of the Canadian barren-ground caribou could have evolved from the same population in the Beringia area and moved east as the ice retreated. The relatively great genetic difference detected between the Canadian barren-ground caribou and the Alaska caribou, indicate however, either a longer time of isolation between the Canadian barren-ground caribou and the Alaska caribou, or genetic influence form other populations with a different genetic pool. There are indications that an unglaciated corridor form Alberta to the Mackenzie Delta was opened at a late period and possibly was occupied by the woodland caribou before the tundra caribou from the Beringia refuge could reach the eastern tundra (Banfield, 1961). As the ice-barriers retreated, the Alaska caribou in the west, the woodland caribou in the north, could hav re-met in the areas of Mackenzie Delta at an relatively early date. The high amount of gentic variation in the Canadian barren-ground caribou, together with considerable genetic difference with both the Alaska caribou and the Peary caribou, could therefore reflect an origin of the Canadian barren-ground caribou from ancestral population which was genetical influenced by all the three main series of North American subspecies of reindeer and caribou.

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Parasite-host relationships of warble fly *(Oedemagena tarandi* L.)[1] and reindeer *(Rangifer tarandus* L.)

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Expanded abstract: Evolutionary adaptation of the warble fly *(Oedemagena tarandi* L.) to parasitism in reindeer has occurred in such a way that survival of the parasite depends completely on the survival of the host. The death of the host will thus cause the death of the parasite larvae. Thus the interspecific relations of the warble fly and reindeer have assumed a character of a lenient parasitism. Many researchers note that almost all reindeer are infested by warble fly and reindeer have assumed a character of a lenient parasitism. Many researchers note that almost all domestic reindeer are more heavily infested than wild reindeer. Infestation rates in young domestic reindeer range from 26 to 324 larvae per animal and in young wild reindeer from 15 to 126 larvae per animal (Tables 1, 2) Mature, domestic reindeer are infested with 25 to 417 larvae per animal and in mature wild reindeer the infestation ranges from 38 to 94 larvae per animal (Solomakha 1983). Infestation rates decrease with age. The proportion of young animals which are infested remains in both domestic and wild reindeer constant throughout winter. Young reindeer are, on average, 2 to 4 times more heavily infested than mature animals exept for mature, domestic reindeer treated with ethacide against oedemagenatosis in the previous season in which the rate of infestation may exceed that of juveniles.

Serum antibody titers against warble fly larvae range from 1:4 to 1:16384 in infested reindeer. The intensity of humoral immunity depends upon the age of the reindeer and the developmental stage of the larvae. Antibody titers are higher in reindeer which have endured 3-7 multiple invasions than in juveniles. Antibody titers are lower in mature draught reindeer than in other mature reindeer.

Serum antibody titers ranging from 1:64 to 1:1024 have been discovered before 15 June in newborn calves, which, due to the time of the year, could never have been in contact with warble flies. Serological studies of wild reindeer fetuses have revealed precipitating antibodies against third instar warble larvae in

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[1] Editors footnote:
The genus *Oedemagena* has recently been renamed *Hypoderma* (Wood 1987)

Table 1. Infestation rate of warble fly larvae in domestic reindeer.

Year	Reindeer/Age	n	Mean number of larvae
1977	Calves, 8 months	65	119
	Males, 1 year 9 months	29	74
	Males, ≧ 3 year	14	49
	Females, ≧ 3 year	10	76
	Draught reindeer	29	87
1979	Calves, 8 months	10	142
	Males, 1 year 8 months	11	96
	Males, ≧ 3year	4	25
	Females, ≧ 3 year	5	70
	Draught reindeer	4	110
1980	Calves, 8 months	34	34
	Males, ≧3 year	42	29
	Females ≧ 3 year	49	26
1981	Calves, 8 months	7	117
	Males, 1 year 8 months	7	324
	Males, ≧3 year	10	212
	Females, ≧3 year	5	417
1982	Calves, 8 months	6	109
	Males, 1 year 8 months	1	95
	Females, ≧ 3 year	3	163
	Draught reindeer	3	180
1983	Calves, 8 months	16	43
	Males, 1 year 8 months	3	29
	Males, ≧ 3 year	2	50
	Females, ≧ 3 year	10	77

titers varying from 1:40 to 1:5120. Passive hemaglutination tests on milk collected from wild reindeer in June revealed antibodies against water-soluble protein fractions of the hemolymph of third stage larvae with titers ranging from 1:16 to 1:32.

Humoral immune responses can be observed in the zone of contact between larvae and reindeer tissues. Mononuclear leucocytes and cell fragments including nuclei are found in smears made from migrating larvae. At the second stage, when a connective tissue capsule is formed, smears contain principally lymphocytes, plasma cells and macrophages. Some neutrophiles and eosinophiles are also present. At this stage leucocytes accumulate around the larvae and acute granulation tissue containing fibroplasts, macrophages and lymphocytes is

Table 2. Infestation rate or warble fly larvae in wild reindeer.

Age of reindeer (years)	n	Mean number of larvae
1	33	98
2	14	123
3	41	72
4	39	61
5	45	56
6	28	59
7	16	38
8	9	52
9	5	94
10-14	5	80

Table 3. Titers of hemolysins and hemoglutinins in the larval hemolymph.

Date	Number of reindeer	Larval developmental stage	Hemolysis or hemoglutination of reindeer erythrocytes by larval hemolymph						
			1:0	1:2	1:4	1:8	1:16	1:32	1:64
23.10 1982	5	I	5	5	5	3	2	—	—
13-15.02 1979	82	II	43	20	1	—	—	—	—
28.06 1980	48	III	48	48	48	46	23	14	7
Protein-free hemolymph	10	III	0	0	0	0	0	0	0

formed. At the third stage, before the end of the parasitic stage, the content of cells in smears consits mostly of polynuclear leucocytes. Simultaneously, an infiltration of leucocytes occurs into the hemolymph of some of the larvae. About 60% of these leucocytes are lymphocytes.

Resistance against the acticve influence of the host immune system is important for larval survival. There are two main types of hemocytes in *O. tarandi* larvae. They differ in their structure and in their ability to stain with azure-eozine. Basophilic hemocytes absorb stain well and their cytoplasm colours blue or bright blue. These hemocytes make up 0.5 - 1.0% of the hemolymph of the first and second stage larvae and 4 - 5% in hemolymph of third stage larvae.

The majority (99.0%) of hemolymph cells in first and second stage larvae and 95 - 96% of the hemolymph cells in the third stage larvae are plasmocytes. These cells have phagocytic and secretory functions. They have characteristic honeycomb structures int the cytoplasm and small nuclei. Small plasmocytes predominant the early stages of the development stages of the larvae. Large plasmocytes are dominant at late stages. These cells are abundant in the hemolymph before the parasitic stage of the flies life cycle in the host organism is complete. Production of large plasmocytes decreases after the larvae have emerged from the fistulae and during the larvae pupation. The plasmocytes disappear totally after seven days. The protective function of the hemocytes is connected with the phagocytosis of the heterogenious substance which penetrates the larvae. Hence, the number of hemocytes increases under the influence of unfavourable factors. In this case, phagocyting hemocytes may be exhausted and thus, the total number of cells in the hemolymph decreases.

In addition to hemocytes, larval defence includes hemoglutinines and hemolysins which agglutinate and hemolyze reindeer erythrocytes. The titer of hemoglutinines and hemolysins in migrating larvae does not exceed 1:16. The titer in third stage larvae reaches 1:64 (Table 3) corresponding with the maximum level of precipitating antibodies against hemolymph antigens in reindeer blood. The secretional function of larval hemocytes increases through both increased size and quantity of secretion drops produced. Increased secretion by the hemocytes is connected with trophic needs and is one of their protection factors. In vitro treatment of the larvae with ethacide results in a decrease of the number of secretion drops produced by the hemocytes within a few hours followed by their complete disappearance.

Serum titers of antibodies increase with increasing age in reindeer. "Camouflage" of the parasite capsule by antigen-antibody complexes promotes survival of the larvae. In addition, larvae have proteolytic enzymes which may destroy immunoglobins with which they come into contact. It is quite probable that larvae may exert an inhibitory effect on their hosts' immune system, thus initiating a sequence of responses promoting the survival of the parasite. In the process of evolution, the host-parasite relationship between reindeer and warble fly larvae has been formed in the way that an interrelation in the larvae-reindeer system developed. For example, warble fly larvae in the subcutaneous tissue excrete products which induce production of specific precipitating antibodies in the host. However, the larvae have the ability to resist the protective factors of the host and to maintain their integrity at the expence of their own cellular and humoral system. After between three and seven invasions the relationship favours the reindeer and the number of infesting larvae decrease with increasing age of the host.

This investigation has revealed previously unknown aspects of the host-parasite relationships between warble fly larvae and reindeer. The results may be useful when the immunobiological relations of the host-parasite system are used for the control of warble flies.

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Characteristics of fatty acid composition of adipose tissue and serum lipids in reindeer calves

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Abstract: Fatty acid composition of adipose tissue and serum lipids were studied in newborn and growing (1.5-month-old) reindeer. Material was collected during 1985 and 1986 at the Kaamanen research station. Lipids were extracted with methanolchloroform and fatty acid methyl esters of lipid fractions were analysed by gas liquid chromatograph. Fatty acids of adipose tissue triglycerides in newborn calves were predominantly unsaturated (51%) referring to fluid properties of brown adipose tissue lipids. The dominant fatty acid was oleic acid (18:1) with 46% followed by palmitic acid (16:0) with 30% and stearic acid (18:0) with 15%. Triglycerides (TG) contained 3% polyunsaturated fatty acids (PUFA), the majority of which was essential fatty acids (EFA). In growing reindeer adipose tissue TG were predominantly saturated (67%). The dominant fatty acid was 16:0 (34%) followed by 18:1 (29%) and 18:0 (25%). Adipose tissue phospholipids (PL) were mainly unsaturated in both age groups. The proportion of PUFA was 23%, of which majority was EFA, necessary to normal structure and function of biomembranes. A high correlation existed between fatty acid composition of adipose tissue TG and PL with serum TG in newborn calves ($r = 0.982$ and 0.924). Fatty acids of serum TG were saturated by 54%. The dominant fatty acids were 18:1, 16:0 and 18:0 with percentages of 38,32 and 12, respectively.

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Histological changes in rumen epithelium of reindeer calves during the winter season

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Abstract: Histological samples were taken from five different parts of the rumen from six reindeer calves in December (Group 1) and from six 1 year old calves in April (Group 2). A digitizer was used to measure the thickness of different cell layers in the rumen papillae. Individual variations were great, but some differences could be seen. The whole epithelium was thicker ($P < 0.05$) in animals belonging to Group 1. This was due to thicker *stratum granulosum* ($P < 0.01$) and other cell layers excluding *stratum basale.* Thickness ratio *stratum basale:* other cell layers was lower ($P < 0.05$) in Group 1. These results indicate that the epithelium of rumen of reindeer calves becomes less active during the winter.

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Neurological disorder in two moose calves (*Alces alces* L.) naturally infected with *Elaphostrongylus alces*

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Abstract: Two months old moose calves exhibiting neurological signs were videotaped, killed and necropsied. The parasite *Elaphostrongylus alces* (Steén et al 1989) was found epidurally along the meninges of the spinal cord, and in the muscle faciae of the thoracic and lumbar regions. Progressive inflammatory processes were present in the epineurium, perineurium and endoneurium. Accumulations of inflammatory cells, eosinophils, lymfocytes and macrophages, were found around eggs and larvae and frequently, around regional blood wessels. The neurological disturbances in the moose calves were pronounced, with locomotive abnormalities and ataxia. They showed weakness in the hindquarters, with uncoordinated and swaying movements of the hind legs. In addition, one of the calves was lame on the left forelimb. The muscles of the leg were visibly atrophic.

The lesions produced by *E. alces* at the lumbar nerve roots and in the *cauda equina* are suggested to be the cause of the clinical signs observed.

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Introduction

Elaphostrongylus spp. are parasitic nematodes associated with the central nervous system and muscle fasciae of a variety of cervids (Cameron 1931, Lyubimov 1945, Mitskevich 1958, Roneus and Nordkvist 1962, Kummeneje 1974, Krutzer and Prosl 1975, Mason et al 1976, Sugar 1978, Steén and Rehbinder 1986, Stuve, 1987).

Elaphostrongylus spp. have been knovn to cause neurologic disorders in wild and domesticated cervidae, as red deer *(Cervus elaphus* L.) (Borg 1979), maral deer *(Cervus elaphus sibiricus)* (Vsevolodov and Pryadko 1964) and reindeer *(Rangifer tarandus tarandus* L.). (Roneus and Nordkvist 1962, Kummeneje 1974).

Experimental infections have been performed in different cervids, as caribou *(Rangifer tarandus caribou)* (Lankester 1977), reindeer (Mitskevich 1964), red deer (Watson 1982) and moose *(Alces alces* L.) (Lankester 1977, Stuve and Skorping 1987.) Watson (1982) reported that *E. cervi* infection in red deer calves, produced exercise intolerance, blindness, hind limb incoordination and nervous disorders. A moose calf infected with L3-larvae obtained from caribou showed pronounced weakness primarily affecting the hindlimbs. The process progressed rapidly until the calf after four months was unable to stand up (Lankester 1977). Stuve and Skorping (1987) experimentally infected a moose calf with *Elaphostrongylus* larvae obtained from moose. The moose calf showed neurological disorders, but recovered

The present study is the first to report on a natural infection with *E. alces* in two wild moose calves with clinical manifestation of neurological disorders.

Material and methods

In May 1987 two approximately 11 months old moose calves, one male and one female, exhibiting neurological signs, were found in the county of Lapland in the northern part of Sweden. They were studied and videotaped before being killed and necropsied.

The brain and the whole spinal cord with nerve roots were removed and examined for *E. alces* and pathological lesions. Skeletal muscles were examined for the occurence of the parasite. Visceral organs were inspected macroscopically and microscopically. The brain, spinal cord, nerve roots, fasciae from skeletal muscles and visceral organs were fixed in 10% formaline and prepared for histology. Nematodes found were fixed in heated 70% ethanol and identified. Bone marrow fat content was examined according to the method of the Nordic Committee on Food analysis (1955).

Results

Neurological signs

Case 1.

The female calf appeared week, uncoordinated and indifferent to human proximity. She rose with difficulty, leaning her cheek against the ground in order to gain and support balance (Fig 1, 2). When standing, her hind limbs were shivering, unsteady and weak, and the lumbar region was lowered (Fig 3).

When rising and standing on her carpal joints, she had difficulties to lift the hind part of her body with the hind legs. She was able to rise to a standing position only by supporting herself against a tree. When standing the hind legs were notably weaker than the front legs, and the left hind leg was often abducted. The calf put most of her weight upon her front legs when walking with unsteady swaying movements of the hind quarters and a broad gait (Fig 4). Forced to move, she lifted the forelimbs abnormally high and brought them down in a stamping fashion. She easily stumbled over when handled or even when walking on slightly uneven ground. The calf did not seem to be mentally affected and was alert.

Case 2.

The male calf was observed in an area of approximately 50 m^2 that was totally browsed. Like the female calf he appeared weak, uncoordinated and indifferent to disturbance. In attempts to rise he often remained in a position of a "sitting dog". He was lame in his left forelimb, which had atrophic muscles (Fig 5). When standing the body weight was mainly supported by the right forelimb and the left hind limb. The left front leg was frequently adduated (Fig 6). When forced to turn, the animal's hind quarters swayed even while standing on both hindlegs (Fig 7, 8, 9). He frequently stumbled over when moving (Fig 10, 11, 12, 13). The hind leg gait was abnormally broad (Fig 6). The calf seemed to be aware and alert.

Gross pathological findings

In both calves several adult *E. alces* were found epidurally in the lumbar region of the spinal canal and in the cauda equina. In the male calf, parasites were also located epidurally in the thoracic region. The presence of *E. alces* was caracterized by hemorrhage and oedema in the surrounding tissues.

Parasites were also found in the fasciae of the thoracic and lumbar muscles without surrounding reactions. The bone marrow fat content was low (0.01%; 3.5% respectively), and both calves were emaciated.

Histopathological findings

In the connective tissue surrounding the spinal cord, close to the nerve roots, aggregates of mainly mononuclear leucocytes around blood vessels were a common finding. The inflammatory reaction was generally characterized by oedema, hemorrhages and infiltrations by lymfocytes, plasma cells, eosinophiles and macrophages. Signs of intensive phagocytosis were seen as macrophages were partly or completely filled by detritus masses.

The inflammatory changes in the meninges often extended to the spinal nerve roots. Granulomas were observed around eggs and larvae. They were surrounded by a thin capsule of connective tissue. Infiltrates by mainly lymfocytes, were frequently found to extend into the nerve tissue, invading the epineurium, perineurium and endoneurium.

Discussion

The locomotive abnormalities with symptoms of ataxia, as incoordination, swaying of the hindquarters, broad and stamping gait and a certain amount of hypermetria suggest paralysis of ascending proprioceptive nerve fibers.

It is known that the long proprioceptive nerve fibers in the spinal cord and in the dorsal ganglia are those to be injured first by compression. (de Lahunta 1977).

The extent of the inflammatory reactions strongly indicates the possibility of a compression of the nerve fibers by hemorrhages, oedemas, granulomas and perivascular cuffings, causing the described functional nervous disturbances. Due to the circumstances during the examination of the animals, paralysis due to compression of efferent nervfibres can not be excluded as the spinal nerves, carry both afferent and efferent nervfibres. The locomotive disturbances described, might also be explained by the lesions shown in the epineurium, perinerium and endonerium, of the spinal nerves.

The epidural location of the nematodes and the inflammatory changes, as seen in moose, differs from that in other cervidae, where the parasites and the histopathological changes are found in the subdural and the subarachnoidal spaces (Roneus and Nordkvist 1962, Polyanskya 1963, Pryadko et al 1963, Mitskevich 1964, Barus and Blazek 1973, Prosl and Kutzer 1980). Whether the locomotive disturbances described in these two cases are solely due to the nervous tissue lesions, or partly caused by inanition and exhaustion, is difficult to evaluate.

It is thus necessary to perform experimental studies in order to obtain more conclusive data on the neurological effects of infestations by *E. alces* in moose.

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Fig. 1. Female moose calf rising with difficulty.

Fig. 2. Leaning her cheek against the ground to gain balance.

Fig. 3. Lumbar region is lowered.

Fig. 4. The gait is broad.

Fig. 5. Male moose calf with lame and atrophic left forelimb.

Fig. 6. Abnormally broad hindleg gait and the left frontleg adducted.

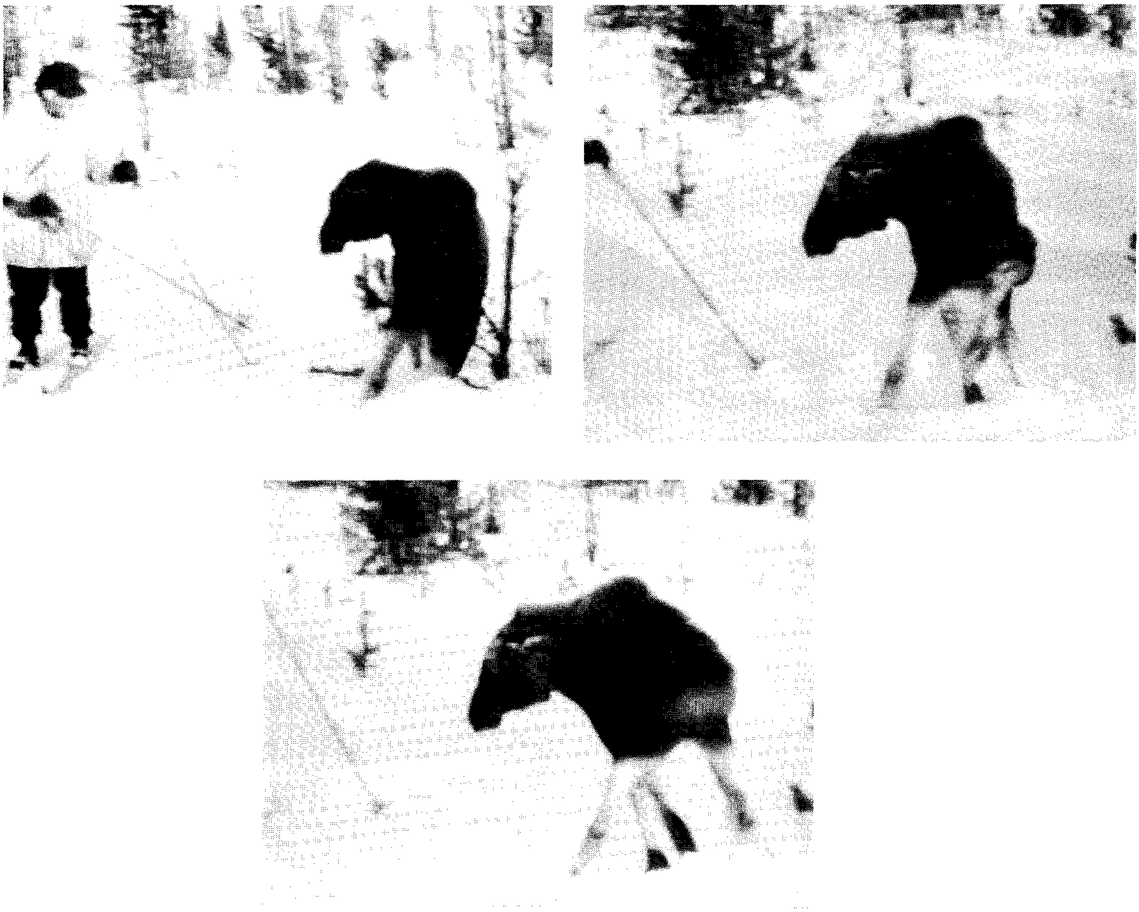

Fig. 7-9. Forced to turn, the hindquarter is swaying, weak and unsteady.

Fig.10-13. When moving, the male moose calfi frequently stumbled over.

Fetal sex ratios in caribou: effect of maternal age and condition

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Abstract: The fetal sex of 76 Peary caribou *(Rangifer tarandus pearyi)* and 421 barren-ground caribou *(R. t. groenlandicus)* were examined with respect to the ages and physical condition of their dams. There was a high proportion (61 and 62%) of female fetuses in young (1 -4 year) female of both subspecies and more males produced by older (>10 years) barren-ground caribou. Maternal physical condition did not affect the sex ratio of fetuses ($P > 0.05$) although indices of condition generally were higher in dams carrying female fetuses than those carrying males. A review of sample sizes required to show deviations from a 50:50 sex ratio indicates that some conclusions about the effects of age and nutritional state of dams on the secondary sex ratios of various species are not statistically sound. The observed sex ratio in caribou makes ecological and perhaps adaptive sense if old females are dominant to younger ones and that behaviour is conveyed to their male offspring.

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Warble infestations in some Canadian caribou and their significance

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Abstract: Warble fly larvae *(Oedemagena tarandi)* occurred in 97-100% of barren-ground caribou *(R.t. groenlandicus)* sampled in March from the Beverly herd. In December, they occurred in 98% of males and 75% of females. Larvae numbers increased up to several-fold from December to March. Within age classes, males generally were more heavily infected than females. Annual differences were small. Larvae occurred in 14 and 26% of two populations of Peary caribou *(Rangifer tarandus pearyi)* on the Canadian Arctic Islands. In them, incidences of larvae were unrelated to sex or age. Greater than average numbers of larvae in barren-ground caribou sometimes were associated with females in relatively poor condition and therefore less fecund. These results are discussed in relation to current hypotheses of the factors that affect warble infections.

Key words: condition, fecundity, *Oedemagena*, *Rangifer*

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Introduction

Data are scarce on the infestation levels of warble parasites in caribou in northern Canada. Kelsall (1975) reported frequencies and numbers of scars and holes in 312 museum hides of caribou obtained throughout Canada. The only other data for barren-ground caribou in north-central Canada were for 132 specimens from various seasons and herds (Kelsall, 1968), including Banfield's (1954) data.

Even less is known about the possible influences of the adult fly and its larvae (Dieterich and Haas, 1981) on the ecology of caribou. Tashnikov (1971) apparently found a positive relationship between numbers of larvae and fat reserves; Huot and Beaulieu (1985) the same for yearlings.

Several reasons were advanced to explain differences in infection levels among caribou herds and age classes and between the sexes. Climatic differences and migratory habits are most frequently implicated (e.g., Kelsall, 1975). Immunological factors are now believed to be important (e.g., Helle, 1980; Solomakha, 1990).

The purpose of this paper is to: (1) examine the effects of latitude, year, season, age, and sex on larval frequencies and numbers in a sample of 1 377 caribou; (2) explore relationships between infestation levels and fat reserves and fecundity; and (3) discuss the factors influencing the infestation levels.

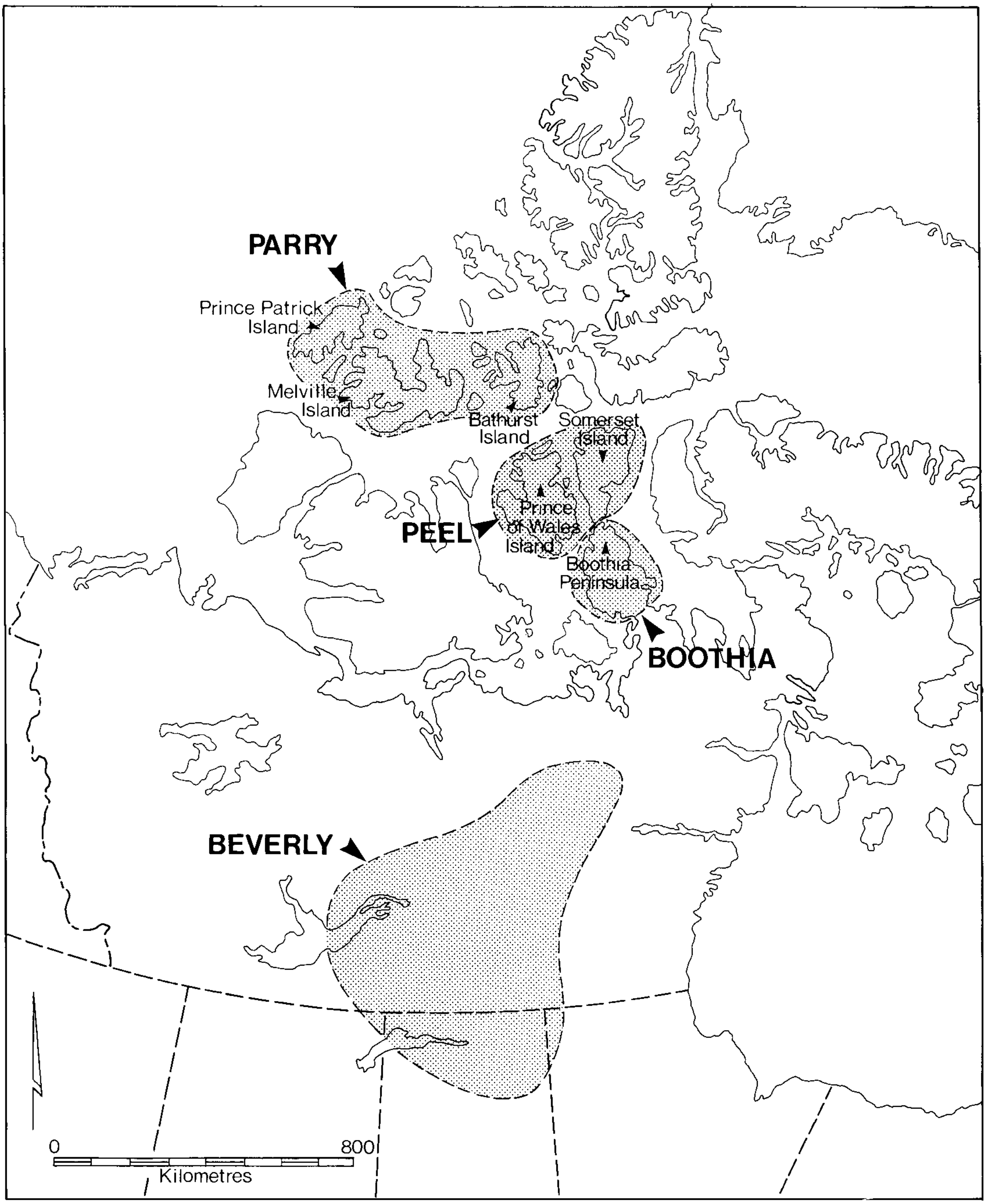

Fig. 1. Geographic locations of caribou populations mentioned in this report.

Methods

The barren-ground caribou were obtained from the Beverly herd in north-central Canada. The insular sample consisted of 203 caribou from the following locations: Boothia Peninsula (n=22); and Somerset (47); Prince of Wales (48); Bathurst (6); Melville (35); Eglinton (7); and Prince Patrick (38) islands. Data analysis revealed that three major groupings of locations could be made to increase sample sizes: Boothia Peninsula, Peel Islands (Somerset and Prince of Wales) and Parry Islands (all the others).

Hides of shot caribou were removed and the larvae or the larval holes were counted. Where numbers were >100, the larvae were counted only on one lateral half of the hide. Numbers of larval holes in hides were bilaterally similar (Kelsall, 1975).

Ages of caribou < 2 years old were obtained by teeth eruption criteria. The ages of older caribou were estimated from counts of lines in the stained cementum of the first incisor and first molar. Age is expressed to the next birthday, i.e., caribou 1 1/2 and 1 3/4 years old in December and March samples, respectively, are presented as 2 years old. Mean numbers of larvae included all caribou in the Beverly herd and only infected animals on the arctic islands. Data for warble larvae are highly variable, which precludes statistical differences between data sets unless the means are markedly different and large samples are available.

The grouping ofı age classes was based on homogeneity of means: generally > 2 years for numbers of warble larvae, back fat depths, and weight of kidney fat; > 3 years for body weight of females; and > 4 years for body weight of males and fecunndity of females. We used Kruskal-Wallis ANOVA and t statistics for comparisons among and between means and regression analysis to explore relationships among variables.

Observations of the behavior of barren-ground and Peary caribou were obtained over several summers. Included were general opportunistic observations and interval scanning of focal individuals.

Results

Occurrence and numbers of warble larvae in barren-ground caribou

Warble larvae were present in all but 1 of 238 males examined in March and 2 of 123 inspected in December. Larvae were present in 97-100% of females in March samples, 1980-87, and in 61-92% of females > 1 year old in December samples, 1982-86. In females > 2 years old, average numbers of larvae were 21, 12, 3, 6, and 8 in December, 1982 through 1986, and 33, 35, 39, 56, 37, 33, 33, and 37 in March, 1980 through 1987. Standard deviations were almost double the means in December and about equal to the March means, e.g., overall means 9.1 (SD 18.8) and 38.3 (SD 42.9). Lack of a statistical difference does not preclude a biological difference in the 1982-83 sample.

In pooled samples for each season (Table 1), the largest numbers of larvae were in males > 5 years old, followed by males 5, 2 and 1 year old, and finally by males 3 and 4 years old. In females, those 1 and 2 years old were most-heavily infected with marginal differences in older classes. There was an overall downward trend ($P<0.05$) with age of females in December and March. Comparable changes were found within winters.

Average numbers of larvae present in March were in some cases orders of magnitude larger than in December (Table 1). A correction for those with no warbles in December would reduce the difference marginally. Larvae were slower to develop in females than in males and slower in females > 3 years than in younger ones.

Occurrence and numbers of warble larvae in Peary caribou

Frequency of occurrence was unrelated to age or sex. E.g., Peel Islands (largest sample): females 1-4 years, 29% (n=34), females > 4 years, 28% (n=29); Boothia 79% for 14 females vs 63% for 8 males, Peel 29% for 63 females vs 26% for 27 males; and Parry 14% for 51 females vs 15% for 20 males. The overall incidences of warble larvae in all ages and both sexes were: Boothia 73% (n=22); Peel 28% (90); and Parry 14% (71). Warble larvae occurred in only 11 and 16% of 35 and 38 caribou sampled on Melville and Prince Patrick islands, respectively. There was a general increase in warble numbers in infected caribou aged 1-4 years on Boothia Peninsula but sample sizes

Table 1. Frequency of occurrence (percent) and mean numbers of warble larvae under the skin of caribou sampled from the Beverly herds in December (1982-86) and March (1980-87).

	Numbers of warble larvae							
Sex/age	December				March			
(yr)	Freq. %	Mean	SE	n	Freq. %	Mean	SE	n
F 1	100	18.8	4.1	5	100	124.7	14.1	29
M 1	100	65.3	14.0	15	100	118.7	18.3	20
F 2	92	23.7	4.1	26	100	114.2	11.6	59
M 2	100	47.6	6.4	26	100	171.1	16.1	57
F 3	87	14.1	3.0	30	98	45.7	5.1	82
M 3	95	18.4	2.8	42	99	93.1	9.4	90
F 4	61	5.8	1.5	38	97	46.2	5.0	61
M 4	100	25.9	5.2	24	100	80.8	10.3	28
F 5	84	12.2	7.2	25	98	28.3	3.8	56
M 5	100	77.0	22.0	10	100	145.5	43.7	20
F 6-8	76	10.5	2.5	58	97	36.1	3.8	153
F 9-11	59	4.2	1.3	22	99	37.1	4.9	91
M > 5	100	147.7	49.1	6	100	222.6	36.4	23
F > 11	61	5.4	2.4	18	97	35.9	5.5	36
F > 3	70	8.2	1.5	161	98	36.8	2.1	397
M > 3	100	56.9	11.6	40	100	144.9	18.6	71
F > 4	72	9.0	1.9	123	98	35.1	2.3	336
M > 4	100	103.5	23.7	16	100	186.7	28.4	43

were small (Table 2). No such trend was present in Peary caribou on the Peel Islands except perhaps in males.

Numbers of larvae relative to condition in barren-ground caribou

Regressions of warble numbers and condition variables for each caribou produced no significant correlation coefficients. The test was unduly influenced by some extreme numbers of larvae. Kruskal-Wallis tests indicated nine significant relationships between warble number frequencies, in 25- and 50-unit intervals, and condition variables: in males and females 2 years old in December (back fat); in males 3 years old in March (weight); in males > 3 years old in March (weight and back fat); and in females > 4 years old in December (weight and back fat) and in March (back fat and kidney fat). Correlations were positive in females and negative in males.

Analysis of data for females 3-5 and >2 years old in the March 1986 sample (Thomas unpubl.) revealed significant ($P<0.05$) differences in back fat depths and kidney fat indices between those with greater than, and less than, the median numbers of warble larvae for those age classes. We pooled the data for all years and made similar comparisons using the mean

Table 2. Mean numbers of warble larvae in infected caribou, mostly *R.t. pearyi*, sampled from three areas of the Canadian Arctic north of 70°, 1974-79.

Age Class (yr)	Mean number of larvae (n)					
	Boothia Pen.		Peel Isl.[a]		Parry Isl.[b]	
	Females	Males	Females	Males	Females	Males
1	13(2)	4(1)	33(1)	5(1)	(0)	(0)
2	28(1)	42(2)	37(5)	18(2)	(0)	(0)
3	(0)	278(1)	29(2)	5(2)	(0)	(0)
4	53(2)	91(1)	36(2)	35(1)	(0)	(0)
> 4	10(6)	(0)	42(8)	153(1)	54(7)	47(3)
1-4	32(5)	91(5)	35(10)	12(6)	(0)	(0)
All	21(11)	91(5)	38(18)	34(7)	54(7)	47(3)

[a] Somerset and Prince of Wales islands.
[b] Bathurst, Melville, Eglinton and Prince Patrick islands.

Table 3. Physical condition variables in females having fewer than, and more than, the mean number of warble larvae in pooled samples in December, 1982-86, and March, 1980-87.

Age (yr)	Condition variable	December			March		
		<mean		>mean	<mean		>mean
2	Weight (kg)	61.1		62.9	60.3		64.0
3	Weight (kg)	74.0		75.8	77.3		76.1
>3	Weight (kg)	84.8	**	79.0	85.2	**	82.2
2	Back fat (mm)	8.1		4.5	3.9		4.3
>2	Back fat (mm)	14.9	**	7.6	15.5	**	11.9
2	Kidney fat (g)	56.6		43.5	55.8		57.6
>2	Kidney fat (g)	83.7	**	67.8	109.5	**	87.9

**$P<0.01$

numbers of larvae. The results indicated higher condition indices in females > 2 and > 3 years old with fewer than the mean number of warble larvae (Table 3). Sample sizes varied from 41 to 147 in December; from 133 to 349 in March. In males 1, 2, 3, 4, and >4 years old, the same condition variables were larger in those with more than the average numbers of larvae in 22 cases (2 significantly so), lower in 7 cases and equal in 1.

In samples from individual years, condition variables differed ($P< 0.05$) between those with more than, and fewer than, the mean number of warble larvae for the sample period in 20 of 36 cases (Table 4). The March 1981 sample was inadequate. The anomalous March 1984 sample was from a different component comprised of fatter and more fecund individuals compared with the December 1983 sample. A pooling of females > 3 years old produced significant back fat differences in all five December samples and in four of the eight March samp-

Table 4. Mean wights (kg) in < 3 year old and back fat depths (mm) and kidney fat (g) in 2 year old female barren-ground caribou with more than, and less than, the mean number of warble larvae in the sample period.

Month	Year	Mean no. larvae	Group vs. $\bar{x}$	Weight n	Weight mean	Back fat n	Back fat mean	Kid. fat n	Kid. fat mean
Dec	1982	21.6	<	27	81.4	28	9.3	31	74.4
			>	7	79.6	7	5.6	7	73.6
Dec	1983	8.8	<	16	82.6	18	16.0	18	95.5
			>	11	79.3	15	9.7	15	76.9
Dec	1984	2.3	<	30	86.1	32	20.1	32	88.1
			>	7	85.7	12	15.2	12	63.0
Dec	1985	4.3	<	29	86.9	32	14.9	30	83.4
				12	80.3**	15	8.7	15	56.8
Dec	1986	6.8	<	19	83.8	22	12.5	22	86.1
			>	8	78.9**	13	7.2	13	79.4
Mar	1980	31.7	<	7	79.7	13	4.9	11	68.7
			>	7	80.3	11	3.3	11	64.2
Mar	1982	36.3	<	30	84.9	32	16.7	31	107.4
			>	22	84.5	26	16.5	24	88.3
Mar	1983	53.3	<	45	81.3	52	11.5	49	94.8
			>	24	76.5**	30	6.1	30	72.3
Mar	1984	30.7	<	60	85.4	66	18.3	66	118.5
			>	17	86.5	24	20.5	24	119.9
Mar	1985	34.2	<	57	88.7	74	19.8	72	126.2
				32	87.1	37	16.2	37	103.4
Mar	1986	32.8	<	50	86.6	58	13.0	58	104.3
			>	25	81.4**	31	8.8	31	79.1
Mar	1987	35.0	<	23	81.2	26	10.7	27	100.7
			>	11	77.0**	14	8.1	14	75.4

**P <0.01

les; equivalent differences for kidney fat occurred in three of the December samples and in five of the March samples.

Warble larvae and fecundity of barren-ground caribou

There was no relationship between fecundity and average numbers of warble larvae in December and in March using the sample means for females 3, 4, and > 4 years old in individual collections. In five of six samples obtained in March, the mean numbers of larvae in females > 4 years varied from only 31 to 34; the pregnancy rate varied from 76 to 98%.

We selected age groupings where the means were similar and compared numbers of warble larvae in pregnant and nonpregnant females (Table 5). Two differences were significant and the trend towards fewer larvae in pregnant fe-

Table 5. Numbers of warble larvae under the skin of pregnant and non-pregnant, female, barren-ground caribou sampled in December (1982-86) and March (1980-87).

Age class (yr)	Month	Numbers of warble larvae					
		Pregnant			Not pregnant		
		$\bar{x}$	SE	n	$\bar{x}$	SE	n
2	Dec	20.0	16.0	2	24.0	4.4	24
3	Dec	11.3	2.5	17	17.7	6.0	13
4	Dec	4.8	1.6	29	8.0	4.3	8
<4	Dec	8.4	2.2	102	12.8	4.0	18
2	Mar	109.9	18.4	8	114.8	13.1	51
3	Mar	40.5	5.0	61	60.6	13.3	21
4	Mar	40.1	4.3	49	71.1	16.7	12
<4	Mar	31.9	2.3	297	59.3	9.3	38

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

males was consistent.

Warble fly avoidance behavior in barren-ground caribou
One observed strategy was to find escape habitat such as sand dunes, to disassociate from other caribou, and to lie still, preferably in a depression, until discovered. Then the caribou runs at full speed in an attempt to lose the fly. Occasionally the caribou stops and quickly lies down. One cow that "flopped" 10 m from an observer was breathing at 110 cycles/min. Cows will temporarily disassociate themselves from their calves in an attempt to avoid flies.

A second strategy common with adult bulls is to stand in about 0.5 m of water, ripple the skin and shake the body whenever a large fly comes near, stompe the legs if a fly attempts to land on them and swing the head back in an attempt to pin the fly against the legs or body. It may then run at full speed for up to 1-2 km and sometimes circle back to the same pond. A third strategy is to stand with the head lowered almost to the surface, usually over sand or in a meadow.

Early in August, when harassment by mosquitoes and warble files overlaps, several caribou may stand together. The warble fly is highly active only on certain days and especially on warm, sunny afternoons. By about 1800 hours (in late July-early August) the attacks cease and the caribou regroup and move away from the escape terrain to feed.

Discussion

A definite relationship was demonstrated between numbers of warble larvae and condition variables in adult (>2 years), female barren-ground caribou. The degree of fatness in turn affected fecundity. Why a trend in the opposite direction exists in males is unknown. Males that expose themselves to more flies in their summer movement patterns may be selecting better feeding conditions, e.g., more optimally following gradients of plant phenology. Parturient females have evolved movement patterns that enhance the survival of their calves.

Our data suggest that harassment by the fly is more important than reactions caused by the larvae. This conclusion is based on similar physical condition differences in December and March between those with more and less than the mean number of larvae. Larvae were small and not numerous in December. Further, the average number of larvae in March is only moderately high and large numbers (200-400) occur in a small proportion of the young (<2 years) of both sexes and in adult males (>3 years). Cause and effect remain unresolved. The likely explanation is that both factors are involved, i.e., that severe fly harassment reduces fat gain in the summer and leaner caribou are more susceptible to having eggs laid on them by the fly.

Infestation levels of warble larvae in caribou appear to be related to at least five factors: (1) climate; (2) caribou density; (3) migratory behavior; and (4) avoidance behavior in caribou; and (5) intrinsic immunological factors. Caribou morphological differences (Kelsall,1975) and the timing of pelage replacement are other possible factors.

The progressively lower incidence of larvae in the Beverly, Boothia, Peel Islands and Parry Islands populations (Tables 1 & 2) implicates climatic and density factors. Summer temperatures and caribou densities also decrease progressively in the series. Mean number per infected female caribou did not vary as much as the percent infected. Climate appears to be the more important of the two because some low density southern populations of woodland caribou *(R.t. caribou)* have large numbers of larvae (Kelsall, 1975). The warble fly appears to be near its distributional limit on the Parry Islands where the maximum temperature seldom attains 13-15°C, the quoted threshold for activity (Brejew, 1956), and sunny days are few.

The later migration of adult males in spring and early summer may explain why they have the largest numbers of larvae (Table 1). They may encounter flies emerging from larvae dropped from earlier migrants. These temporal relationships are consistent with the earlier development of larvae in males versus females (Table 1) and the slower development of larvae in older females versus younger ones (old females are believed to migrate the earliest). This factor explains the large numbers of larvae in relatively sedentary caribou such as those in the Rocky Mountains (Kelsall, 1975). Movement distance from larval shedding areas influenced infection incidences in reindeer in Norway (Folstad and Nilssen, 1990).

The avoidance behavior of caribou to warble flies includes pronounced changes in group size and tactics by individuals. There is a sharp decrease in group size from mid-July to early August. Avoidance strategies for mosquitoes and warble flies are opposite in terms of caribou group size (Roby, 1978). The individual is the optimum unit in avoiding warble flies as indicated by observations of behavior. Some of this behavior obviously has a genetic basis. A learned component might explain some of the variation in larval numbers and the relatively high numbers in caribou up to 2 years old.

A gradual acquisition of immunity to warble larvae also is consistent with the higher numbers of larvae in young caribou of the Beverly herd (Table 1). Solomakha (1990) revealed that antibodies to warble larvae were transferred from the dam to the fetus and via the milk to the calf, The absence of any age-related relationship with warble numbers i Peary caribou is consistent with lower intrinsic resistance in the less frequently infected subspecies.

This review points to the complex nature of the subject. Phenomena can be explained by more than one factor in most cases. For example, the decline in warble numbers with age in females (Parker, 1981; this study) can be explained by differences inmovement patterns (time of infection), avoidance behavior, and acquired immunological resistance. We suggesst that all of the discussed factors are implicated and their relative contributions may vary regionally.

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Effects of running and immobilization on blood constituents in the reindeer.

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Abstract: Reindeer have regularly to run long distances in round-ups which may also involve immobilization or transportation in lorries. To evaluate the round-up stress accumulation of some metabolites in the blood 64 free-living animals were studied, divided into 8 groups in connection with slaughtering. Animals in two groups were forced to run at 15 km/h^{-1} for 4 h, and in two groups for 8 h. Two groups ran for 8 h and were then allowed to rest 16h. One group was immobilized and transported in a lorry for 4 h. The haemoglobin concentration or red cell count did not vary in any group. The catecholamines showed minor changes. Sodium, magnesium, potassium, calcium or inorganic phosphorus did not change. Blood glucose was lower in exercise groups than in the control or immobilization group. ASAT and ALAT increased in the exercise groups showing a tendency to recover after exercise and increased in the immobilization group. Alkaline phosphatase increased in all test groups as did HBD and urea. Amylase increased in the excercise groups. Creatine phosphokinase increased during the exercise and immobilization period but normalized during the recovery period. Creatinine increased in all groups. Ammonia concentration was lowest in the immobilization group. Body temperature increased after prolonged (8 h) exercise only. In conclusion, the liver enzymes increased during exercise and immobilization. Changes in creatine kinase were most prominent and returned to normal during the recovery period.

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Reindeer Management and Utilization/Predation/Behaviour

Key note address:

Reindeer in the USSR: problems of protection and rational use

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Abstract: There are approximately 2.2 million domestic and 1 million wild reindeer in the USSR today. It is unlikely that the number of domestic reindeer will increase further but there is a tendency for further growth in several large populations of wild reindeer. All middle-sized and small populations of wild reindeer need protection. During the whole initial period of penetration and adaptation of man to the north, the life of ancient inhabitants was closely linked to hunting wild reindeer. Neolithic relics of North Eurasia witness the wide distribution of a relatively monotonous Stone Age reindeer hunting culture. Domestication of reindeer began not less than a thousand years ago. Large-scale reindeer husbandry developed only 300-400 years ago and prospered for about 200 years. Social changes impeded its development after the 1950s, resulting in the restoration of wild riendeer herds.

Key words: distribution, number, migration

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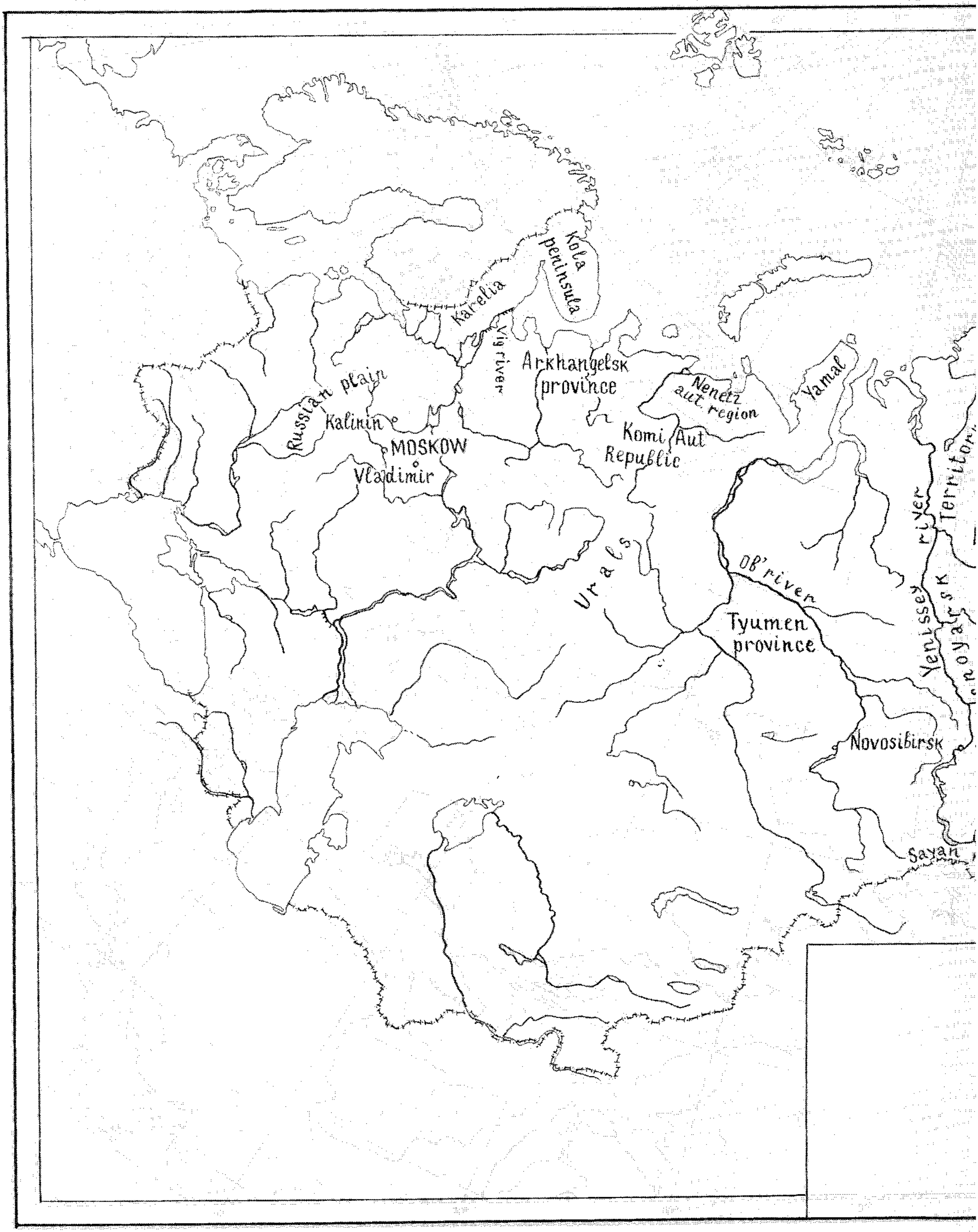
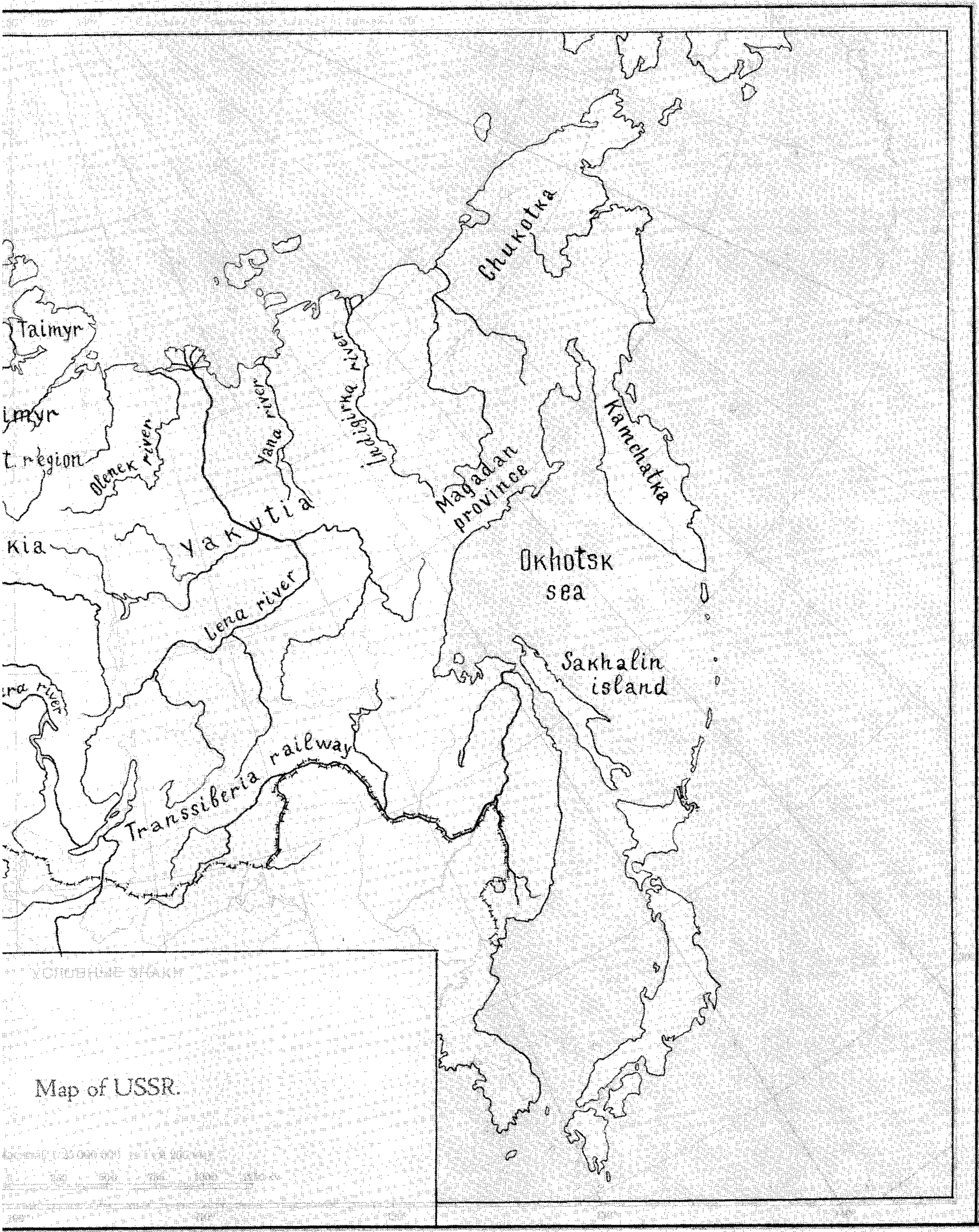
Introduction

Management of reindeer is complicated by the fact that both in the USSR and in Eurasia as a whole the species occurs in two forms; populations of wild reindeer and herds of semi-domesticated ones. These two forms use the same habitats and occupy practically the same ecological niche in the tundra and taiga ecosystems. Effective management, however, is impossible where both wild and domesticated reindeer occur together on the same ranges. Hence an urgent problem arises. What is preferable; development of reindeer husbandry or protection and rational use of wild reindeer populations? This problem is both acute and complex. In addition to the economic value of the animals, their great ecological and cultural significance as well as the interests of conservation must be considered.

The main ecological distinctions between the two forms of reindeer are as follows. First, wild reindeer (especially tundra forms) are nomadic and undertake long migrations. Domestic reindeer also migrate but over much shorter distances. Keeping these animals within strictly


Kola peninsula
Karelia
Vig river
Arkhangelsk province
Nenetz aut. region
Yamal
Russian plain
Kalinin
MOSKOW
Vladimir
Komi Aut Republic
Urals
Ob' river
Tyumen province
Yenissey river
noyarsk
Territor
Novosibirsk
Sayan



Map of USSR.

Taimyr
imyr
t region
Olenek river
Yana river
Indigirka river
Chukotka
Kamchatka
Magadan province
Yakutia
kia
Lena river
Okhotsk sea
Sakhalin island
ra river
Transsiberia railway

limited areas, especially within fences, is quite contrary to the genetically consolidated ecological and physiological characterictics of the species.

Secondly, wild reindeer eat much less lichen than domestic ones. Dependence on lichens is a secondary phenomenon linked with the first stages of domestication. Lichens do not provide full nutrition for reindeer. They are rich in carbohydrates but very poor on protein and relatively poor in vitamins. Lichens for reindeer are, according to their chemical composition, analogous to root crops for cattle. When reindeer feed on lichens alone they have to draw on their reserves of important nutrients; protein, calcium and phosphorus. As a result physiological starvation occurs even though the animals eat well; starvation ceases when they begin to consume green vegetation. Lichens cannot support reindeer all the year round, even though the animals like them very much.

The natives of the north domesticated reindeer using this ecological "lichen factor". It was easier to feed reindeer on the ranges rich in lichens, where it was both more convenient to pasture them as well as being easier to retain them at the same place. As a result, populations of domesticated animals, formed over many centuries, prefer lichen habitats and lichen feeding.

Lichens are often only an accessory component of the diet of wild reindeer. This makes wild reindeer much more ecologically flexible than domestic ones. Wild reindeer, with less specialized nutrition, can use a large variety of foods and are therefore capable of exploiting the tundra and taiga more fully than domesticated reindeer.

Domesticated reindeer can manage with only a small portion of lichens in their diet or even without them. For example, domesticated reindeer introduced on to subantarctic islands have successfully colonised ranges without lichens. In the north-east of the USSR a special form of domesticated reindeer, the so-called "kharghin", has been bred successfully almost without lichen feeding.

The conflict between wild and domesticated riendeer has developed during last 300-400 years, simultaneously with the development of large-scale reindeer husbandry in North Eurasia.

During the initial period of penetration and adaptation of man to the north a special circumpolar hunting culture arose which relied mainly on hunting wild reindeer. One can say with certainty that here, on the edges of Eukumene, the man lived in close contact with wild reindeer. The norther peoples depended almost completely on this animal. Traces of this hunting culture existed until the beginning of the 20th century among the Nganassana (Taimyr).

The initial number of wild reindeer in the USSR is unknown but it may have reached 5-7 million in the period before the development of reindeer husbandry. Reindeer husbandry developed probably not less than a thousend years ago but it remained relatively small-scale and important chiefly for transport until the 17th century. Large- scale reindeer husbandry began to develop in the 18th century. In the 17th - 18th centuries there were probably never more than one million domesticated reindeer in Russia but large-scale reindeer herding began to force out wild reindeer form the beginning of the 18th century. The number of wild reindeer diminished sharply.

At present (1988) there are about 2.2 million domesticated reindeer in the USSR and about 1 million wild ones. Numbers of semi-domesticated reindeer have stabilized or even declined during the last decades. At the same time wild reindeer populations have increased rapidly; from 200-250000, in 1961-1962 to one million today. At present there is a tendency of further growth of wild reindeer number in the USSR. It is unlikely that the number of domesticated reindeer will increase much more, mainly for socio-economical reasons.

Reindeer herders live either a nomadic life in tundra and taiga or use the so-called "shift method" in which individual herders go to remote ranges only for short periods before changing with one another. In the case of the "shift method" the herdsmen's families remain in their settlements for a considerable time. Neither method conforms with modern social demands or with the standard of life which the native inhabitants of the North now expect. Consequently, the reindeer husbandry is now suffering from an acute shortage of labour.

Geographical distribution and number of wild and domesticated reindeer in the USSR

The historical distribution of wild reindeer in the USSR was considerably more extensive than it is at present. In the past wild reindeer inhabited the whole taiga zone from the tree line to the zone of dense taiga forests. The abundance of wild reindeer is now considerably reduced thorughout much of their former range anc especially in the European part of the USSR At the end of the 10th century, wild reindeer existed southwards to the latitude of Moscow and Vladimir and in the vast bogs of the Kalinin province.

At preset wild reindeer are found only locally in European USSR, in the Urals and in isolated spots within their former areas in most parts of West Siberia. In West Siberia wild reindeer were formerly found southwards to Novosibirsk. In East Siberia and in the Far East the southern limit of their area remains unchanged. Wild reindeer occur locally in the mountains in the south of Siberia. In the large territory near the economic zone of the Transsiberian railway wild reindeer have vanished completely. None of the changes in their distribution in the forest zone of the changes in their distributin in the forest zone of the European part of the country are due to competition from semi-domestic reindeer but are, instead, the result of direct extermination, of excessive hunting and of loss of habitat.

Wild reindeer disappeared almost completely in the tundra and forest-tundra zones of the north as it was here, in the European and West Siberian tundras and Chukotka that the largest centres of reindeer husbandry was found. These centres were thus responsible for the dissappearance of wild reindeer from West Siberia, Evenkia, Yakutia and in the taiga westwards to the Okhotsk Sea in the 18th and 19th century. And today, although reindeer husbandry is declining nearby everywhere the number of wild reindeer is still increasing either only very slowly or not at all owning to industrial development of the taiga zone.

The largest populations of wild reindeer in the USSR at present are in the northern part of Central Siberia (Taimyr) and in Yakutia. Zoologists traditionally distinguish Yakut populations from Taimyr ones, basing their division on the administrative boundary between Yakutia and Krasnoyarsk Territory. Actually the animal use a vast, common area streching 2500 km from the Yenissey in the west to the Indigirka river in the east. The distribution of wild reindeer is not continuous here at present, especially in Yakutia where reindeer husbandry is more developed. About 300 years ago, when there was no large-scale reindeer husbandry east of the Yenissey, this Chukotka area, was particularly important for wild reindeer. However, the area was not occupied by reindeer permanently during summer in the tundra zone but when they went on long migrations to winter ranges in forest-tundra zone and northern taiga subzone. To the east of the Indgirka river Chukchi reindeer husbandry forced wild reindeer practically completely out. In tundras of Yakutia only small populations on wild reindeer remained.

The biggest wild reindeer population in the USSR today is the Taimyr one. According to recent aerial census data this population comprises more than half a million animals. During the last 25 years the population grew 5 times and has probably now reached close to its maximum. This is a migratory population, preforming an annual roundtrip of 1000 kilometers. The main summer ranges and calving grounds of this immense herd are in the western Taimyr. The winter ranges are in northern taiga subzone of Eastern Evenkia. Recently, Taimyr wild reindeer have started to penetrate in to adjacent regions of Yakutia in winter, and now some times as many as 300 000 animals pass the winter here.

Until relatively recently it was thought that wild reindeer migration routes, calving grounds and winter ranges were constant. However, it now appears that reindeer change their summer and winter ranges, as well as routes ofimigration quite regularly. By changing ranges they preserve their food resourses and use the vast territories of the north more rationally.

The changing pattern of range use by groups of animals within the limits of a population area is called by us a "kaleidoscopic effect". This may occur annually, when reindeer change their ranges on a small scale, or, more rarely, on a large scale, when a herd changes its winter or summer ranges by moving into an adjucent geographic region (for example, from Evenkia to Yakutia). This phenomenon can be related to the so-called "pendulous fluctuations" of changing migration routes and wintering grounds (Syroechkovski, 1975, 1986). The "kaleidoscopic effect" is charactristic for all populations of reindeer, especially large herds. It is a remarkable adaptation by the animals to severe natural conditions of the north. Only with a such behaviour can reindeer successfully use the poor ranges of the north, grazing vast territories without destroying their food supply and thus accumulating the mighty biological potential of one big, mobile population. The famous Taimyr herd is one such population.

Knowledge of the spatial dynamics of herds is very important for reindeer management and forms the basis of recommendations for the rational use of ranges. Failures in the organization of reindeer hunting can be avoided, given adequate knowledge. Great failures took place in game management in 1985-1986, for example. For many years tens of thousends of reindeer were killed at crossing points over the Pyassina river in Taimyr during the migration with no account being taken of possible pendulous fluctuations of the herd. Eventually, and especially in 1986, the animals moved east, away from their ordinary routs, and buildings specially equipped for processing and storing their carcases were left far from the routes.

Many historical facts indicate that migration routes are labile. In the years when reindeer "did not come" (i.e. changed their migration routes) ethnic peoples of the north, e.g. Nganassans (Taimyr) and Yukaghirs (Northern Yakutia), starved.

There is no significant conflict between wild and domestic reindeer in Taimyr at present. Taimyr and adjacent Evenkia have never been regions of large- scale reindeer husbandry for economic-ethnographical reasons. Between 1965 and 1970 there were approximately 120000 domestic reindeer here but today there are only 20000 animals. The decline was due partly to changes in the lifestyle of the reindeer herding people and partly to compentition with wild reindeer. Taimyr natives own approximately 30 000 domestic reindeer. Most of these occupy ranges on the Ghydan peninsula (Tyumen province), on the left bank of the Yenissey. Wild reindeer are no longer able to reach the left bank because their migration is cut off by ice- breakers which navigate as far as Dudinka along the Yenissey all the year round.

The second major area occupied by wild reindeer in the USSR is Northern Yakutia. Here there is a signigicant conflict between wild and domestic reindeer. At present there are about 150 000 wild reindeer and about 130 000 domestic reindeer in the Yakutian tundras. The number of domestic reindeer is not increasing. Wild reindeer occur in several separate populations which formerly occupied the tundra of the north-east USSR.

The number of wild reindeer in Yakutia increased to 180 000 by 1975. Biological prosperity of these herds is shown by their high annual rate of increase (up to 12%). The animal here began to be harvested from the early 1970s but the shooting, in contrast with Taimyr, was not organized well. The shooting was carried out by people specialized in reindeer husbandry not in hunting, as in Taimyr. These people had little sympathy for wild reindeer and their increase in numbers stopped as a result of irrational, unreasoned hunting. The number of wild reindeer in Yakut tundras could theoretically have reached 350 000 - 354 000 by 1985 and ultimately 500 - 600 000 owing to an average annual rate of increase of these populations of up to 10%. Under such circumstances there would have been almost twice as many wild tundra reindeer as domestic reindeer in Yakutia. However, this is not the case owing to the irrational hunting.

Yakutia is the second largest zone of habitation of wild reindeer after Krasnoyarsk Territory. There are 250 000 tundra and taiga animals here. The current estimate of 100 000 wild taiga reindeer is not reliable because aerial census of the Yakut taiga populations has not been carried out properly. Numbers seem to be overestimated.

The reindeer husbandry in USSR is concentrated at present in the tundra and forest-tundra zones - mainly in regions where wild reindeer are absent or rare. The greatest area of reindeer husbandry in the USSR (and in the World) is situated in the north-east of the USSR, within the limits of Chukotka (Magadan province), Koryak autonomous region (adjacent districts of Kamchatka) and the north-west Yakutia. There are more than one million domestic reindeer in this area. The second great centre of reindeer husbandry is in the northern part of west Siberia and in the tundras of the north Russian plain. There are approximately 700 000 domestic reindeer here, mainly within the limits of Tyumen and Arkhangelsk provinces and Komi Autonomous Republic. Five ethnic groups are involved in large scale reindeer husbandry in the USSR today. In the North-Eastern region there are mainly Chukchi, Koryaks and Yakuts. In the Europe-west Siberian region there are mainly Nenetzs but also some Komis.

Circumpolar culture of wild reindeer hunters

The traditional view that the life of native peoples of the North is closely connected with reindeer husbandry is true only for the relatively recent past. It was not like this before. The adaptation of the ancient inhabitants of the north was closely connected with wild reindeer hunting. Reindeer provided food, clothes and shelter. Literally speaking, man moved north side by side with reindeer following the retreating ice. Both penetrated the cold steppes, tundra-like landscapes and sparse forests of the Holocene when these were still populated by mammoths and hairy rhinoceros.

The period of populating the north lasted many thousands years during which northern peoples were largely dependent on wild reindeer. They migrated with these herds, they made long-lasting camps in places where migrating animals gathered and where it were possible to arrange mass hunting. In autumn and spring the ancient hunters killed a lot of reindeer often at the river crossings, and stored the meat. The places of the mass hunts were considered scared and were carefully protected. Natives did not scare reindeer and they did not kill more animals than they could store. There was ecological equilibrium between Nature and Man.

The origin and formation of the culture of reindeer hunters is poorly studied and remanis controversial among archaeologists and ethnographers. First the tundras of the old world were populated. Then, 11 - 38 000 years ago, Man penetrated through the Bering Strait to North America. Siberia was populated during the epoch of a highly developed hunting culture of the upper palaeolith which formed in north eastern Europe and east of the Urals. It is from here that the most ancient inhabitants of northern Asia moved east and according to academician A.P. Okladnikov, "made their fires for the first time on the banks of the great Siberian rivers - Ob', Yenissey, Angara and Lena". There is recent archaelogical evidence from the Taimyr of a non-ceramic culture of wild reindeer hunters dating from as early as the IV-III th millenia B.C.

Unfortunately, neolithic petroglyphs with images of hunting the wild reindeer are unknown to the continental part of north Siberian but they are relatively numerous in Fenno-Scandia, espicially Karelia, where many images of reindeer an reindeer hunting were found of the shores of Lake Onega and the Vyg river. Similar petroglyphs have recently been found in the Kola peninsula and on rocks in Chukotka.

All these facts witness that the tundra and the taiga were inhabited by stone age hunting cultures long before the formation of the present peoples and nationalities of north Eurasia. The ethnogenesis of these tribes is not clear but, according to many ethnographers, neolithic relics in northern Europe and west Siberia are assosiated with ancient inhabitants of the western Urals. The Yukaghirs of east Siberia and Chukotka may be related to the neolithic inhabitants of that area.

The neolithic relics of north Eurasia witness the wide distribution of a relatively uniform wild reindeer hunting culture on the enormous territory of the Old World and North America.

The domestication of reindeer began probablay two thousand years ago in wester Eurasia. However, the ecological equilibrium between Man and wild rindeer began to be destroyed only with the arrival of a large scale husbandry approximately 300 years ago. At the same time, the Nenetzs, who were reindeer breeders, populated the east european and west-Siberian north, ousting out both wild reindeer and the pre-Samodiy tribes which were dependent on them. Reindeer hunters like the Yukaghirs remained in the northern part of east Siberia until the 17th century when the warlike Chuckchi began to force them out form the east. The Chukchi quickly developed a large-scale reindeer husbandry. Evenks and Yakuts advanced from the taiga and the Central Yakut steppes in the south and south-east and defeated the Yukaghirs owing to the superiority of their weapons; they had lances and arrows with iron heads, and their fighting detachments rode on reindeer. The wild reindeer was the enemy of reindeer husbandry, and this was the main reason for its rapid extermination. Reindeer husbandry, however, prospered only for about 200 years. Social factors impeded its development after the middle of the present century and as a result wild reindeer herds have begun to increase again.

Not all northern natives developed reindeer husbandry. The native peoples of North America never domesticated reindeer. In north Eurasia two peoples, the Nganassans and Yukaghirs, out of eight or nine ethnic groups which once inhabited the tundras and the northern sparse forests maintained their dependence on wild reindeer almost to the present day. We do not know why these two peoples never developed reindeer husbandry. These peoples, remnants of an encient circumpolar hunting culture declined simultaneously with the disappearance of big herds of wild reindeer.

The protection and conservation of wild reindeer is urgent and closely connected with the principles of their use. At present all middle-sized and small populations of wild reindeer in the USSR i.e. those with <5000 animals need protection. Thus, all our wild reindeer populations, except the Taimyr and big North Yakutian ones, need protection. The following populations are endangered and should be included in the Red Data Books of the USSR and the RSFSR: Sayan; Sakhalin island; Central-Chukotsk; the taiga populations of west Siberia and the Eurpean part of the USSR. The latter belong to the subspecies *Rangifer tarandus fennicus* which is carefully protected in Western Europe. A unique population of wild tundra reindeer of the Nenetz autonomous region also needs the urgent conservation. This is the only remaining population of the typical tundra subspecies of reinder described by Linneus in 1758.

Ecological-economic basis for rational use of wild reindeer

We have estimated that the maximum potential number of wild and domestic reindeer in the USSR is 5-7 million animals. If numbers of domestic reindeer are held constant, then the number of wild reindeer can be trebled. So we have good reason to develop a specialized economy based on the rational use of wild reindeer: a "the hunting reindeer husbandry" (Syroechkowski, 1982, 1986).

Such management is already in practice. In 1971 a State hunting farm "Taimyrski" was organized to exploit the Taimyr population. Later on the State farms of Taimyr joined the wild reindeer hunting. Between 1971 and 1981 these farms shot more than 600 000 wild reindeer yielding 25 000 tons of meat. Nevertheless, the population continued to grow. We estimate that it is possible to shoot up to 100 000 wild reindeer annually without damaging the population. It would therefore be possible to produce annually, in addition to meat, 100 000 skins, 400 000 kamusses (skins form reindeers' legs which are valued highly by hunters) and a lot of stuff for souvenirs and pharmaceutical industries, provided the population is managed rationally. The present output of Taimyr hunting reindeer husbandry is many times greater than the output of domestic reindeer husbandry in Taimyr, Evenkia, west and central Siberia. This does not mean that the development of domestic reindeer husbandry in Taimyr and Evenkia must be stopped. Domestic reindeer husbandry is necessary for the native peoples for food, for transport etc. Hunting wild reinder, however, is also an important traditional activity which can provide native peoples with a stable prosperity.

The hunting reindeer husbandry cannot be considered as a purley economic pursuit. It must be closey connected with the native peoples of the north. The chief objective of hunting reindeer husbandry is social and economic progress of thier lives. Economic advantage must not prevent the main social objective.

Successful exploitation of wild reindeer requires a herd of not less than 40 - 50 000 animals. Such a herd can yield about 4 - 5 000 reindeer annually and will soon pay for itself.

Hunting husbandry involves more than just organization of a hunt. Ecological monitoring of the herd is indispensible. This must include regular census of reindeer in all seasons; trackin the migration, preferably by aerial radiotelemetry and mass marking of animals; control of the sex- and age-structure of the population; control of morpho-pysiological state of animals and veterinary control. In addition it is important to control the state of the habitat and to develop a system for its protection and restoration.

Co-existence of wild and domestic reindeer on the same ranges is impossible. Where this already occurs we propose a geographical division of the two forms of husbandry according to the "preference foci" of habitation of wild and domestic animals. "Preference foci" are determined by taking into account social, ecological and ethnographical factors. The recognition of a definite region as a "preference focus" for hunting reindeer husbandry does not necessarily require the complete absence of domestic reindeer. The obvious "preference foci" of hunting reindeer husbandry is Taimyr with the adjacent parts of Evenkia, and the Lena-Indigirka part of Yakutia. The obvious "preference foci" of domestic reindeer husbandry are Chukotka, Koryak and Nenetz autonomous regions, Yamal and the rest of Yakutia.

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Aquisiton and management of reindeer herd data

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Abstract: Obtaining and maintaining accurate records of reindeer *(Rangifer tarandus)* herd data has become a necessary tool for efficient herd management. A computerized record keeping and reporting system was developed due to the speed which which animals were seen at the seasonal handlings. Custom software was written using the dBASE III+ data management package to handle the special needs of herd record keeping. The software was then compiled using the Clipper compiler. The resulting program and data were implemented in ramdisk on a Toshiba 3100 microcomputer. Data structures were carefully chosen to provide for recording of tag identification, sex, age, body weight, abnormalities, disease testing, and treatments for each deer. Additionally, fields were provided to maintain records of ongoing biologic experiments. A report generation program was written to provide a current herd status report to the herders.

Key words: Alaska, U.S.A.

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Introduction

Reindeer herding in western Alaska has long been identified with the traditional culture and subsistence lifestyle of the Eskimos in that region. The introduction of current technology and advanced animal husbandry practices to this native industry has provided a benefit to the Eskimo herders while not detracting from their lifestyle. The use of helicopters has increased roundup efficiency, and the administration of parasite treatments has greatly enhanced overall herd health. Also, as will be seen in this paper, the computer is playing an important new role in the area of herds record keeping and management strategies.

Computers have been used as a means of data storage and retrieval for many years in such diverse activities as criminal identification and librarary book circulation (Cotterman,1974). The need for accurate record keeping on a large scale in the Alaskan reindeer industry became apparent when herds became so large that handwritten records became unmanagable. The first use of computers in the Alaskan reindeer industry as a record keeping tool was in 1982 when the University of Alaska's Reindeer Research Program implemented a portable-computer based system for field use as part of an applied resarch project (Kokjer, Ray-Landis, and Dieterich, 1985). Generators or a 12 volt battery/transformer combination were used for a power source. This system was designed around commercially available computer hardware and software that suited the needs of this application. Portability and processing speed were the major criteria to be fullfilled. Tag identification numbers, sex, age, weight, vaccinations, treatments, physical abnormalities, and serologic results were among the data that were entered into the computer for each deer.

By 1986 a hardware and software upgrade was needed to keep pace with increasing demands on the system. A new generation of IBM compatible, portable microcomputers with extremely fast processors had become available at the time and, in additon, the Ashton-Tate[2] company had just released its latest data management software package, dBASE III+. Three Toshiba[3] portable microcomputers, dBASE III+, and a compiler were purchased. These upgrades together with rewriting the system pograms provided the speed and memory capabilities to handle large amounts of data while maintaining the portability necessary for field operations.

Data aquisition and data entry

The first step in the processing of any data for analysis is the aquisition of the data itself and its entry into the computer. During a reindeer corralling, as many as 100 reindeer can be handled in an hour making the job of aquiring and recording data for each reindeer very time critical. Often only a few seconds are allowed for observing the animal and recording the data. As well as recording new data for each reindeer, old data records for the animal are displayed so that a history for an animal may be viewed. Thus, full advantage must be taken of the speed potential of the given computer hardware and software in order to match the speed of incoming data and to search for and display the old data. By choosing how the data is stored in the computer and by using process known as program compilation, the response time of the system can be greatly improved.

In any computer system, access to a database (an organized collection of data) that is stored on disk is typically 3000 times more time consuming than access to a database stored in computer memory (Ciminier and Adrianio, 1987) . While a program that manipulates a database is running, there may by hundreds of such accesses per minute. Therefore, if the database is stored in computer memory instead of disk while the program is running, a substantial decrease in access time can be achieved. An area of memory set aside for this purpose is known as a RAM (Random Access Memory) disk or ramdisk. A two megabyte extended memory package was added to the microcomputers that provided a large memory area to be used as a ramdisk.

Before running the program, the database for the selected herd is copied from disk to ramdisk. Then while the program is running, the database is accessed in the ramdisk and new data is added. When the program is finished, the updated database is then copied over the old database on the disk. This new copy is now the current version of the database.

If the program itself is also copied from disk into ramdisk, the processing speed can be further increased. The inherent risk in this process, however, is that if power is lost before the database can be copied from ramdisk back to disk the updates are lost and only the database that was originally on the disk before the program ran will remain. The upgraded system uses a R&D [4]12 volt to 110 volt power transformer with a low power alarm. When the source (a 12 volt airplane battery) drops below 12 volts, the alarm is tiggered allowing for several minutes to exit the program normally and save updates to disk.

In addition to using ramdisk as a storage area, the use of a compiler to convert the programming code into machine language greatly

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[3] Toshiba America, Inc., 9740 Irvine Blvd., Irvine, CA 92718 U.S.A.

[4] R & D Corporation, 1194 Pacific St., Suite 201, San Luis Obispo, CA 93401, U.S.A.

increases the overall response of the system. dBASE III+ is a powerful database management software package that contains a proprietary programming language capable of being compiled. In this initial form, this programming language is " interpretive" meaning that each line of programming code must be interpreted and converted separately to machine language while the program is running. Interpretation each line of code while the program is running is time consuming and delays the response of the system.

The process of compilation alleviates this problem in two ways. First, a compiler converts each line of code to machine language before the program is run so that the timeconsuming conversion process is eliminated. Secondly, compiled code takes up less memory space than interpretive code leaving more room in memory for the database (Coats, 1982). The Clipper[5] compiler was chosen because it is specifically designed to work with dBASE III+. By combining the use of memory as a storage area and running compiled programs, the response time of the system was greatly increased.

Database structure

Data entry programs that were written for the original system were modified to take advantage of the use of ramdisk and compilation in the upgraded system. The original database structure was not changed in order to simplify the modification process. The data for each herd was maintained in a series of files which together comprised the database structure.

The primary file in the database structure for a herd is called ANIMALS.DBF represents a reindeer and contains the ear tag identification number (tag id), sex, and birth year for that deer. This record is refered to as the header record. Each header record in ANIMALS.DBF contains a "pointer" called EXPTR which points to a record in another file called EXAMS.DBF containing the handling records for all the deer. The pointer is simply a number that indicates which handling record in EXAMS.DBF is the first in a series of handling records for a particular deer. Each record in EXAMS.DFB contains the date of a handling and the data observed and recorded for a deer for that date. The header record in ANIMALS.DFB also contains a number, NUMB, indicating how many handling records are recorded in EXAMS.DBF for a deer.

Another pointer in the header record is called NEWPTR and points to a record in a file called NEWRECS.DBF which contains the most recently entered data for a deer. Each record in NEWRECS.DBF contains the current handling date and the data observed and recorded for a deer for the current date. A database which maintains a series of files (EXAMS.DBF, NEWRECS.DBF) that are pointed to from another file (ANIMALS.DFB) is known as a hierarchal database (McFadden and Hoffer, 1985).

In addition to ANIMALS.DBF, EXAMS.DBF, and NEWRECS.DBF, two more files comprise the rest of the database structure. NEWANIMS.DBF is used to store handling records for animals that appear at a handling for the first time and thus are not in ANIMALS.DBF. FAWNS.DBF is used to store handling records for fawns only if they are handled in a separate area from adults. Each record in NEWANIMS.DBF and FAWNS.DBF has a format that is a combination of the header record format and the handling record format so that tag id, sex, birth year, and the handling data may be recorded into one record. NEWANIMS.DBF and FAWNS.DBF are part of the database structure but are not pointed to by any of the other files and are therefore

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[5] Nantucket Corporation, P.O. Box 3621, Culver City, CA 90230, U.S.A.

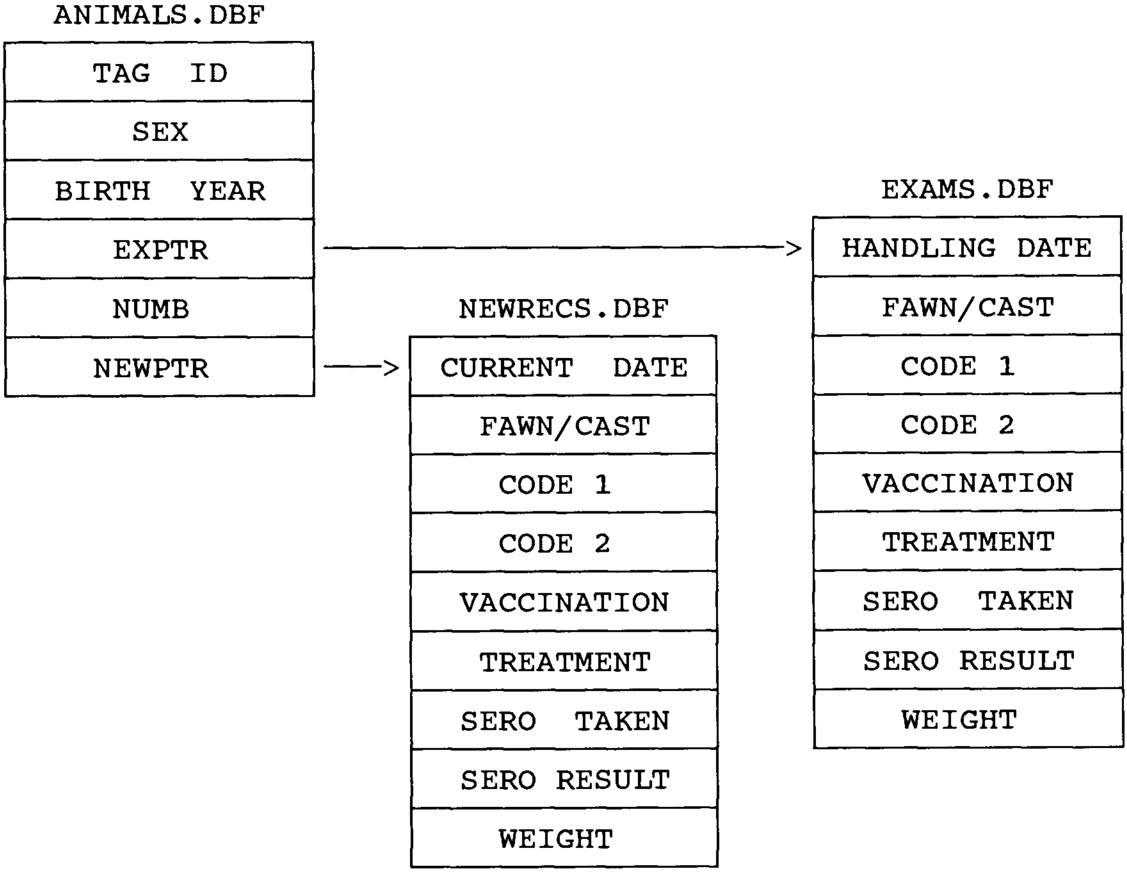


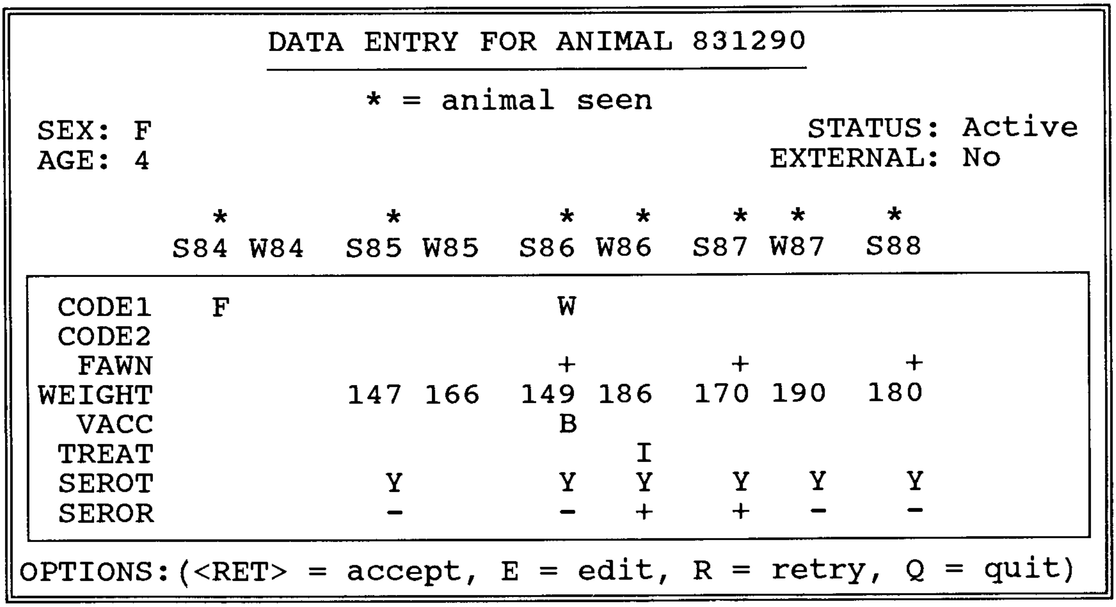
Fig. 1. Hierarchal database structure for herd data.

not part of the hierarchy. Thus, the five files, ANIMALS.DBF, EXAMS.DBF, NEWRECS.DBF, NEWANIMS.DBF, and FAWNS.DBF comprise the entire database structure for each herd database that is maintained in the system.

Data entry programs

Data entry programs that are run during a reindeer handling utilize the structures described above. As a deer is handled, it's tag id is called out and entered into the computer. ANIMALS.DBF is searched until the record containing the tag id is found. EXAMS.DBF is then searched for the handling records for that deer which are displayed on a formatted screen. If a tag id is searched for in ANIMALS.DBF and not found, the animal is considered to be a new animal (or maverick) and the new data is placed in NEWANIMS.DBF. There is no search process for fawns as the data for a fawn is by default placed in FAWNS.DBF. This process in the upgraded system takes about 1 second even for the largest herd databses (24,000 records or 6000 animals). This compares to 12 seconds in the original system. While a difference of 11 seconds per animal may not appear to have much impact in system performance, when compounded over a typical handling time of 12 hours, the differencd is substantial.

When the handling is complete,ANIMALS.DBF contains pointers to NEWANIMS.DBF and FAWNS.DBF contain data for any new animals and fawns that were seen. These files are ready to be merged into a single indexed master file called a relational database. A relational database is one in which sets of re-



```
                DATA ENTRY FOR ANIMAL 831290

                     * = animal seen
SEX: F                                       STATUS: Active
AGE: 4                                     EXTERNAL: No

           *        *        *   *    *   *    *
          S84 W84  S85 W85  S86 W86  S87 W87  S88

  CODE1    F                W
  CODE2
   FAWN                      +        +        +
WEIGHT             147 166  149 186  170 190  180
   VACC                      B
  TREAT                          I
  SEROT             Y        Y   Y    Y   Y    Y
  SEROR             -        -   +    +   -    -

OPTIONS:(<RET> = accept, E = edit, R = retry, Q = quit)
```

```
   S84: Summer 1984.
 CODE1: F = broken antler; W = Had warbles.
  FAWN: + = female had a bag
  VACC: B = vaccinated for Brucellosis
 TREAT: I = treated for warbles with Ivermectin
 SEROT: Y = a blood sample was taken and analyzed
 SEROR: + = blood test was positive;
        - = blood test was negative;
```

Fig. 2. Formatted data entry screen.

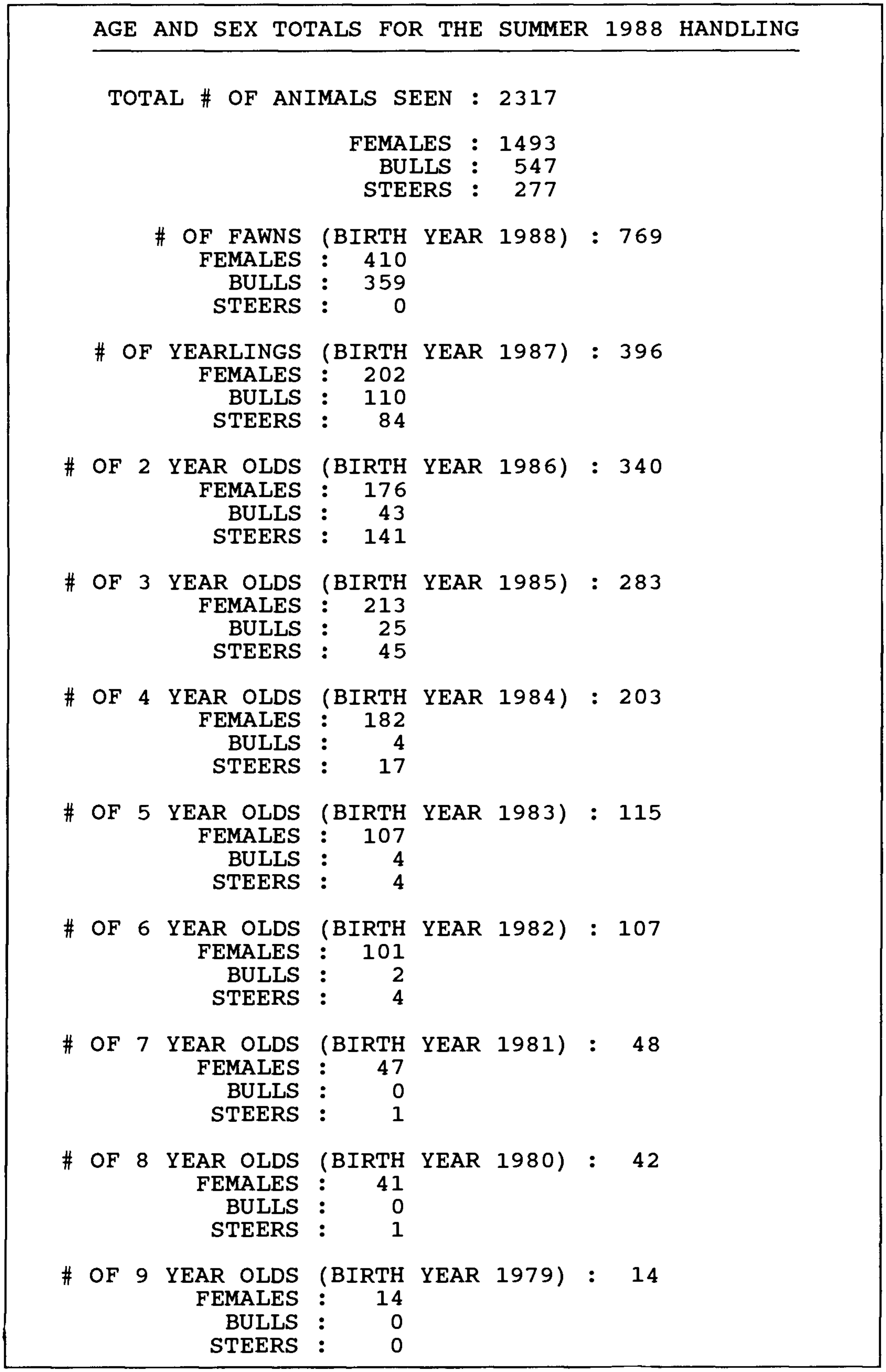
cords have a common relationship to one another (McFadden and Hoffer,1985). In the case of the indexed master file, the common relationship is the tag id. This indexed master file will be used for report generation and analysis.

Report generation

It is possible with the upgraded system to produce a report of the handling and a summary of the herd data within minutes after the last deer has been handled. This report contains information about the handling that just occured and produces a herd summary based on new data and data previously entered. In addition, a tally is generated which displays the number of animals seen at the handling. The tally is catagorized into sex and age classes.

Before a report can be generated, the five database files must be merged into the single indexed master file. This is done using the merge program. The first step in the merging process is to step through ANIMALS.DBF and obtain all of the old records for each deer. EXPTR is used to locate the first handling record in EXAMS.DBF for a particular deer and NUMB indicates how many records to obtain. The header record from ANIMALS.DBF is then combined with each of the handling records from EXAMS.DBF and appended to the master file. As a result, each record in the master file contains the tag id, sex, and birth year for a deer in addition to the handling data for a given handling date.

If a deer was seen at the current handling, the new record for that deer is obtained from NEWRECS.DBF and is appended to the master file as the last record in the series for that deer. Finally, the new animal records from



```
AGE AND SEX TOTALS FOR THE SUMMER 1988 HANDLING

  TOTAL # OF ANIMALS SEEN : 2317

                  FEMALES : 1493
                    BULLS :  547
                   STEERS :  277

     # OF FAWNS (BIRTH YEAR 1988) : 769
        FEMALES :  410
          BULLS :  359
         STEERS :    0

 # OF YEARLINGS (BIRTH YEAR 1987) : 396
        FEMALES :  202
          BULLS :  110
         STEERS :   84

# OF 2 YEAR OLDS (BIRTH YEAR 1986) : 340
        FEMALES :  176
          BULLS :   43
         STEERS :  141

# OF 3 YEAR OLDS (BIRTH YEAR 1985) : 283
        FEMALES :  213
          BULLS :   25
         STEERS :   45

# OF 4 YEAR OLDS (BIRTH YEAR 1984) : 203
        FEMALES :  182
          BULLS :    4
         STEERS :   17

# OF 5 YEAR OLDS (BIRTH YEAR 1983) : 115
        FEMALES :  107
          BULLS :    4
         STEERS :    4

# OF 6 YEAR OLDS (BIRTH YEAR 1982) : 107
        FEMALES :  101
          BULLS :    2
         STEERS :    4

# OF 7 YEAR OLDS (BIRTH YEAR 1981) :  48
        FEMALES :   47
          BULLS :    0
         STEERS :    1

# OF 8 YEAR OLDS (BIRTH YEAR 1980) :  42
        FEMALES :   41
          BULLS :    0
         STEERS :    1

# OF 9 YEAR OLDS (BIRTH YEAR 1979) :  14
        FEMALES :   14
          BULLS :    0
         STEERS :    0
```

Fig. 3. Age/sex totals for sample reindeer handling.

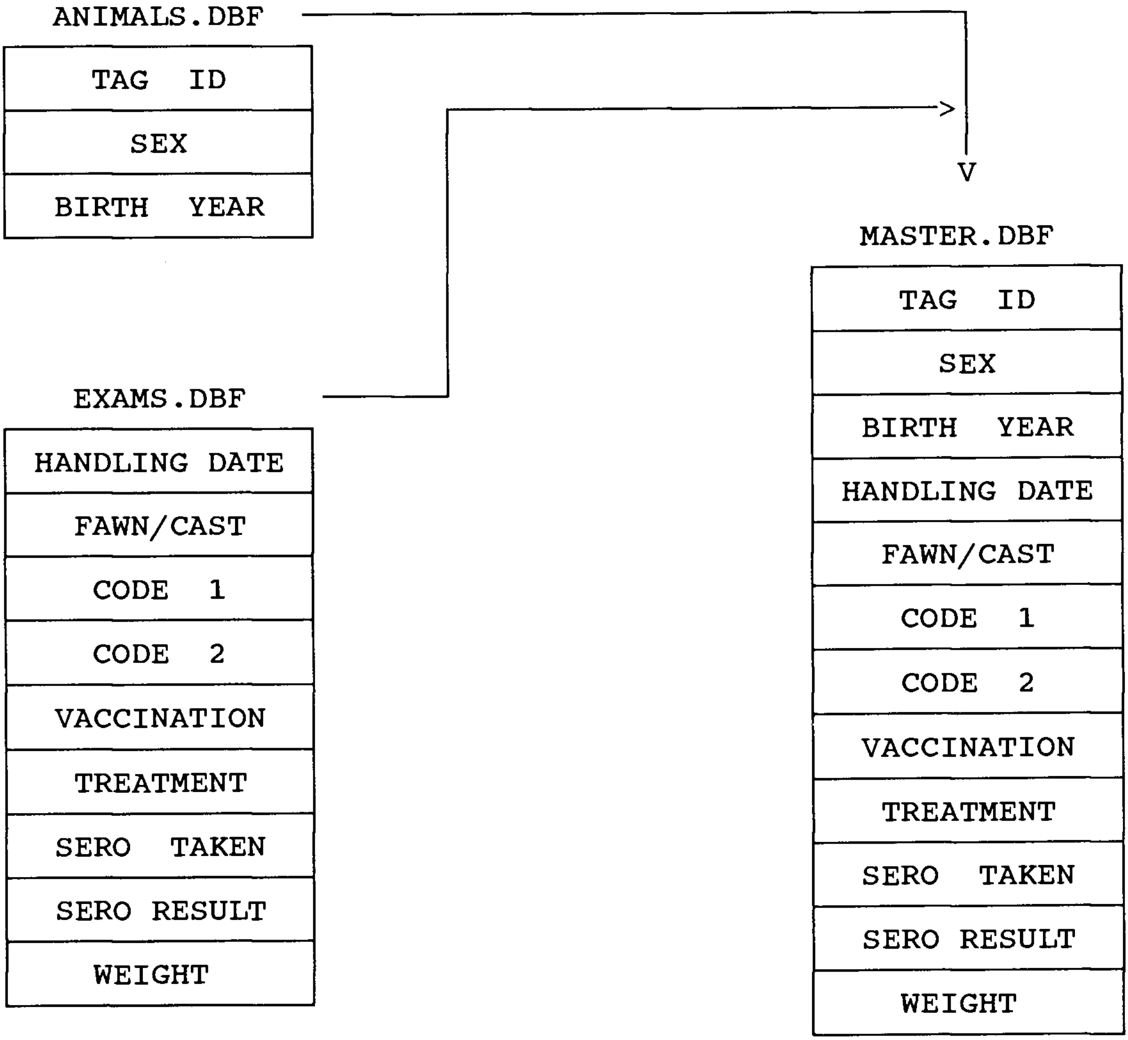


Fig. 4. Generation of master file from ANIMALS.DBF and EXAMS.DBF.

NEWANIMS.DBF and FAWNS.DBF are appended to the master file. The records from NEWANIMS.DBF and FAWNS.DBF contain both header information and handling information and are identical to the record format in the master file.

The master file is then sorted so that the tag id numbers and handling dates are in ascending order. An index file is generated using the tag id numbers as the key. The sorted master file and its associated index file represent the relational database for a given herd. The advantage in using a relational database instead of the hierarchal database is speed. In the hierarchal database, the data can only be obtained by following a series of pointers to different files. This is time consuming and for large databases the delay is critical.

The indexed master file is used to generate the handling tally and herd summary. Each record in the master file is examined by the program and information such as the number of fawns per 100 adult females, the number of bulls per 100 females, the number of females slaughtered, and the number of deer with injuries is extracted and printed out. This report can be great aid to applied research and a valuable guide for making decisions about herd management.

Conclusion

It is beyond the scope of this paper to discuss all of the variables and questions involved in creating a herd management strategy. There are a lot of factors such as market conditions for meat products and range utilization that make developing a comprehensive management strategy a complex process. Maintaining a database for a herd over several years and producing relevant informaton on a regular basis provides a valuable tool for analysis of herd dynamics. This is a job that the computer is particularly well suited for.

It is important to note that consistency in data collection and reliability of software and hardware are the two most important criteria in using this system to make decisions based upon the data. Handlings must be regularly attended by data collection personnel in order to maintain a continous record and the programs written must be proven to work correctly and produce reliable results. The hardware must not fail at critical moments (such as a disk unit "crashing" before the ramdisk can be copied back to it!). If these criteria are met, a computer based data aquisition and management system can be a valuable asset to research and herd management.

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The Evenkia reindeer and its rational use

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Abstract: In taiga areas of Siberia and the Far East the animals of the Evenkia breed are reared. Their quantity reaches more than 150 000 animals. These are the largest reindeer. Cows weight is 110-120 kg, mature males 150-170 kg that is 15-30% higher as compared with other breeds. Purposeful use of genetic potential of this area reindeer will be realized by means of development and introduction of scientifically grounded plan of pedigree work with this breed till 2000. Deterrents of reindeer rational use in this region are the traditional methods of reindeer management (free-range methods in summer-autumn period) which lead to annual large unproductive losses of animals, high barrenness of cows and reduction of stock. In this connection we have developed the more progressive technology of their management in the taiga region. This technology base is the constant controlled animals pasturing in winter period on unfenced ranges and daily controlled pasturing on fenced seasonal ranges during the rest period that secures the rational use of reindeer of the Evenkia breed.

Rangifer, Special Issue No. 3, 1990: 441

The inventory of reindeer pastures in Kaamanen Research Station and in Muotkatunturi co-operative in northern Finland

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Abstract: A project was founded in April 1987 to develop new and easily repeated methods to evaluate vast reindeer pastures. The study area is located in Muotkatunturi co-operative in the Forest and the Fell Lapland vegetation zones. The pine forest limit runs trough the area. In Muotkatunturi co-operative the density of reindeer is average 4.8 reindeer/km^2. Comparison of reindeer pastures was made between Kaamanen research station (75 km^2), on average 150 reindeer, and its surroundings (124 km^2). The training areas (24) were selected by using the areal photographs and the topographic maps. Most of the training areas (17) were in the pasture of the research station. Tree stand and undervegetation was inventoried by 20 quadrats. In Kaamanen 7 sample areas were very dry sites, 11 dry sites, 5 subdry sites and 1 sample was almost bare mountain region. Eleven training areas were subalpine birch forests and 12 Scotch pine forests. In the training areas the older, mature stands (38%) and young thinning stands (17%) were dominated. Dwarf shrubs was dominated in field layer *(Empetrum nigrum* ssp., *Vaccinium myrtillus, V. vitis-idaea).* The bottom layer was dominated by mosses *(Dicranum* sp., *Polytricbum* sp.) and hornlichens and *Cladina stellaris, C. mitis,* and *C. rangiferina.*

Rangifer, Special Issue No. 3, 1990: 443

Improvement of meat production capacity in reindeer farming

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Abstract: The poster describes the main activities in a joint Swedish-Norwegian research project. The ultimate purpose is to develope tools for individual production control and flock management in domestic reindeer production.

Key words: indentification system, recording, culling, selection, production parameters, flock dynamics

Rangifer, Special Issue No. 3, 1990: 445-447

Purpose

Meat production with free-ranging semi-domesticated reindeer *(Rangifer tarandus)* is practiced in the nothern forest and mountain areas of Scandinavia and Finland. The animals are kept in large flocks with little individual handling. Due to the management conditions mating and calving cannot be controlled.

The objectives of this joint Swedish-Norwegian research and development project are to:

(a) develop identification, handling and production recording systems to enable improvement of the animal stock and the production ability of the flock through culling and selection
(b) provide information in the biological production parameters of farmed reindeer on Scandinavia
(c) develop a simulation model for optimization of reindeer flock structure with respect to long range production capacity.

Identification system

Traditional ear marks (cuts) show only the ownership of the animals. A new system with a unique ID-code for every animal has been introduced. The code includes:

(a) country and district as a two-letter combiantion
(b) owner number within the district
(c) birth year both as letter and tag colour
(d) identity number (ID) within birth year
(e) sex given by even or odd ID-number

Table 1. Example on simulation results; meat production in three different flock structures:
A = mainly slaughter of 1.5 year old adults
B = mainly slaughter of calves
C = mainly slaughter of calves, less males in the flock.

	Flock structure		
	A	B	C
No. of animals			
males	400	400	250
females	600	600	750
Total losses			
males	65	64	63
females	85	84	105
No. slaughtered			
males	112	116	163
females	79	96	120
Meat production, kg/year			
males	3 884	3 958	4 804
females	2 497	3 007	3 759
totally	6 381	6 965	8 563

The code is intended for identification in the field and for use in computerized production recording. Totally 25,000 reindeer calves are tagged every year in Norway and Sweden at special gatherings in July-August at an age of 2-3 months.

A difficulty is that calf and dam cannot be caught together for identification. Therefore calves are first given provisional ID- collars and observed in the flock in order to identify the dam. After all calves (200-400 in each batch) have had their dams identified they are gathered again and given the permanent ear tag.

Females intended for breeding are given an additonal marking with a plastic collar at 1.5 years of age. The collars are labelled with their identity code in reflective material, which allows identification from long distances. The collars are vital for the identification of dams of calves.

Production recording

Important information for selection and management decisions are calving rates, weight gains of calves, weights of adult females and survival.

Data are collected in the summer gathering and slaughter gatherings in September and during November-December.

The information is assembled and stored in computerized data bases, allowing life-time production records to be retrieved for females, including the performance ofi their calves. For calves and young animals their growth performance and the dam's producing ability will be displayed.

Weighing equipment suitable for reindeer has been developed for the weight recording in field.

Culling and selection

High-producing winter flocks are maintained by culling at slaughter in the late autumn. Females are culled according to their predicted production ability the following year.

A culling index, that will include fertility, mothering ability and growth ability will be introduced for practical application. The information used is the previous calf crops and calves' survival and growth rates. Proper adjustments for female's (dam's) age and weight is required.

Calves are selected for production and breeding purposes on their own and dam's results. For practical application the information will be summarized in a selection index.

The objective of the culling and selection is to achieve a high phenotypic production ability and generate long term genetic improvements in vitality, fertility, mothering ability and growth capacity. The ability to build up enough body fat reserves for the winter is important.

Production parameters

The available information on the production biology of the reindeer is scarce compared with ordinary farm animals. However, efforts to improve this are being made by analysing data from the production recording. Vital information is for example:

(a) age effects on survival rates, weight gains and calving rates

(b) within age class relationships between female's weight and calving rate as well as the calf's size, survival and weight gain

(c) "genetic" and phenotyic variations in various production characters

(d) effects of flock structure (e.g. number and age of males) on calving rate in various female age classes.

Simulation of flock producing ability

A dynamic simulation model for the reindeer flock has been developed on the basis of preliminary production parameters.

The main purpose is to optimize sex and age structure with respect to the production capacity of the flock under different production conditions. The optimal structure determines the culling and slaughter policy.

Other questions of interest are the dynamic behaviour of a reindeer flock after changes in, for example, slaughter and management policies or due to severe losses during a hard winter season.

The simulation model also enables economic assessment of changes in production components, for example due to selection.

The model will allow the development of computerized calculation tools for future prediction of flock production. Such tools could be useful in the advisory service or for the reindeer owners themselves.

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Rangifer is dealing with topics about reindeer husbandry, reindeer biology and -pastures.
Articles can be of 4 types: original scientific articles, preliminary reports, summary articles or short notices.