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O B I T U A R Y

JOUNI TIMISJÄRVI

9.2.1947-15.3.2004

Jouni Heikki Timisjärvi died suddenly at his home in Haukipudas, Kello, Finland on the 15th of March 2004.

He was born on the 9th of February 1947 in reindeer herder's family which lived on the shore of beautiful Lake Timisjärvi in Posio. Timisjärvi's father was at one time director of the herders' co-operative of Timisjärvi.

Jouni Timisjärvi was a doctor of both medicine and surgery. He was one of the first teachers of the Institute of Physiology at the University of Oulu. His teaching career started in 1971 and he acted as both assistant professor and professor. He was an esteemed teacher and scientist who specialised in heart diseases and the history of medicine on which he was writing a book. Jouni Timisjärvi was an excellent, critical tutor of graduate students working on cardiac physiology at the University of Oulu.

Jouni Timisjärvi was a pioneer of reindeer physiology in Finland. His doctoral thesis, "The blood circulation of the reindeer", was completed in 1978. I completed my own doctoral study of condition and blood composition in reindeer under his tutorship. Timisjärvi was given the honorary title as the docent of physiology in the University of Oulu in 1985. He published more than 50 scientific papers, many of these concerning reindeer physiology.

Timisjärvi encouraged reindeer research in Finland. In spring 1977 we started the joint trips to the Kaamanen experimental farm owned by the Reindeer Herders' Association. Together we studied the growth and survival of calves and the development of their immune system. We also studied a variety of vital functions and aspects of the endocrine system of reindeer. Timisjärvi's expert knowledge was made good use of when planning and developing the Reindeer Station of the Finnish Game and Fisheries Research Institute into an international research station. He took part in many international meetings including meetings and other events organised by the Nordic Council of Reindeer Husbandry Research (NOR). The last mutual scientific meeting was the 11th Arctic Ungulate Conference in Saariselkä, Finland, where he acted as a member of the Scientific Committee and chairman of session on physiology.



Mauri Nieminen

11th Arctic Ungulate Conference (AUC)

The 11th Arctic Ungulate Conference (AUC) was organised by the Finnish Game and Fisheries Research Institute (RKTL) in Saariselkä, in the Heart of Lapland, Finland, 24-28 August 2003. The conference continued a series of ten conferences devoted to Arctic Ungulates, including five Reindeer/Caribou Symposia, two Muskox Symposia and three Arctic Ungulate Conferences. The series began with the 1st International Reindeer/Caribou Symposium held in Fairbanks, Alaska, in 1972. The 3rd International Reindeer/Caribou Symposium was held in Saariselkä, in 1982. First Arctic Ungulate Conference was arranged in Nuuk, Greenland, in 1991, and 2nd in Fairbanks, in 1995. The 10th AUC was held in Tromsø, Norway, in 1999. When returning to Saariselkä, we decided to call our meeting the "11th Arctic Ungulate Conference" to emphasize the tradition and continuity of this series.

Totally 160 delegates from 16 countries attended the Saariselkä conference and they presented more than 130 scientific papers. The scientific and social programme as well as the abstracts has been published in *Rangifer* Report No. 7, 2003.

The conference emphasized all aspects of the management and biology of arctic ungulates and especially disciplines traditionally not so well represented in this series of conferences, including animal health and welfare, predation, history and

multiple land use, management and marketing, and hunting and reindeer husbandry. So we invited key note speakers, most of who normally worked with arctic ungulates. Some of their papers are published in this volume. Some of the delegates' papers have already been issued in *Rangifer* Vol. 24, Nos. 3 and 4, 2004 and some will be published in next issues of the journal.

During the conference in evening programme, participants got information about Urho Kekkonen National Park and also about reindeer husbandry and tourism in Saariselkä area. Guided tours were made to the Sami museum, "Siida", in Inari and to the Reindeer Research Station of the Finnish Game and Fisheries Research Institute in Kaamanen.

The conference also included a Circumpolar PhD-Network in Arctic Environmental Studies (CAES) workshop.

The conference was sponsored by the Finnish Academy, the Nordic Council for Reindeer Husbandry Research and the Finnish Game and Fisheries Research Institute.

In the meeting 26 August 2003, the Executive committee of the Arctic Ungulate Society agreed, that the next conference will be held in the Republic Sakha, in Russia, in 2007.

Mauri Nieminen
Chairman of the Scientific Committee

Effects of reindeer density on vascular plant diversity on North Scandinavian mountains

Johan Olofsson & Lauri Oksanen

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Abstract: We studied the effects of reindeer grazing on species richness and diversity of vascular plants on dolomite influenced low alpine sites in the species rich northern part of the Scandes using 8 sites with different reindeer densities. Two sites were situated inside Malla Strict Nature Reserve, where reindeer grazing have been totally prohibited since 1981, and strongly restricted since 1950s. The six other sites were located in other species rich hotspot sites standardized to be as similar to the dolomite-influenced sites in Malla Strict Reserve as possible but varying in reindeer densities commonly found in the Fennoscandian mountain chain. Each site with a habitat complex especially rich in rare vascular plants (the *Dryas* heath – low herb meadow complex) was systematically sampled in four plots of 2 m x 10 m. The plots were divided to 20 squares of 1 m x 1 m, and complete species lists of vascular plants were compiled for each of the squares. The first DCA (detrended correspondence analysis) axis was strongly related to an index of reindeer grazing, indicating that grazing has a strong impact on the composition of the vegetation. None of the characteristics indices of biodiversity (species richness, evenness or Shannon-Wiener H') was correlated with reindeer density. The local abundances of categories consisting of relatively rare plants (Ca favored plants and red listed plants of Finland) showed significant, positive correlation with the intensity of reindeer grazing. We conclude that even though the density of reindeer has no influence on the total species richness or diversity of vascular plants, reindeer may still be important for regional biodiversity as it seems to favour rare and threatened plants. Moreover, our results imply that standard diversity indices may have limited value in the context of conservation biology, as these indices are equally influenced by rarities and by trivial species.

Key words: arctic, alpine, diversity, disturbance, grazing, *Rangifer tarandus*, vascular plants.

Rangifer, 25 (1): 5-18

Introduction

One of the established ecological principles is the Intermediate Disturbance Hypothesis (IDH), stating that for each habitat, there is an optimum level of disturbance, leading to highest plant species diversity by allowing the coexistence of both disturbance-adapted plants and plants adapted to various durations of transient dynamics initiated by the disturbance (Grime, 1973; 1979; Connell, 1978). As the optimum level supposedly depends on the

intensity of environmental stresses, the dominating impact of disturbance on local species diversity changes from positive to negative along gradients of decreasing primary productivity (Grime, 1979; Proulx & Mazumder, 1998; Austrheim & Eriksson, 2001).

Among the forms of disturbance where humans play a role, reindeer grazing is the most extensive form in northern Fennoscandia, influencing prac-

tically all parts of the area save some islands and coastal areas of northern Norway (especially in Nordland, see Bernes, 1996; Suominen & Olofsson, 2000). Given the prevailing view that arctic-alpine plants live in a stressful environment, where the intensity of disturbance that maximize diversity should be low, reindeer grazing have often been regarded as a negative factor that overexploits arctic-alpine habitats, decreases biodiversity and causes erosion (see Moen & Danell, 2003).

Studies on the impact of reindeer on Fennoscandian arctic-alpine nature have improved our knowledge on the impact of reindeer on the coverage of lichens (Johansen *et al.*, 1995; Ihse & Allard, 1995; Johansen & Karlsen, 1996; 1998; Allard *et al.*, 1998), on nutrient mineralization rate and primary production (Stark *et al.*, 2000; Olofsson *et al.*, 2001; Olofsson & Oksanen, 2002; Stark & Grellmann, 2002), on ground temperatures (Olofsson *et al.*, 2003) and on abundances of ground-dwelling (Suominen *et al.*, 1999a; Suominen *et al.*, 1999b) and galling (Olofsson & Strengbom, 2000; Herder *et al.*, 2004) invertebrates. Vegetation studies have corroborated the predictions of IDH in the context of lichen rich heathlands, which become overwhelmingly dominated by *Cladina stellaris* in the absence of reindeer, whereas only crustose lichens survive on the most grazed and trampled sites along reindeer fences. Highest diversity is found under intermediate grazing conditions, *e.g.* on fairly intensely used winter ranges, characterized by a species-rich mixture of fruticose lichens, cup lichens, crustose lichens and bryophytes (Du Rietz, 1925; Dahl, 1957; Helle & Aspi, 1983; Oksanen, 1978; Oksanen & Virtanen, 1995; Olofsson *et al.*, 2001; Väre *et al.*, 1995; Suominen *et al.*, 1999a).

However, there are few studies focusing on the effects of reindeer grazing on the diversity of vascular vegetation and on the flourishing of rare arctic-alpine plants, even though sustainable reindeer grazing, which promotes a high biodiversity, is an environmental quality objective of the Swedish Government for mountain areas (Swedish Environmental Protection Agency, 1999). Recall also that reindeer is a native herbivore in Fennoscandia, and that wild ungulates in arctic areas in North America often have been found to be resource limited and thus pronouncedly influenced the vegetation (Caughly & Gunn, 1993; Crête & Manseau, 1996).

Moreover, grazing pressure in the arctic may have been even higher in the evolutionary past than today (Zimov *et al.*, 1995). Thus, another view of the tundra is that it is an ecosystem where grazing has always been intense and where the survival of many currently rare plants may be critically dependent on the actions of the last arctic ungulate that has survived in Eurasia – the reindeer (see Oksanen, 1990; Oksanen & Ranta, 1992; Oksanen & Virtanen, 1997; Oksanen & Oksanen, 2000).

Most of the reported effects of reindeer grazing are from winter-grazed or year-around grazed areas, but reindeer also influences the vegetation in summer-grazed areas (Oksanen, 1978; Bråthen & Oksanen, 2001; Olofsson *et al.*, 2001; Moen *et al.*, 2003). In the context of protecting rare vascular plants, the impacts of summer grazing are focal, since our arctic-alpine rarities are found in the mountain chain, which is primarily used for summer grazing. The effect of summer grazing on biodiversity can be studied by constructing exclosures (Oksanen & Moen, 1994; Virtanen *et al.*, 1997; Moen & Oksanen, 1998; Virtanen, 1998; 2000; Bråthen & Oksanen, 2001) but this approach is so slow that impacts on biodiversity can only be inferred by extrapolation, based on initial stages of transient dynamics.

Old large-scale fences, constructed for non-scientific purposes, provide another opportunity. Results obtained by using them as makeshift experiments indicated that the diversity of vascular plants and bryophytes increases in some locations in response to moderate and sometimes even in response to extremely intense grazing by reindeer, while it in other locations species diversity does not differ between grazing regimes (Olofsson *et al.*, 2001). Unfortunately, such studies are burdened by design problems (*e.g.* fixed directions of grazing gradients). In this study, we have thus used a comparative approach in the context of the species-rich habitats of North Scandinavian mountains by treating the varying grazing intensity in the area as independent variable and patterns in plant species diversity as dependent variable.

The study area and outlines of our approach

Northernmost Fennoscandia is characterized by large variations in species richness, which is especially pronounced for arctic-alpine plants and for

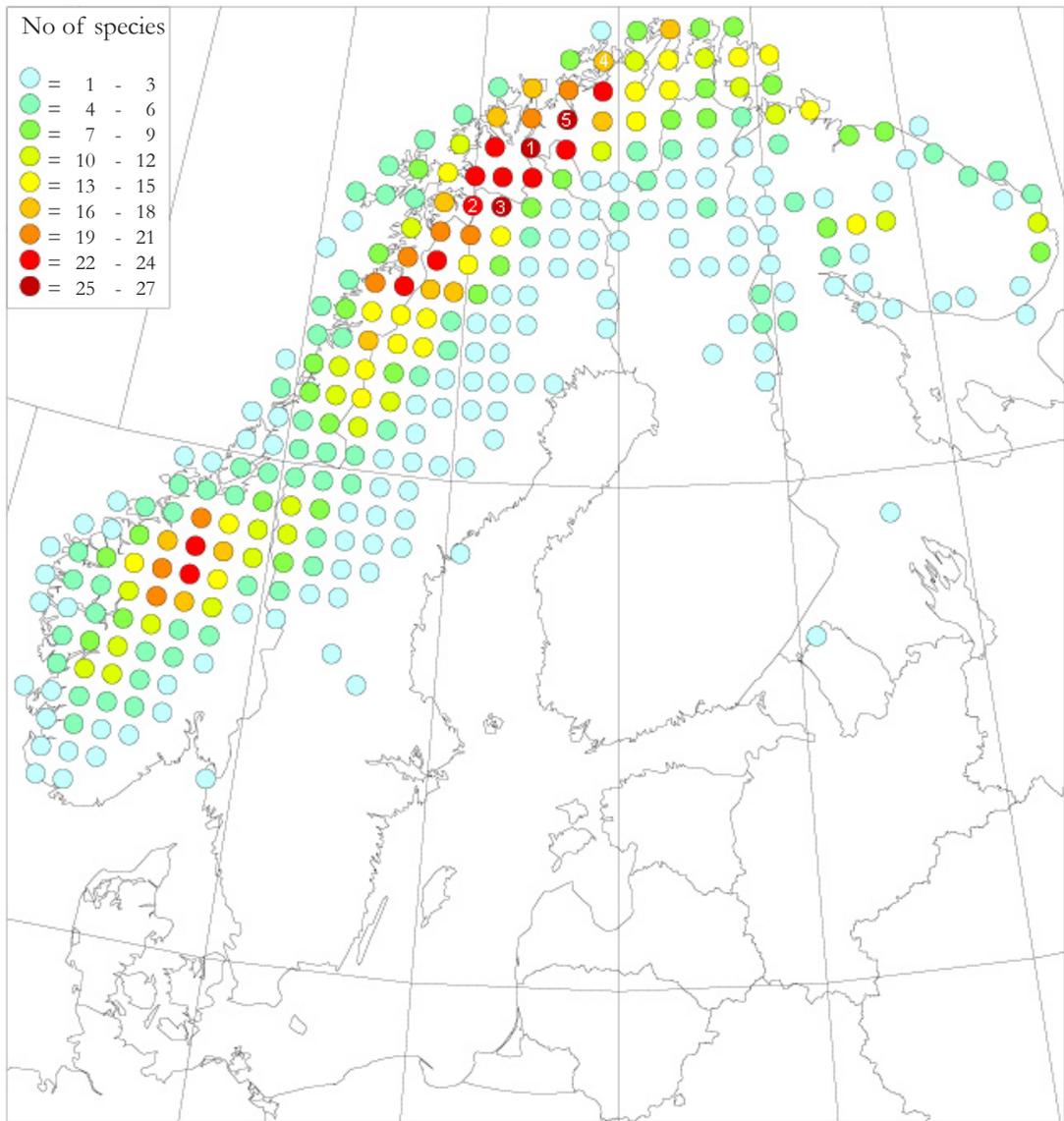


Fig. 1. Occurrence of lime favored arctic-alpine species in different northern grids of Atlas Florae Europaea (Jalas *et al.* 1972-99). The number on the maps refer to the following sites: 1. Pikku-Malla, Iso-Malla and Saana, 2. Geadgečorro and Boazuvárri, 3. Vággečohkka, 4. Jeahkkir, 5. Jávrjoaivit.

plants favoured by lime rich bedrock. To illustrate the general pattern in an objective way, we have compiled data on the occurrence of arctic-alpine phanerogams (criterion: Fennoscandian localities presented by Hultén (1971) are primarily above the timberline) and phanerogams noted as lime favored by Mossberg *et al.* (1992) in different parts of the northern parts of Fennoscandia and Kola, in accordance to the currently available part of Atlas Florae

Europaea (Jalas *et al.*, 1972-1999), now covering the phanerogams of in the beginning of the customary systematic rank order (including families Brassicaceae, Papaveraceae, Crassulaceae and Saxifragaceae; species without known localities north of 68°N were excluded).

The pattern emerging from this data set is clear indeed. The occurrence of arctic-alpine plants that are lime-favored (Fig. 1) is strongly concentrated to

a relatively small 'hot spot area' in the eastern and interior part of the mountain chain, stretching from the Abisko area in northernmost Swedish Lapland to Altafjord in Finnmark, Norway. The highest species richness is found on the grid encompassing the surroundings of Lake Kilpisjärvi (Gilbbisjávri), but values obtained for surroundings of Torneträsk (Duortnosjávri) and Reisadalen (Raisávžži) are only marginally lower. The underlying reason for the floristic richness of the area is the rich occurrence of dolomite in the lowermost and oldest overthrust plate of the Scandinavian mountain chain (Du Rietz, 1924), and the relatively continental climate, which counteracts leaching.

The use of this hot spot area for reindeer grazing is variable (Bernes, 1996). In Sweden and in northernmost Norway, the migratory herding system allows relatively high reindeer densities, as the lichen grounds are saved from unnecessary trampling. Densities on summer ranges are thus typically of the order of 5 to 10 reindeer per km². On the Finnish side, where grazing is stationary, reindeer densities are only 1 to 2 animals per km². Moreover, the Finnish side harbors the Malla Strict Nature Reserve, located right in the 'hottest' part of the hot spot – on the western shores of Lake Kilpisjärvi. One of the main scopes of the reserve was to protect the rich flora against the supposedly negative impacts of reindeer husbandry (Montell, 1914). Hence, reindeer grazing in the reserve has been restricted since early, 1900s, though the ambition to reduce reindeer grazing and associated human activities was not especially successful before the late, 1950s (Itkonen, 1948; Kokko, 1969). In, 1981, reindeer grazing in the reserve became totally forbidden, but even afterwards, some grazing has occurred in the western part of the reserve (Iso-Malla, see below).

The northern hot spot area thus provides unique opportunities for studying the impact of reindeer grazing on the rare elements of the North Fennoscandian flora. Unfortunately, however, the 'Malla experiment' has major design problems, which had to be solved before this opportunity could be exploited. The point of departure for establishing the Malla Reserve was Montell's personal excitement about the rich flora and fascinating vegetation of this mountain. To translate this into a random sampling process and to define the statis-

tical population, from which the reserve could be regarded to be drawn, is not easy. Yet, this is vital for the obtainance of replicated controls, without which the 'Malla experiment' would be scientifically worthless. To obtain this replication, we overlooked current national borders, which are of no relevance to the distributions of plants, and tried to imagine what mountains would been likely to fascinate Montell chosen any if he had got acquainted with some other part of North Fennoscandian hot spot. From the general areas thus defined, we searched for sites geologically and topographically maximally similar to Malla, with exposed dolomite rock belonging to the oldest overthrust plate being exposed above but no more than 350 meters above the treeline. To avoid pseudoreplication, we did not allow for selection of two sites from the same side of the same valley formation, unless one represented the edge of the mountain chain, while then other was located along the perimeter of a 'window' (outcropping granite area), where the dolomite-rich geological formation became exposed again. As precipitation, altitude from the timberline and latitude differed between the sites anyhow; the sites were chosen so that the sites inside Malla Reserve, with the lowest grazing pressure, were in the middle of the environmental gradients. When the Malla sites lost their average position along some of these gradients, the next grazed site was selected from the underrepresented parts of the gradient. By these criteria, we found one 'Malla replicate' from the Finnish part of the Kilpisjärvi Basin, three from the Swedish Torneträsk area and one from Reisadalen in Norway. As we had decided to have at least six areas with reindeer grazing, we had to extend our sampling area and to include one site from the outer parts of Altafjord in Norway, in the periphery of the hot spot.

The locations of the study sites are presented in Fig. 2. The general characteristics of these eight sites, ranked in accordance to the intensity of reindeer grazing (pellet group index), are summarized in Table 1. As an index of species pool, we used the numbers for the Atlas grid in question (Jalas *et al.*, 1972-99), except for sites less than 5 km from a grid boundary, whose pools were computed by averaging the numbers of species for both grids, rounded integers to the direction of the values on the grid where the site was located.

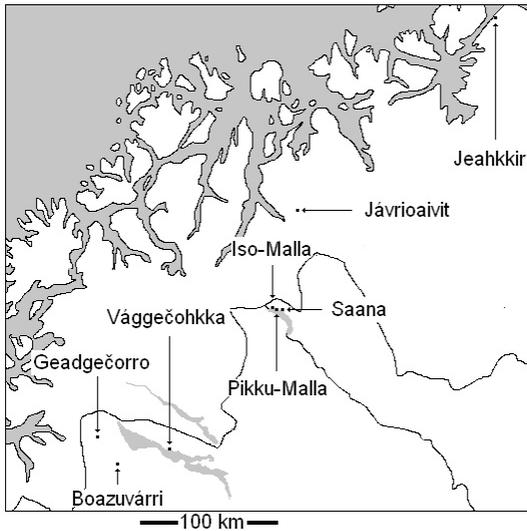


Fig. 2. Map over the study area, showing the locations of the study sites in northernmost Fennoscandia (Boazuvári, Geadgečorro and Vággečohkka in Sweden; Pikku-Malla, Iso-Malla and Saana in Finland; Jávrioavit and Jeahkkir in Norway).

Methods

In these eight areas, we have quantified the intensities of reindeer grazing and studied the composition of the vascular vegetation within the pivotal habitat for the majority of the rare vascular plants – the *Dryas* heath - low herb meadow complex, created by the impact of base rich bedrocks, especially dolomite (Du Rietz, 1924). Data on vascular plant species richness were collected between 10th July and 12th August, 2001. In each site, sampling started by identification of exposed dolomite rocks, which in northern Scandinavia occur primarily as discontinuous horizontal strands, outcropping from the softer shales. Sampling started from the midpoint of the first encountered dolomite strand and proceeded as follows. A grid of 10 m x 2 m was laid out 2 m to 12 m below the edge of the exposed dolomite rock, the long side of the grid pointing straight down the slope. The grid was divided into 20 plots on 1 m x 1 m. This sampling method ensured that the grid became located within the *Dryas* heath - low herb meadow complex and included a fair amount of habitat variation. When the first grid had been located, three more grids were sampled from the same area moving horizontally along the dolomite rich part of the slope and choosing the nearest exposed rocks which were at least 100 m

from the first sampling site and from each other. For each of the 80 (1 m x 1 m) subplots at each of the 8 sites, a complete list of all vascular plant species was compiled. Abundances of vascular plants within a grid were calculated as the % of subplots within each grid, with the plant present.

Since the reindeer data compiled by Bernes (1996) and those obtainable from national authorities refer to entire districts, their representativeness for local areas is imperfect at its best. We thus used a pellets group abundance index as our primary estimate of reindeer density. Normally, this technique is applied so that the numbers of dropping groups are counted along long transects (Van der Wal *et al.*, 2001; Moen *et al.*, 2003). While appropriate for studies focusing on widespread habitats, this technique is less suitable for our study, focusing on patchily occurring lime-rich habitats. Instead, presence/absence of reindeer pellets was recorded for each of the 1 m x 1 m plots, used in the vascular plant study and the natural logarithm of the number of plots with reindeer pellets was used as an index of reindeer density. The natural logarithm of 1+ the number of plots with pellets was used to down-weight the importance of the sites with the highest reindeer density, which would otherwise dominate in the computations of regressions. Reindeer pellets decompose slowly and remain visible for several years. The abundance of reindeer pellets is thus indicative of the reindeer density over, at least, the last 10 years.

To describe over-all species diversity of the grids, we used the exponential form of the Shannon-Wiener function. We used the Shannon-Wiener function, as it is sensitive to rare species, and presented it in the exponential form, as this is a unit more understandable to ecologists (Krebs, 1998). We used Smith and Wilson's index of evenness, as this is robust to differences in quality of the abundance estimates of common and rare species (Krebs, 1998). Plants were defined as calcium favored respectively arctic and alpine according to Mossberg *et al.* (1992), Hultén (1971) and Nilsson (1986). To obtain a set of rare plants, which definitely belonged to the species pool of the Finnish sites, we even focused on the occurrence of vascular plants belonging to the Finnish red-list (Ryttäri & Kettunen, 1997), excluding species not encountered in the 'Finnish wedge' (*Gymnocarpium robertianum*, *Gentianella campestris* ssp. *campestris*

Table 1. Position, altitude, precipitation (climate stations: 1 = Kilpisjärvi, 2 = Katterjokk, 3 = Abisko, 4 = Ankerlien, 5 = Porsa Gruber), number of arctic-alpine and lime favoured phanerogams species in the Atlas Florae Europae (Jalas *et al.*, 1972-99) grid to which the site belongs within the taxa for which the Atlas work has been completed, and reindeer grazing pressure in accordance to official statistics (reindeer per km², Bernes, 1996) and reindeer pellet counts. The reindeer densities of Jávrioarvit are adjusted for the real size of the summer range and are thus different to the number presented by Bernes (1996).

Site	Position	Altitude m.a.s.l. (and m above treeline)	Precipitation mm/yr (climate stations)	Arctic alpine plants (pool)	Lime favored plants (pool)	Lime favored alpine plants (pool)	Rein- deer density per km ²	Reindeer pellet count	
								raw	ln trans- fm
Pikku-Malla	69°05'N, 20°45'E	640 (90)	450 (1)	49	32	27	0	0	0
Iso-Malla	69°05'N, 20°40'E	700 (150)	450 (1)	49	32	27	0	0.75	0.56
Saana	69°00'N, 20°50'E	720 (170)	450 (1)	48	30	25	1-2	2	1.10
Geadgečorro	68°24'N, 18°20'E	700 (200)	848 (2)	47	30	24	5-10	2	1.10
Boazuvárri	68°16'N, 18°32'E	780 (130)	330 (3)	47	31	25	5-10	2.5	1.25
Vággečohkka	68°24'N, 19°05'E	760 (160)	330 (3)	47	31	25	3-5	4.5	1.70
Jeahkkir	70°27'N, 23°47'E	200 (-50 ⁽¹⁾)	748 (4)	40	21	18	5-10	4.0	1.61
Jávrioaivit	69°31'N, 21°15'E	860 (360)	455 (5)	47	31	25	>10 ⁽²⁾	15	2.77

- 1) The site is treeless due to long-lasting intense grazing, but in sites inaccessible to reindeer, tree-sized birches are encountered up to 250 m.a.s.l.
- 2) Size of summer range erroneously marked 4 times larger than it is by including most of the autumn-spring range; reindeer density corrected accordingly.

and *Allium schoenoprasum* var. *sibiricum*). In this part of the study, we used the red list concept both in narrow sense (categories 1-3, *i.e.* extinct, critically endangered and threatened species), and broad sense (categories 1-4, including even species considered as near to be threatened). Comparisons focusing on these categories of plants are thus biased in the favor of finding highest numbers of occurrences in the Finnish sites, everything else being equal.

The structure of the data set was described with a DCA (detrended correspondence analyzes) and the correlation of the axis with grazing was tested. All ordination analyses were performed with the software package CANOCO (ter Braak, 1998). We tested the effect of reindeer density on species richness with linear regression, with sites as sampling units.

Results

The reindeer pellet abundance indices reveal that there is a clear gradient of grazing pressure between the eight study sites, with the lowest reindeer density, as expected, on Pikku-Malla and Iso-Malla, and the highest grazing pressure on Jávrioait (Table 1). The local indices of grazing pressure are, by and large, consistent with the district level data on reindeer densities. The DCA was able to detect 4 significant gradients (Table 2). The first axis describes most of the variation and is mainly related to reindeer density (Fig. 3). The second and third axes are of fairly similar importance and seem to be mainly related to altitude and moisture respectively.

There was no significant correlation between reindeer density and any of the conventional indices of biodiversity (species richness, the Shannon-Wiener index of species diversity or the Smith and Wilson index of evenness, Fig. 4, Table 3). On the other hand, reindeer density was significantly and positive correlated with the richness of Ca-favored species and Finnish red-listed species in narrow sense (1-3) (Fig. 5). Moreover, there were a tendency for a positive relationship between reindeer density and species richness of arctic and alpine species and Finnish red-listed species in broad sense (1-4). Notice that these correlations emerged in spite of the fact that the area with the third

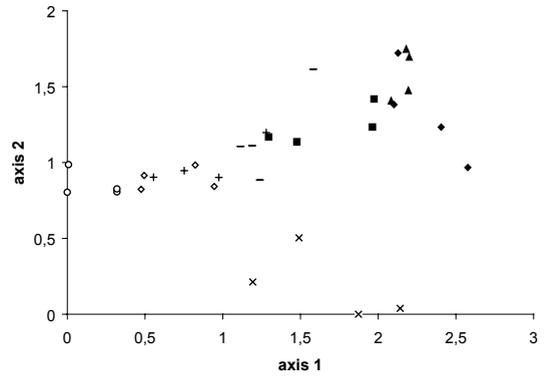


Fig. 3. Ordination plot from the DCA (detrended correspondence analysis), based on sample grids (32 grids in 8 sites). ■ Pikku-Malla, ▲ Iso-Malla, ◆ Saana, + Geadgečorro, - Boazuvárri, ◇ Vággečohkka, ○ Jeahkkir, × Jávrioait.

highest grazing intensity – Jeahkkir – harbored considerably fewer arctic alpine species and lime-favored species than the other study sites (Table 1).

The occurrence of individual species was too variable between the various study sites to allow statistically established inferences concerning their relation to grazing pressure. To allow for tentative conclusions and to provide background for inter-

Table 2. Eigenvalues and variance explained by the first four axes in the DCA analyses and regression coefficients between environmental variables and the 4 axes.

Axis	1	2	3	4
Eigenvalue	0.347	0.188	0.114	0.062
Community composition:				
Variance explained (%)	15.8	8.5	5.2	2.8
Cumulative variance (%)	15.8	24.3	29.5	32.3
Species-environment relation:				
Variance explained (%)	31.5	15.7	-	-
Cumulative variance (%)	31.5	47.2	-	-
Regression coefficients:				
Reindeer density	-0.4291	-0.2349	0.1152	0.1056
Precipitation	-0.1489	-0.0152	-0.2242	-0.1752
Altitude	-0.2382	0.3408	-0.0867	-0.1002
Inclination	0.0642	0.0126	0.1558	0.027

Table 3. Linear and quadratic regressions between the reindeer density index and the various measurements of richness and diversity.

		R^2	$d.f.$	F	P
Species richness	Linear	0.073	6	0.47	0.518
Diversity (N')	Linear	0.006	6	0.038	0.851
Evenness (E-var)	Linear	0.022	6	0.14	0.723
Ca favored species	Linear	0.510	6	6.3	0.047
Arctic-alpine species	Linear	0.310	6	5.17	0.151
Red listed (1-4) species	Linear	0.287	6	2.214	0.171
Red listed (1-3) species	Linear	0.512	6	6.3	0.046

preting the observed correlations, we nevertheless summarize the occurrences of Finnish; Swedish or Norwegian red listed species or genera including many such species represented by at least ten records (Table 4). We see that all the taxa showing any

clear relationship to grazing were more abundant on the most grazed mountains.

Discussion

Reindeer grazing is clearly related to plant community composition, as the first axis of the ordination, which explained a large part of the variance, mainly correlates with reindeer density. By itself, this relation does not tell what the cause is and what is the consequence. For the Swedish and Norwegian data points, the relation could even be interpreted so that rich occurrences of lime are both favorable for certain groups of plants and make the mountains attractive for reindeer. However, this explanation does not apply to the Finnish data points, since the stationary grazing practices account for the low grazing pressure on the Finnish mountains and the virtual absence of reindeer from the Malla reserve is a consequence of administrative decisions.

In spite of the clear relation between plant community structure and grazing pressure, reindeer-grazing pressure is totally unrelated to the standard measures of biodiversity - species richness, the Shannon-Wiener diversity index and the index of evenness. Correspondingly, Moen *et al.* (2003) have not found any differences in diversity between summer grazed heathlands and heathlands with relaxed grazing pressure in the summer. However, the numbers of calcium favored species and Finnish red listed (1-3) species is positively correlated with reindeer density and even the number of arctic-alpine species showed a similar tendency. This indicates that even though reindeer has no detectable effect on the local species richness of all vascular plants, reindeer grazing increases the number of those species, which make the largest contribution to γ -diversity (biodiversity in northern Europe).

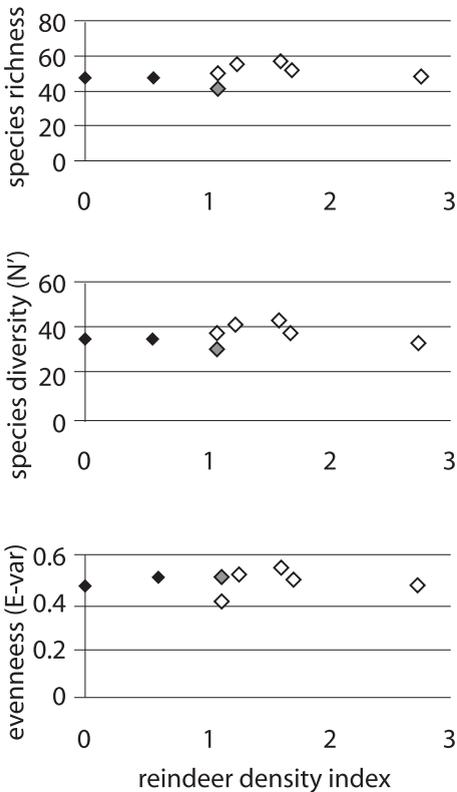


Fig. 4. Relationship between reindeer density and species richness, species diversity and species evenness. The two sites inside Malla Reserve are marked with black squares and Saana is marked with gray squares.

While correlative data have their inherent weaknesses, we cannot see any reasonable alternative explanation but regard differences in reindeer densities as causal for the pattern observed here, except for random variation in site conditions. This explanation can be rejected by standard statistical criteria ($P < 0.05$). The four most intensely grazed sites include the southernmost and northernmost sites, the sites with the most oceanic and most continental climates, and the sites with lowest and highest altitudes, both from the sea level and from the timberline. Geological conditions were standardized by the sampling method. It seems thus implausible that any shared physical attributes of these sites would account for the rich occurrence of calcium-favored species and Finnish red listed species in the strict sense (categories 1-3) in the intensely grazed sites. Differences in species pool cannot possibly account for the pattern, since the pool of calcium favored species in the Kilpisjärvi area is at least equally large as around Torneträsk (Boazuvári, Vággečohkka, Geađgečorro) and Reisdalen (Jávríoavít) and larger than in outer Altafjord (Jeahkkir).

The discrepancy between the results concerning over-all diversity and flourishing of rare and threatened plants indicates that collective indices like the number of species present or the Shannon-Wiener H' have limited value in the context of nature protection. It is at least equally important to look at the identity of the species, their local abundances and at their protection status.

Although the species level data must be treated with caution, as the lack of replication prevents us from testing these patterns statistically, they can be used to clarify how grazing might influence the dynamics of arctic-alpine plant populations. All the taxa for which the grazing favouredness index was higher than +80 consisted of relatively small plants with low-lying foliage and primarily or exclusively sexual reproduction, a combination of traits typical for red-listed arctic alpine plants. (Ryttäri & Kettunen, 1997). That herbivory can increase the abundance of such plants by preventing competitive exclusion is not especially surprising (Grime, 1973; 1979; Connell, 1978; Oksanen & Virtanen, 1997; Olff & Ritchie, 1998; Pärtel *et al.*, 1999).

Even abundance of lime favored plants correlated positively with grazing pressure. Moreover,

R. Virtanen (pers. comm.) pointed out that the species showing clearest positive relation to grazing are relatively drought-adapted. Intense reindeer grazing may indeed make the sites drier as reindeer paths even work as drainage channels in rainy weather. Moreover, grazing-inflicted erosion may spread lime and nutrients from exposed rocks to their surroundings and grazing even speeds up nutrient mineralization (Olofsson *et al.*, 2004). However, the causal factors responsible for these correlations can be indirect. The lime-favored plants occurring in our material are, in practice, a subset of arctic and alpine plants and contain many red-listed species. Moreover, the characteristic features of drought-adapted plants - low stature and small or narrow leaves - increase grazing-tolerance while making the plants weak competitors in closed vegetation. The most parsimonious interpretation of our results is thus that in the habitats sampled by us (heaths and meadows close to dolomite outcrops), grazing and associated mechanical disturbance favors small plants, which are weak competitors and require disturbed ground for successful reproduction, as even shown in the experiments conducted in the other alpine habitats in the Kilpisjärvi area (Virtanen, 1998; 2000; Virtanen *et al.*, 1997) and in northernmost Norway (Moen & Oksanen, 1998; Olofsson *et al.*, 2002).

Management perspectives

The present study was motivated by the need of a scientific basis for the future management of the Malla Strict Reserve. The results reported here pertain to one of the goals of these preserves: to protect rare and threatened species. Even a maximally conservative interpretation of our results implies that reindeer densities prevailing in northwestern Finnish Lapland cannot be regarded as harmful for the survival of Fennoscandian arctic-alpine rarities. To the contrary, our results indicate that the majority of these species thrive best on maximally intensely grazed mountains. Scientifically, this indication is hardly surprising. The arctic and its subarctic-alpine extensions are characterized by intense grazer-plant interactions, with lemmings and reindeer/caribou in main roles (Tihomirov, 1958; Wielgolaski, 1975; Baztli *et al.*, 1981; Crête & Manseau, 1996, Oksanen & Oksanen, 2000), and elimination of a strong interactor tends to reduce biodiversity (Paine, 1974; 2000).

Table 4. Occurrences of plants red listed plants in Finland, Sweden or Norway on the grids representing the four least intensely grazed areas (Pikku-Malla, Iso-Malla, Saana, Geadžęčorro) and in the four most intensely grazed areas (Boazuvárri, Vággečohkka, Jeahkkir, Jávrioaivit). Numbers refer to the total number of subplots where the taxon was encountered. The index of grazing favouredness is computed as $100(N_i - N_w) / \max(N_i, N_w)$, where N_i is the number of subplots in the intensely grazed areas where the taxon in question was encountered and N_w is the corresponding number for the weakly grazed areas.

Taxon	Weak Grazing	Intense Grazing	Grazing Favouredness
<i>Viola rupestris</i> ssp. <i>relicta</i>	0	20	+100
<i>Armeria maritima</i> ssp. <i>sibirica</i>	0	14	+100
<i>Veronica fruticans</i>	2	19	+89
<i>Euphrasia salisburgensis</i>	7	58	+88
<i>Rhododendron lapponicum</i>	4	26	+85
<i>Minuartia</i> spp.	6	35	+83
<i>Chamorchis alpina</i>	4	7	+57
<i>Antennaria</i> spp.	31	48	+35
<i>Erigeron</i> spp.	36	55	+35
<i>Botrychium</i> spp.	10	10	0
<i>Campanula uniflora</i>	67	42	-37

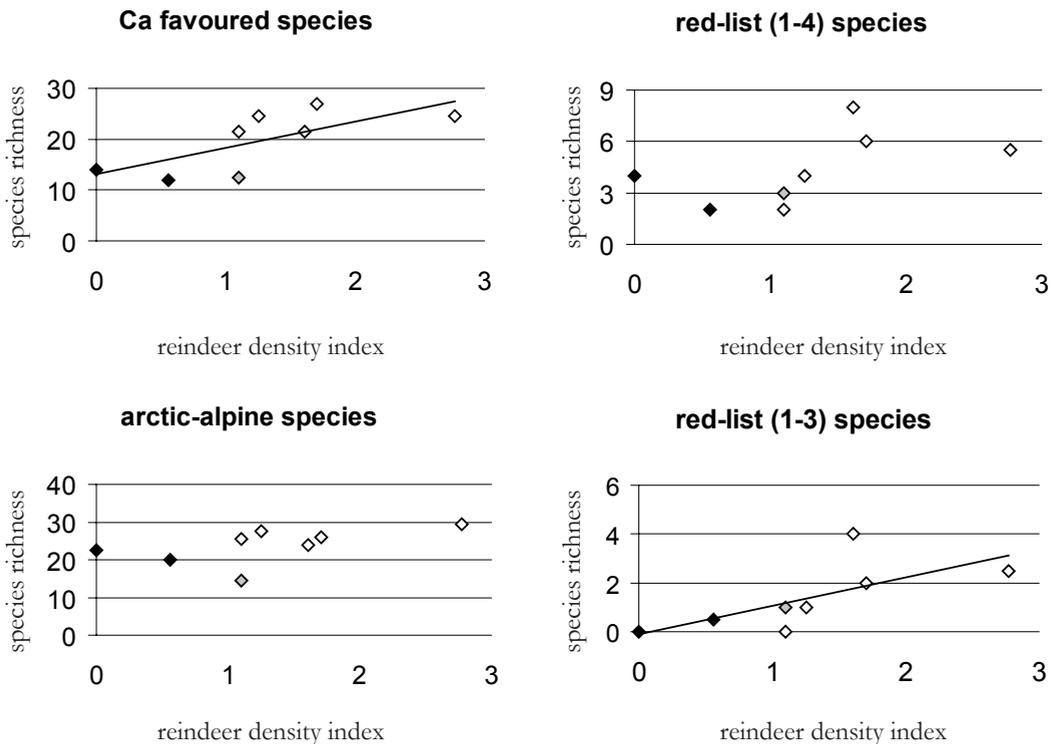


Fig. 5. Relationship between reindeer density and richness of arctic and alpine, Ca favoured and red listed plants. The two sites inside Malla Reserve are marked with black squares and Saana is marked with gray squares.

Whether and in which time scale the current lack of reindeer grazing on Malla can be regarded as perilous for our arctic-alpine plants is nevertheless a complicated issue. The rare species found on our plots on the intensely grazed mountains, are present on Malla, too, but have more restricted habitat range. On Malla, they occur primarily in habitats, where the density of taller plants is low for reasons other than grazing, such as rock outcrops and wind-deflated gravel fields (own observations, and personal communication with H. Väre, R. Virtanen and H. Kauhanen). In these habitats, the majority of the rarities seem to be doing quite well on Malla, too. However, small, local populations face the risk of extinction and the rate recolonization depends on the abundance of the species in the area (Hanski & Gyllenberg, 1993). In a longer time perspective, habitat loss and reduced abundance can thus threaten the persistence of arctic-alpine rarities on Malla via impacts on metapopulation dynamics, even if their current populations were not in immediate peril.

While the risks outlined above should be taken seriously, the current situation gives no reason to panic. As for the future of arctic-alpine rarities on Malla, there is time to test the interpretations presented above by studies conducted along local gradients of grazing intensity and by manipulative experiments. Recall that our results concerning the relation between reindeer grazing and abundance of arctic-alpine rarities depend on the assumption that, with respect to abiotic factors, the reference areas and Malla can be regarded as random samples, drawn from a single statistical population. The premise that such a statistical population can be defined *a posteriori* is central for the whole idea that Malla is scientifically valuable as a reindeer-free reference area. Unfortunately, however, there is no totally dependable way to mimic random sampling, if the treatment has not been drawn randomly from an *a priori* defined statistical population. This is indeed a major weakness for the entire 'Malla experiment', which must be taken in account when evaluating the messages of comparisons between Malla and grazed mountains.

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Abstract in Swedish / Sammandrag:

Vi studerade hur renbete påverkar kärlväxtfloras artrikedom och diversitet på dolomitpåverkade lågalpina lokaler i de artrikaste delarna av norra Fennoskandien. Vi inventerade 8 lokaler med olika rentätheter. Två lokaler ligger inom Malla Nationalpark, där renar har varit förbjudna sedan 1981 och starkt begränsade sedan 1950-talet. De sex andra lokalerna ligger i andra artrika områden med samma dolomitdominerade berggrund, men är betade av renar. Rentätheterna vid de studerade lokalerna varierar från helt obefintligt till bland de högsta rentätheter man kan finna i Fennoskandien. Inventeringen utfördes genom att systematiskt undersöka fyra 2 m x 10 m stora ytor i varje lokal i en habitattyp som är speciellt rik i ovanliga kärlväxter (fjällsippehed-lågörtsäng komplex). Varje yta delades upp i 20 småytor (1m x 1m), och en total artlista upprättades för var och en av dessa småytor. Den första axeln i DCA (detrended correspondence analysis) analysen korrelerade med rentätheten. Det visar att renar påverkar sammansättningen av växtsamhället. Ingen av de vanliga måtten på biodiversitet (artrikedom eller Shannon-Wiener diversitetsindex) var korrelerade med rentätheten. Trots detta, var tätheterna av Ca-gynnade växter och arter rödlistade i Finland positivt korrelerade med rentätheten. Trots att renarna inte påverkade totala artrikedomen, kan de vara betydelsefulla för regionala biodiversiteten eftersom de gynnar ovanliga och hotade arter. De vanliga måtten på biodiversitet har begränsat värde för bevarandebiologiska frågeställningar, eftersom de är lika känsliga för ovanliga och vanliga arter.

Refugial origin and postglacial colonization of holarctic reindeer and caribou

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Abstract: The classification and colonization of reindeer and caribou (*Rangifer tarandus*) was assessed from analysis of both proteins, nuclear DNA and mitochondrial DNA. I demonstrate that the current subspecies designations are not compatible with the differentiation at these markers, suggesting that the morphological differences among extant subspecies did not evolve in separate glacial refugia. Thus, morphological differences among extant subspecies probably evolved as adaptive responses to post-glacial environmental changes. An exception to this is the North American woodland caribou, where all three marker systems support a subspecies-specific refugium as the ancestral origin of these animals. Three major mtDNA haplogroups reported, represent three separate origins of the species during the last glaciation. The most influential origin has contributed to the gene pool of all extant subspecies, suggesting the existence of a large and continuous glacial population ranging across extensive areas of tundra in Eurasia and Beringia. The North American tundra forms (*R.t. granti* and *groenlandicus*) and the arctic forms (*R.t. platyrhynchus*, *R.t. pearyi* and *R.t. eogroenlandicus*) almost exclusively comprise haplotypes of such an origin. Another small and isolated refugium seems to have arisen in western Eurasia in close connection to the extensive ice sheet that covered Fennoscandia. The two Eurasian subspecies *R.t. tarandus* and *R.t. fennicus* appear to have a diphyletic origin as both the putatively small and isolated Eurasian refugium and the large Beringia refugium have contributed to their gene pools. A third distinct and geographically well-defined refugial area was probably located south to the extensive North American continental ice sheet from where the ancestors of the present North American woodland caribou (*R.t. caribou*) likely originated.

Key words: interglacial refugia, microsatellites, mitochondrial DNA, phylogeography, recolonization, transferrin.

Introduction

Reindeer and caribou (*Rangifer tarandus*) are distributed throughout the northern holarctic and are representatives of the fauna in this region. Besides serving a vital role in the socio-economics of many present human settlements, *R. tarandus* was probably the key species for the human immigration and colonization in arctic and sub-arctic by retreat of the ice at the end of the last glacial period. An understanding of the post-glacial re-colonization of *R. tarandus* therefore contributes knowledge towards our own early immigration and colonization.

Rangifer, 25 (1): 19-30

The classification of *R. tarandus* has been greatly debated. Historically, there has been almost as much confusion in vernacular names for the species as in scientific names. Alternating use of two vernacular names for this species - reindeer and caribou - has certainly contributed to the confusion. However, present view is that both refer to the same species and that caribou includes all wild specimens in North America, while reindeer refers to both wild and domestic animals in Eurasia. Domestic animals in North America of Eurasian origin are also called reindeer.

Different terms have also been used for *R. tarandus* corresponding to ecological adaptations *i.e.* the woodland or forest form, the barrenground or tundra form, and the arctic form. The woodland or forest reindeer/caribou appear to be adapted to forested areas, characterized morphologically by large body size, relatively long legs and with short distance between their antlers. The barrenground or tundra form primarily inhabits open tundra habitat or mountain regions, with a medium sized body size and larger space between their antlers. The Arctic reindeer and caribou appear to be adapted to colder and harsher environments. They are usually relatively small-bodied with short legs and rostrum and maintain thick insulating winter pelage. The distinctiveness of the different ecotypes however is not absolute, and a gradually transition between the different morphs in a mainly south-north direction appears to exist in both Eurasia and North America.

The subspecies classification of *R. tarandus* has been dominated by a high number of described subspecies without well-defined subspecific char-

acteristics. However, Banfield's (1961) revision and summary of the classification of reindeer and caribou based mainly on craniometrical measurements, is widely used as a guideline for the now living or recently extinct subspecies of reindeer and caribou. These include (see Fig. 1 for distribution): The Eurasian tundra reindeer (*R.t. tarandus*), distributed almost continuously across the tundra region, including the three lines and mountain areas across Eurasia. It is difficult to draw a southern boundary for the distribution of this subspecies in northern Europe and Asia because of possible overlap with the Eurasian forest reindeer (*R.t. fennicus*). The most typical form of this subspecies is to be found in the taiga in the Karelia at the boarder region between Finland and Russia. However, similar forest reindeer inhabit other areas in Russia. It is debatable whether these should be classified within the same subspecies. In the New World, the Alaska tundra caribou (*R.t. granti*) are distributed throughout the Alaskan Peninsula and partly into Yukon, Canada. The Canadian barrenground caribou (*R.t. groenlandicus*) are distributed east to the Alaska tundra caribou

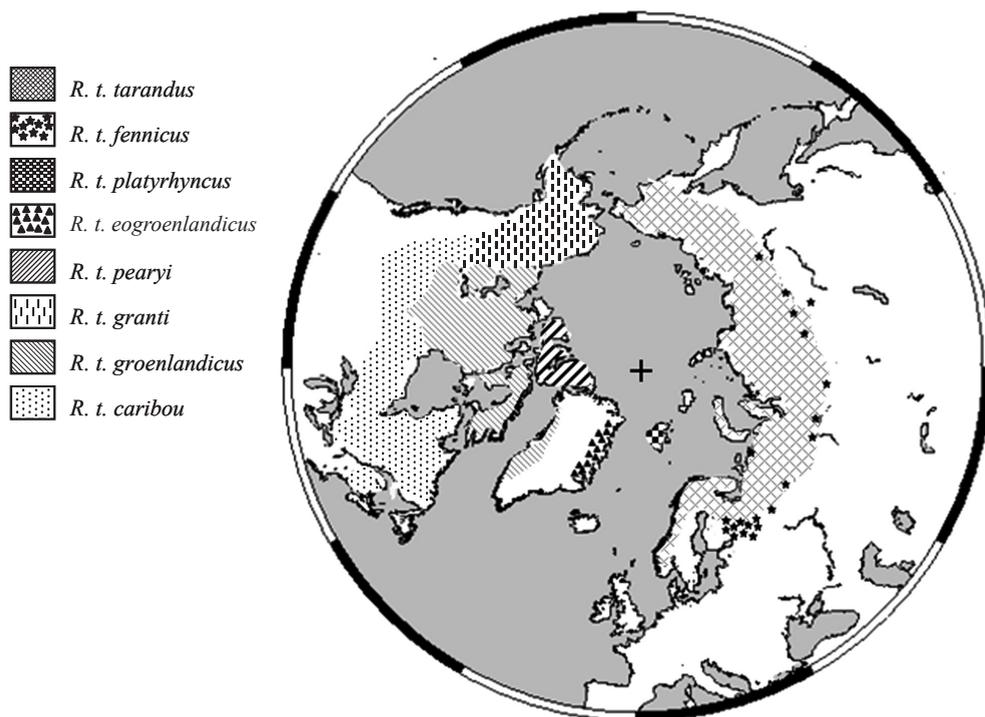


Fig. 1. Geographic distribution of the different subspecies of reindeer. Although additional subspecies have been suggested, these eight constitute the conventional taxonomic classification of the species.

across the tundra region in mainland northern Canada, including the Baffin Island and the west coast of Greenland. The American woodland caribou (*R.t. caribou*) are distributed mainly in the taiga region south to the distribution of the Canadian barren-ground caribou from Newfoundland, Labrador and northern Québec in the East through British Columbia and southern Yukon in the West. Among the arctic ecotypes, there are the Peary caribou (*R.t. pearyi*) living on the Arctic Islands of northern Canada, and the Svalbard reindeer (*R.t. platyrhynchus*)

isolated on the Spitsbergen Archipelago. The now extinct East-Greenland reindeer (*R.t. eegroenlandicus*) also belonged to an Arctic ecotype. This subspecies inhabited the east coast of Greenland and became extinct approximately 100 years ago. The recently extinct *R.t. dawsoni* that occupied Queen Charlotte Island of western Canada was also classified as a separate subspecies (Banfield, 1961).

To what extent the present classification of *R. tarandus* correctly represents the different refugial origin has been an open question. Here, I summa-

Table 1. Populations of reindeer and caribou analysed for serum transferrin polymorphism. The numbers quote the geographic locations of the population provided in Fig. 2.

No.	Population/location	Subspecies	Reference
1	Wild reindeer, Norway	<i>R.t. tarandus</i>	From Røed (1998a)
2	Domestic reindeer, Norway	<i>R.t. tarandus</i>	From Røed (1998a)
3	Domestic reindeer, Kola, Russia	<i>R.t. tarandus</i>	Present study
4	Domestic reindeer, Yakutia, Russia	<i>R.t. tarandus</i>	Present study
5	Domestic reindeer, Alaska	<i>R.t. tarandus</i>	Røed & Whitten (1986)
6	Forest reindeer, Kuhmo, Finland	<i>R.t. fennicus</i>	Present study
7	Svalbard reindeer, Nordenskiölland	<i>R.t. platyrhynchus</i>	Røed <i>et al.</i> (1986)
8	Western Arctic Herd, Alaska	<i>R.t. granti</i>	Present study
9	Central Arctic Herd, Alaska	<i>R.t. granti</i>	Present study
10	Porcupine Herd, Alaska/Canada	<i>R.t. granti</i>	Present study
11	Denali Herd, Alaska	<i>R.t. granti</i>	Present study
12	Nelchina Herd, Alaska	<i>R.t. granti</i>	Present study
13	Forty-mile Herd, Alaska	<i>R.t. granti</i>	Present study
14	Jasper, eastern Alberta, Canada	<i>R.t. granti</i>	Present study
15	Central Alberta, Canada	<i>R.t. granti</i>	Present study
16	Beverly Herd, Canada	<i>R.t. groenlandicus</i>	Røed & Thomas (1990)
17	Baffin Island, Canada	<i>R.t. groenlandicus</i>	Røed <i>et al.</i> (1991)
18	Kaminuriak Herd, Canada	<i>R.t. groenlandicus</i>	Present study
19	Boothia Peninsula, Canada	<i>R.t. groenlandicus</i>	Røed <i>et al.</i> (1986)
20	Victoria Island, Canada	<i>R.t. groenlandicus</i>	Present study
21	Akia, Greenland	<i>R.t. groenlandicus</i>	Present study
22	Kangerlussaq, Grennland	<i>R.t. groenlandicus</i>	Present study
23	Peary caribou, Parry pop., Canada	<i>R.t. pearyi</i>	Røed <i>et al.</i> (1986)
24	Peary caribou, Peel pop., Canada	<i>R.t. pearyi</i>	Røed <i>et al.</i> (1986)
25	Northern Saskatchewan, Canada	<i>R.t. caribou</i>	Present study
26	Eastern Manitoba, Canada	<i>R.t. caribou</i>	Røed <i>et al.</i> (1991)
27	Slate Island, Ontario, Canada	<i>R.t. caribou</i>	Røed <i>et al.</i> (1991)
28	Leaf River Herd, Québec, Canada	<i>R.t. caribou</i>	Røed <i>et al.</i> (1991)
29	George River Herd, Québec, Canada	<i>R.t. caribou</i>	Røed <i>et al.</i> (1991)
30	Gaspe Herd, Québec, Canada	<i>R.t. caribou</i>	Røed <i>et al.</i> (1991)
31	Brunette Island, Labrador, Canada	<i>R.t. caribou</i>	Røed <i>et al.</i> (1991)
32	Newfoundland, Labrador, Canada	<i>R.t. caribou</i>	Present study

size previous studies together with new data, using both proteins, nuclear DNA and mitochondrial DNA as genetic markers to assess the classification and post-glacial colonization of reindeer and caribou.

Transferrin variability.

The populations of reindeer and caribou analysed for serum transferrin polymorphism, both here and in previous studies, are provided in Table 1. All presently living subspecies are included, covering most of *R. tarandus*'s distribution in North America and Eurasia. The methods for analysis of the transferrin polymorphism can be found in Røed *et al.* (1991) and references therein. Altogether, 30 transferrin alleles were detected. The genetic patterns revealed considerable heterogeneity among the populations analysed, both with regard to the number of alleles detected and the allele frequency distribution. However, the main pattern of the frequency distribution previously detected, with a major dichotomy between the *R.t. caribou* on the one hand and various populations of all the other

subspecies on the other (Røed *et al.*, 1991), was also detected after including several more populations. This is illustrated by the frequency distribution of pooled frequencies of three alleles that was almost exclusively found among populations of American woodland caribou (Fig. 2). This supports the hypothesis that during the Wisconsin glaciation, the ancestral populations of *R.t. caribou* survived in a refugium separate from that of the ancestral populations of the other subspecies. However, precaution is required when interpreting evolutionary events from genetic patterns at one locus only. The various transferrin alleles may also have different adaptive values (*cf.* Zhurkevich & Fomicheva, 1976; Røed, 1987) with the possibility that the allele frequency distribution reflects selective forces rather than phylogenetic events.

Microsatellite variation

Over the last decade, new DNA-based methods have become available, offering a greater potential than earlier marker systems. Microsatellites, a class of simple tandemly repeated sequences (Litt &

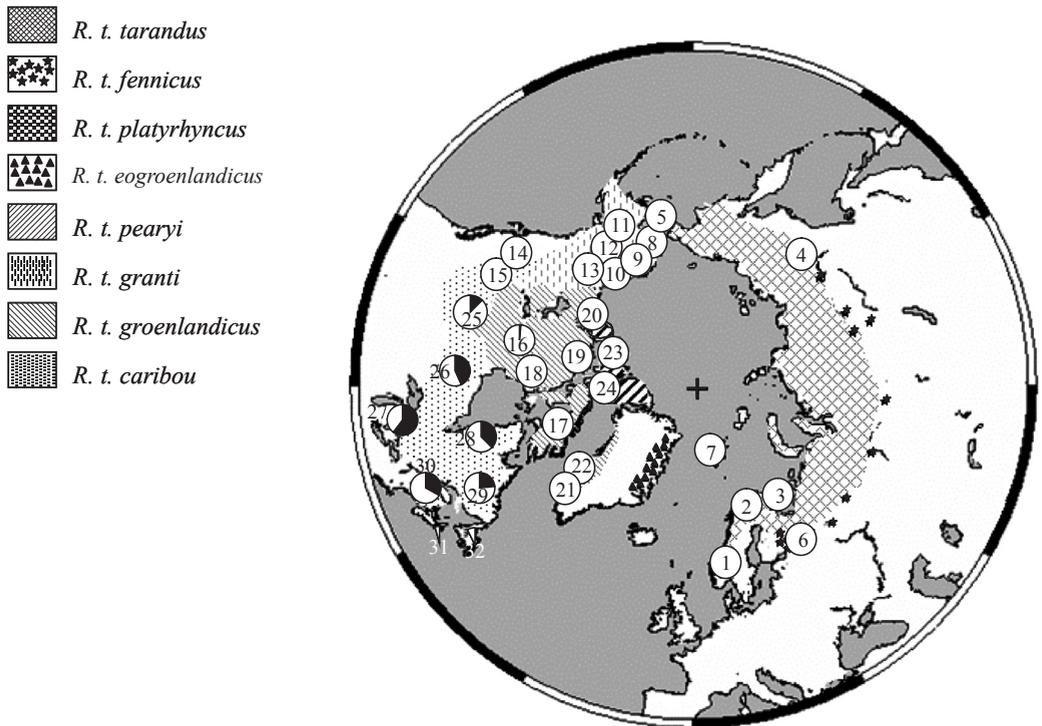


Fig. 2. Frequency distribution of three pooled transferrin alleles (Tf^{A-3} , Tf^{A-2} and Tf^{A-1}) given as section of pies. Numbers refer to the sampled population provided in Table 1. The indicated subspecies distribution is as for Fig. 1.

Table 2. Genetic variability in 13 microsatellite loci in subspecies of reindeer and caribou.

Subspecies	Population	Mean sample size per locus	Mean no. of alleles per locus	Mean heterozygosity
<i>R.t. tarandus</i>	Norway, domestic	201	9.2	0.73
<i>R.t. tarandus</i>	Norway, wild	181	9.7	0.76
<i>R.t. tarandus</i>	Finland, domestic	57	8.2	0.77
<i>R.t. fennicus</i>	Finland, wild	33	7.4	0.71
<i>R.t. platyrhynchus</i>	Svalbard reindeer	20	1.8	0.26
<i>R.t. granti</i>	Alaska caribou	36	10.2	0.77
<i>R.t. groenlandicus</i>	Canada, NWT	20	8.8	0.80
<i>R.t. groenlandicus</i>	Canada, Victoria Isl.	25	8.4	0.78
<i>R.t. groenlandicus</i>	West Greenland	18	4.9	0.46
<i>R.t. pearyi</i>	Peary caribou	11	6.0	0.68
<i>R.t. caribou</i>	Canada, Ontario	13	5.0	0.61
<i>R.t. caribou</i>	Canada, Québec	25	6.5	0.61

Luty, 1989; Tautz, 1989; Weber & May, 1989) have been described as ideal markers since they are highly polymorphic, codominant, abundant throughout the genome and amenable to polymerase chain reaction (PCR) technology. Most microsatellites are effectively neutral loci and thus, their geographical distribution will reflect the patterns of genetic drift and gene flow in populations. One major advantage of using the microsatellites are their rapid evolutionary rate, evolving 10-100 times faster than much of the coding nuclear DNA. Their high evolutionary rate provides an ideal genetic tool for population studies covering relatively short evolutionary time spans.

Microsatellites are increasingly used as genetic markers in reindeer and caribou (Kushny *et al.*, 1996; Wilson *et al.*, 1997; Røed, 1998b; Røed & Midthjell, 1998; Zittlau *et al.*, 2000; Côté *et al.*, 2002; Jepsen *et al.*, 2002; Røed *et al.*, 2002; Courtois *et al.*, 2003; Cronin *et al.*, 2003; McLoughlin *et al.*, 2004). I will present microsatellite analyses for different populations of *R. tarandus* representing all present living subspecies (Table 2).

Template DNA was extracted by standard procedures including proteinase K digestion and phenol/chloroform extraction. Thirteen reindeer-specific microsatellite loci were analysed for polymorphism (NVHRT-01, -03, -16, -24, -31, -48, -73 and -76, Røed & Midthjell, 1998, and RT-1, -5, -6, -9 and -27, Wilson *et al.*, 1997). All forward prim-

ers were end-labelled with fluorescent tags and the PCR products were electrophoresed using an ABI Prism 310 Genetic-Analyser.

Altogether, 184 alleles were detected among the thirteen markers. All loci were polymorphic in all populations except for Svalbard reindeer (*R.t. platyrhynchus*), where five loci were monomorphic. Both mean number of alleles per locus and mean heterozygosity were low for this subspecies compared with all the other populations analysed (Table 2). Reduced genetic variation in this subspecies is in accordance with previously studies, both on protein polymorphism (Storset *et al.*, 1978; Soldal & Staaland 1980; Røed, 1985; Røed *et al.*, 1986) and microsatellite variation (Côté *et al.*, 2002). Svalbard reindeer have apparently been isolated for a long period, during which genetic drift and loss of genetic variability occurred. Similar processes likely occurred for West Greenland caribou (*R.t. groenlandicus*). This subspecies also has relatively low levels of genetic variability (Table 2). Reduced genetic variability for caribou on Greenland, as also detected by Gravlund *et al.* (1998) and by Jepsen *et al.* (2002), could be a result of the many natural barriers as glaciers and wide fjords in this area together with extreme fluctuations in population size (Jepsen *et al.*, 2002). Somewhat reduced variability was also indicated in the two populations of woodland caribou (*R.t. caribou*), and to some extent also in the Peary caribou (*R.t. pearyi*) (Table 2). However, caution is needed

Table 3. Genetic distance (Nei, 1978) based on microsatellite variation in 13 loci in subspecies of reindeer and caribou.

Subspecies-Population	1	2	3	4	5	6	7	8	9	10	11
1. <i>R.t. tarandus</i> (Norway, domestic)	****										
2. <i>R.t. tarandus</i> (Norway, wild)	0.15	****									
3. <i>R.t. tarandus</i> (Finland, domestic)	0.09	0.15	****								
4. <i>R.t. fennicus</i> (Finland, wild)	0.21	0.14	0.09	****							
5. <i>R.t. platyrhynchus</i> (Svalbard)	0.93	0.83	0.99	0.99	****						
6. <i>R.t. granti</i> (Alaska)	0.29	0.17	0.23	0.14	0.74	****					
7. <i>R.t. groenlandicus</i> (Canada, NWT)	0.27	0.20	0.19	0.16	0.62	0.05	****				
8. <i>R.t. groenlandicus</i> (Canada, Victoria)	0.33	0.29	0.21	0.21	0.88	0.13	0.12	****			
9. <i>R.t. groenlandicus</i> (West Greenland)	0.97	0.83	0.81	0.76	2.21	0.75	0.69	0.83	****		
10. <i>R.t. pearyi</i> (Peary caribou)	0.35	0.42	0.30	0.37	0.70	0.65	0.18	0.31	0.79	****	
11. <i>R.t. caribou</i> (Canada, Ontario)	0.59	0.35	0.45	0.38	0.97	0.19	0.26	0.32	1.54	0.65	****
12. <i>R.t. caribou</i> (Canada, Québec)	0.59	0.39	0.46	0.36	1.06	0.14	0.20	0.28	1.24	0.46	0.14

when interpreting the relatively few individuals analysed for the Peary caribou. Besides, the microsatellite variation pattern among these samples showed an excess of homozygotes as compared to Hardy Weinberg expectations, a pattern also previously seen in the transferrin variation (Røed *et al.*, 1986). This possibly reflects genetic structuring within the sampled material.

The microsatellite allele frequency distribution comparison among the sampled populations was performed by estimates of the genetic distance (Nei, 1978) (Table 3). The genetic distances ranged from 0.05 between the two subspecies Alaska caribou (*R.t. granti*) and Canadian barren-ground caribou from the North West Territories (*R.t. groenlandicus*), to 2.21 between the Svalbard reindeer (*R.t. platyrhynchus*) and caribou from West Greenland (*R.t. groenlandicus*). The West Greenland caribou showed generally large distance to all the analysed populations. Relatively low genetic distance was detected among the Scandinavian samples, including both the Eurasian tundra reindeer (*R.t. tarandus*) and the Finish forest reindeer (*R.t. fennicus*). In North America, the genetic distance between the woodland caribou (*R.t. caribou*) and the other populations was generally large (Table 3).

A dendrogram (Fig. 3) summarizing the genetic distances was constructed using the UPGMA cluster method (Sneath & Sokal, 1973). This analysis illustrates the genetic distinctiveness of the caribou on West Greenland (*R.t. groenlandicus*) and Svalbard

reindeer (*R.t. platyrhynchus*) that both clustered out from the others. However, the low genetic variation detected in these populations suggests that their distinctive genetic pattern reflects some relatively recent bottleneck effects rather than phylogenetic events. Among all the other populations, the two woodland caribou (*R.t. caribou*) populations clustered away from the others supporting a separate origin for this subspecies. Also Peary caribou (*R.t. pearyi*) separated out from the others (Fig. 3). However, this subspecies was clearly most genetically similar to the Canadian barren-ground caribou (*R.t. groenlandicus*) from North West Territories (Table 3), suggesting common origin of the ancestors of these populations. The European populations and the three samples of barren-ground caribou in Alaska and Canada clustered away from each other, possibly reflecting relatively recent isolation processes. The opening of the Bering Strait in late Weichselian / Wisconsin might be such a process.

Mitochondrial DNA sequences

Mitochondria are specialised organelles located in the cytoplasm. Most somatic cells have thousands of copies of mitochondrial DNA (mtDNA) that provides a large number of starting copies for amplification. However the cytoplasmic contribution of the male and the female parent is generally unequal; the egg contributes the bulk of the cytoplasm and the sperm essentially none. The mitochondrial genes are therefore strictly maternal

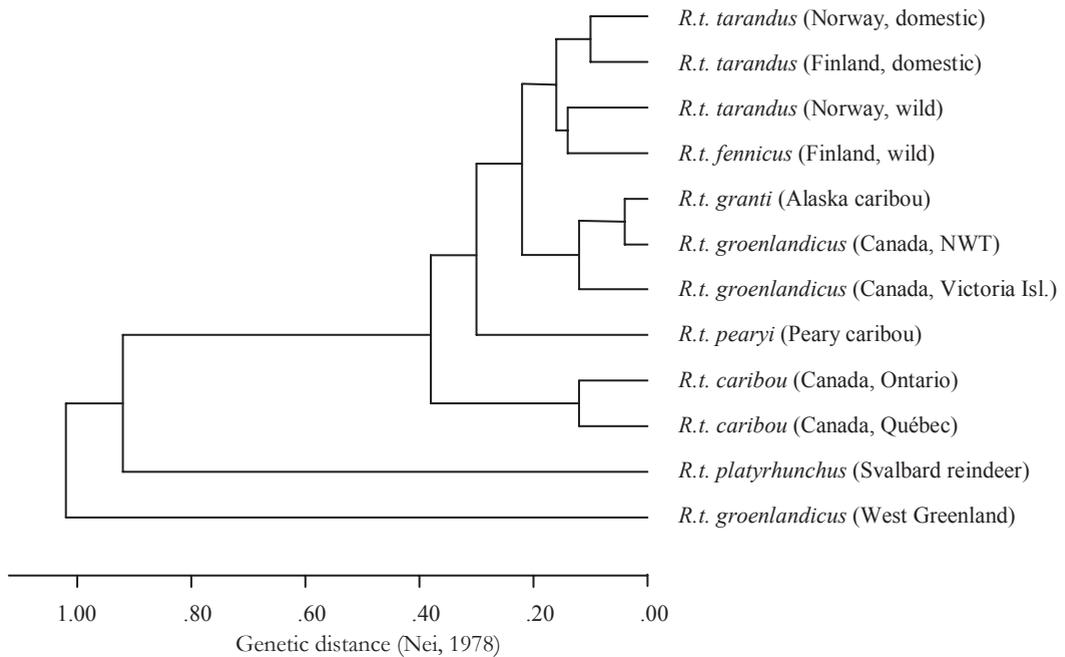


Fig. 3. Cluster analysis of the genetic distance (Nei, 1978) between subspecies of reindeer and caribou based on variability in 13 microsatellite loci.

inherited. This indicates simple heredity and no interpretation problems due to recombination. The rate at which the mitochondrial genome evolves through mutations is faster than most of the coding regions of the nuclear DNA, but slower than microsatellite DNA. It is an ideal genetic tool for inter-population phylogeographical studies covering intermediate evolutionary time span. Another advantage of using the mtDNA is that much of the analysis is based on the presence of haplotypes and haplogroups, and less dependent on frequencies of haplotypes. This makes the interpretation of such data more independent of recent bottleneck effects.

MtDNA sequence variation in the control region have recently been reported for all the extant subspecies of reindeer and caribou (Flagstad & Røed, 2003). The phylogenetic relationships among the different haplotypes were estimated and three distinct major haplogroups were indicated, presumably representing three separate populations during the last glaciation. These three haplogroups are illustrated in Fig. 4, providing a minimum spanning network (MSN) using the statistical parsimony approach described by Templeton *et al.* (1992).

As indicated, haplogroup I exclusively consisted of haplotypes found among the Fennoscandian individuals represented by both *R. t. tarandus* and *R. t. fennicus*. Haplogroup II comprised haplotypes found mainly among the North American woodland caribou (*R. t. caribou*) together with two haplotypes found in two individuals of barren-ground origin (Gro7 and Gro101). Haplogroup III constitutes a wide sub-network of cross-linked haplotypes located between haplogroups I and II in the network. All the subspecies were well represented in this haplogroup (Fig. 4).

The mtDNA sequences were also analysed for molecular variance to examine the amount of genetic variability partitioned within and among populations, as well as groups of populations (Flagstad & Røed, 2003). There was no relationship between the current subspecies designations and differentiation at the mtDNA level (Table 4). The current subspecies designations are therefore not compatible with the differentiation at the mtDNA level. In fact, 0% of the variability was explained at the subspecies level, strongly suggesting that the morphological differences among extant subspecies did not evolve in separate glacial refugia. Similarly, weak

Table 4. Analysis of molecular variance of mtDNA haplotypes of reindeer and caribou based on several possible groupings of the populations examined.

Grouping criteria	Groups of populations	Proportion of total variation assigned to groups	Significance level of grouping (<i>P</i>)
Subspecies	[<i>tarandus</i>] [<i>fennicus</i>] [<i>platyrhynchus</i>] [<i>pearyi</i>] [<i>caribou</i>] [<i>groenlandicus</i>] [<i>granti</i>]	0%	0.52
Ecotype	[<i>tarandus</i> , <i>groenlandicus</i> , <i>granti</i>] [<i>platyrhynchus</i> , <i>pearyi</i>] [<i>fennicus</i> , <i>caribou</i>]	0.2%	0.43
Geographic distribution (Eurasia <i>vs.</i> North America)	[<i>tarandus</i> , <i>fennicus</i> , <i>platyrhynchus</i>] [<i>pearyi</i> , <i>granti</i> , <i>groenlandicus</i> , <i>caribou</i>]	1.4%	0.34
Northern <i>vs.</i> southern haplogroups	[haplogroup I, haplogroup III] [haplogroup II]	32.8%	0.09
Eurasian <i>vs.</i> North American haplogroups	[haplogroup I] [haplogroup II, haplogroup III]	41.9%	< 0.001
Three main haplogroups	[haplogroup I] [haplogroup II] [haplogroup III]	49.0%	< 0.001

relationships were found when grouping the populations according to the ecotypes of tundra, arctic and woodland types, or geographic distribution of Eurasia and North America. The only convincing figures appeared when populations were grouped in various ways according to the main haplogroups as suggested from the phylogenetic analyses. When considering the three groups as separate entities, almost 50% of the total variability was explained at the group level (Table 4), supporting the actual existence of three main mtDNA lineages.

In the same study, the three mtDNA lineages, as revealed from the phylogenetic analysis, were also tested for sudden population expansion using the mismatch distribution approach as given by Slatkin & Hudson (1991) and by Rogers & Harpending (1992). The mismatch distribution is the distribution of the observed number of differences between pairs of haplotypes. The mismatch distributions of haplogroups I and III were clearly

unimodal, a pattern compatible with a historical population expansion. Contrastingly, haplogroup II showed a multimodal mismatch distribution, suggesting stable population size through time or that this haplogroup comprised several sub-groups. The average number of nucleotide differences was much higher for haplogroup III as compared to that of haplogroup I, indicating that the ancestral populations of the two haplogroups expanded at different times. Assuming a divergence rate of 16% per million years, the putative expansion of haplogroup I was dated to 15 000 years before present (BP), while that of haplogroup III was estimated to have occurred at approximately 115 000 years BP (Flagstad & Røed, 2003).

Discussion

As shown for both the microsatellite frequency variation and the mtDNA haplotype distribution, the current subspecies designations are not com-

ranging across vast areas of tundra in Eurasia and extending into North America across the Beringian land bridge. The large sequence diversity and unimodal distribution of sequence differences suggest that the population remained large and continuous after an initial demographic expansion dated to approximately 115 000 years BP. As ice cover retreated by the end of the Weichselian / Wisconsin, representatives from this population appear to have recolonized exposed habitat on the continental mainland in North America, Siberia and Fennoscandia. All current subspecies are to some extent affected by this origin. The North American tundra forms (*R.t. granti* and *R.t. groenlandicus*) and the Arctic forms (*R.t. platyrhynchus*, *R.t. pearyi* and *R.t. eogroenlandicus*) almost exclusively comprise haplotypes of such an origin.

The mtDNA haplogroup I was suggested to have been established as a result of a rather different evolutionary history, characterized by high degrees of recent isolation (Flagstad & Røed, 2003). As haplotypes belonging to this group were not represented among any of the North American samples, a pure Eurasian origin was indicated. A recent origin in a small refugium probably isolated in connection with ice expansion in Eurasia during the Weichselian was discussed. The two Eurasian subspecies *R.t. tarandus* and *R.t. fennicus* appear to have a diphyletic origin, as both the putatively small and isolated Eurasian refugium and the large Beringia refugium have contributed to their gene pools. Accordingly, adaptation to woodland conditions for *R.t. fennicus* seems to be a recent phenomenon, possibly taking place in connection with post-glacial forest expansion.

In North America, another distinct and geographically well-defined refugial area is indicated by all three marker systems. Virtually all haplotypes belonging to mtDNA haplogroup II were found among the southerly distributed woodland caribou. This, together with the dichotomy in both the transferrin and the microsatellite variability pattern, suggests that this subspecies has its main origin in refugia located south to the Wisconsin ice sheet. The multimodal mismatch distribution of this mtDNA haplogroup provides evidence of a large stable population size through time or that this haplogroup comprised several subgroups (*cf.* Flagstad & Røed, 2003).

For the Arctic forms, a common North American origin is particularly well supported for *eogroenlandicus* and *pearyi*, as these subspecies shared a common mtDNA haplotype as reported by Gravlund *et al.* (1998). When the ice retreated, colonizers appear to have migrated across the Canadian archipelago and eventually reached Eastern Greenland. Gravlund *et al.* (1998) reported similar mtDNA haplotype among Svalbard reindeer and a specimen from the Taimyr peninsula in northern Russia and suggested a diphyletic origin of the Arctic ecotype with an Eurasian origin of the Svalbard reindeer. However, in the extensive study by Flagstad & Røed (2003), the most common mtDNA haplotype found on Svalbard was identical to the only haplotype found more than once in the Quebec region in Canada, supporting a North American colonization route towards Svalbard. This was in accordance with the previously reported distinct similarities at the transferrin locus between Svalbard reindeer and Peary caribou and with both having some similarities with the American woodland caribou (Røed *et al.*, 1986; 1991). The microsatellite variability pattern in the Svalbard reindeer (*R.t. platyrhynchus*) was characterized by reduced genetic variability. However, the genetic distance estimates were slightly higher against the Eurasian subspecies than against the North American subspecies, although the distances were generally high towards all other populations (Table 3). It appears therefore that the available data based on genetic variability in both transferrin, microsatellites and mtDNA points toward an origin of the Svalbard reindeer from ancestors in North America.

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Abstract in Norwegian / Sammendrag:

Systematisk inndeling og kolonisering av rein (*Rangifer tarandus*) ble bestemt ved å analysere for variasjon i genetiske markører som proteiner, kjerneDNA og mitokondrieDNA. Dagens oppdeling av rein i underarter viser liten overensstemmelse med variasjonsmønsteret i de undersøkte markørene, noe som viser at de morfologiske forskjellene som karakteriserer dagens underarter ikke har utviklet seg i atskilte refugier i løpet av siste istid. Unntak fra dette er nordamerikansk skogsrein (woodland caribou-*R.t. caribou*) hvor alle tre markørsystemene indikerer at denne har utviklet seg i et refugium forskjellig fra andre underarter. De tre registrerte hovedhaplogruppene i mitokondrie-DNA representerer tre atskilte opprinnelser av rein i løpet av siste istid. Den mest innflytelsesrike av disse bidro vesentlig til genbanken til alle dagens underarter av rein, noe som tyder på at det under siste istid eksisterte en stor reinpopulasjon med kontinuerlig utbredelse gjennom store deler av tundraen i Eurasia og Beringia. De nordamerikanske tundrareintypene (*R.t. granti* og *R.t. groenlandicus*), samt de arktiske typene (*R.t. platyrhynchus*, *R.t. pearyi* og *R.t. eogroenlandicus*) består nærmest utelukkende av haplotyper med denne opprinnelse. Et annet lite og isolert refugium syntes å ha oppstått i Vest-Europa i nærheten av den omfattende isbreen som dekket Fennoskandia. De to europeiske underarter, *R.t. tarandus* og *R.t. fennicus*, syntes å ha en todelt opprinnelse med genetisk påvirkning fra både det antatt lille og isolerte refugiet i Eurasia samt fra det store Beringia refugiet. Et tredje geografisk distinkt refugium var antagelig lokalisert sør for den omfattende isbreen i Nord Amerika hvorfra forfedrene til dagens nordamerikanske skogsrein (*R.t. caribou*) har sin mest sannsynlige opprinnelse.

Seasonal changes in reindeer physiology

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Abstract. The seasonal changes in the photoperiod, temperature and availability of food need to be converted to hormonal signals in order to induce adaptations in the physiology of the reindeer. The most reliable of the seasonal changes in the environment is the photoperiod, which affects the reindeer physiology through pineal gland and its hormone, melatonin. Usually there are large diurnal changes in the concentration of melatonin, but in the reindeer the daily rhythm disappears during the arctic summer to return again in the autumn. Seasonal changes in melatonin secretion are involved in the regulation of reproduction, the growth of pelage, thermogenesis, body mass and immune function. Melatonin may exert its effects through gene activation, but the mechanisms are not completely understood. Other hormones that show seasonality are thyroid hormones, insulin and leptin. Thus the observed physiological changes are a result of actions of several hormones. Appetite, energy production and thermogenesis are all vital for survival. During winter, when energy balance is negative, the reindeer uses mainly body fat for energy production. The use of fat stores is economical as the rate of lipolysis is controlled and the use of fatty acids in tissues such as muscle decreases. Only in severe starvation the rate of lipolysis increases enough to give rise to accumulation of ketone bodies. The protein mass is maintained and only in starved individuals muscle protein is used for energy production. The winter feed of the reindeer, the lichens, is poor in nitrogen and the nitrogen balance during winter is strongly negative. Reindeer responds to limited availability of nitrogen by increasing the recycling of urea into rumen. In general the adaptation of reindeer physiology enables the reindeer to survive the winter and although several aspects are known many others require further studies.

Key words: energy consumption, feed intake, leptin, lipolysis, melatonin, proteolysis, *Rangifer tarandus*, starvation.

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Introduction

Survival, growth and production of offspring are of key importance for every animal species. In arctic species, such as reindeer, these basic physiological functions are modulated by the seasonal changes in the availability and quality of food, wide changes in the temperature and photoperiod. Also in reindeer the response to these environmental cues is manifested in the seasonal changes in its physiology (Fig. 1). To be effective, the changes in physiology have to be initiated before the changes occur in the

living conditions, *i.e.* the changes have to be predictive. For example the growth of winter fur coat has to begin well before the cold season. In order to predict the changes in season the reindeer has to respond to changes in their surroundings, the most important of which are temperature, availability of food and the length of the photoperiod. Among these the length of the photoperiod is the most reliable indicator of the change of the season and therefore seasonality of many physiological phenomenon is based on the length of the day.

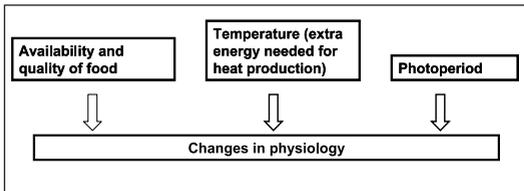


Fig. 1. Seasonal changes in photoperiod, temperature, and availability of food are the main environmental cues that through hormones induce the adaptive changes that enable the reindeer to survive the winter.

Seasonal changes in melatonin and other hormones

The daylight or its absence has to be transduced to a chemical signal and this occurs in the pineal gland to which the information is carried from retina via a multisynaptic pathway. In the pineal gland the information of illumination is converted to a hormone, melatonin that in turn serves as a messenger to every organ in the body. Melatonin is synthesized during the dark period and the synthesis ceases rapidly in light (for reviews see Nelson & Demas, 1997; Malpaux *et al.*, 2001; Bartness *et al.*, 2002; Thiéry *et al.*, 2002).

The synthesis of melatonin starts from the amino acid tryptophan, which is first converted to serotonin, a neurotransmitter (Fig. 2). Two enzymes are needed to convert serotonin to melatonin. The first is arylalcyamine N-acetyltransferase (NAT, EC 2.3.1.87) which catalyzes acetylation of the amino group, and the other is hydroxyindole-O-methyltransferase (EC 2.1.1.4), which adds a methyl group to the hydroxyl group. The regulation of synthesis occurs through daily changes in the activity of NAT, which appear to be endogeneous, because the fluctuation continues even if the animals are kept in constant darkness (Vanacek, 1998). Also when the continuous illumination during the summer abolishes the circadian rhythm of melatonin secretion in reindeer, the pineal gland has not lost its capacity to release of melatonin, which starts rapidly if the reindeer are exposed to darkness (Eloranta *et al.*, 1992).

Melatonin is a small lipophilic molecule, which allows it to leave the cells of the pineal gland by diffusion and also to enter the target cells by the same method. The half-life of melatonin in serum is short, about 10 min. Melatonin is removed from

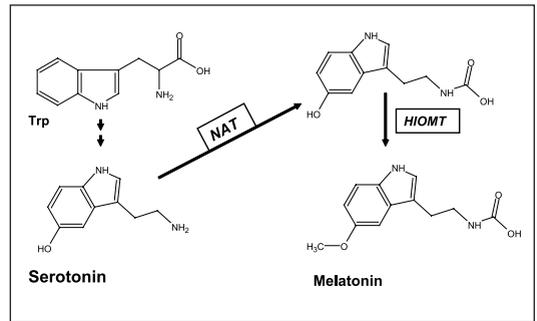


Fig. 2. Synthesis of melatonin. NAT = arylalcyamine N-acetyltransferase, HIOMT = hydroxyindole-O-methyltransferase.

circulation by the liver, which converts it to sulphate or glucuronide that are biologically inactive, no more lipophilic, and can be excreted in the urine (Vanacek, 1998).

Eloranta *et al.* (1995) have studied the seasonal changes in the daily fluctuations of melatonin concentrations in reindeer. During the dark winter season, the melatonin pulse is long and its amplitude is high, while during the summer release of melatonin is negligible. The duration of the pulse allows the reindeer to distinguish seasons with short daylight from those of long daylight. But along the year, in the spring and in the autumn the photoperiod is equally long and also the amplitude and length of the melatonin pulses around the equinoxes do not differ. To be able to distinguish whether it is spring or autumn, *i.e.* whether the duration of the pulse is increasing or decreasing, the reindeer has to have a memory of previous melatonin pulses. Malpaux *et al.* (2001) have in their review listed that the three main points that are the prerequisite for the effective role of melatonin in the regulation of circadian and more importantly the circannual cycles are (i) the absence or presence of melatonin, which enables to distinguish day from night, (ii) the duration of the pulse that is needed to distinguish short days from long ones and (iii) the direction of the change that is necessary to distinguish the season. There is evidence to support the view that the direction of the change is the most important factor to synchronize the physiological functions. In sheep it has been shown that the lengthening of days is critical to synchronize the reproductive rhythm and the shortening is necessary to time the rut and also to maintain its full duration (Woodfill *et al.*, 1991).

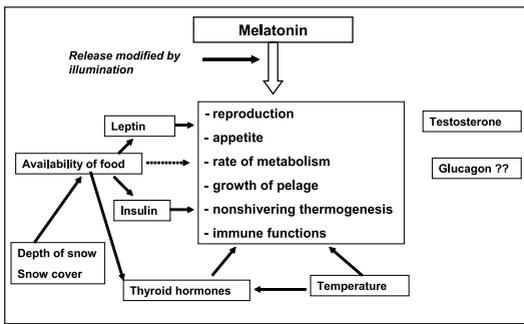


Fig. 3. Release of melatonin from the pineal gland is regulated by photoperiod, and the physiological effects of the melatonin are modified by several other hormones the concentrations of which also show seasonal variation.

The list of seasonal changes regulated or initiated by melatonin is long (Nelson & Demas, 1997; Carlberg, 2000; Malpoux *et al.*, 2001; Thiery *et al.*, 2002). Melatonin is needed to synchronize the rut so that calving occurs in the spring and enables better possibilities of survival for the offspring. Melatonin is also involved in the regulation of body mass, changes in voluntary feed intake, regulation of metabolic rate, nonshivering thermogenesis and growth of pelage. In the target tissue melatonin exerts its effect through binding to receptors which have been found both on the plasma membrane and in the nucleus (Williams *et al.*, 1996; Vanacek, 1998; Carlberg, 2000). Membrane receptors are found in the central nervous system, while in other tissues the receptors are inside the cells. Membrane receptors are found mainly in the pars tuberalis of the anterior pituitary and in many species also in the hypothalamus, although red deer and other ungulates may be devoid of the latter (Williams *et al.*, 1996). Membrane receptors of melatonin are coupled to a G-protein and binding of melatonin decreases the concentration of cAMP in the cell. The actions of melatonin are not mediated only through cAMP, because concentrations of several other signal molecules, such as those of the calcium-calmodulin signalling pathway, may be altered as well (Vanacek, 1998). The knowledge of the mechanisms of action of melatonin at the cellular level is scarce, although the reproductive and circadian actions at the level of central nervous system are assumed to be regulated through membrane receptors (Vanacek, 1998; Carlberg, 2000).

The intracellular receptors are probably present in all cells (Carlberg, 2000). When bound to the receptor, melatonin alters the phosphorylation of a group of transcription factors RZR/ROR that are known to regulate transcription of several genes. However, the physiological role of these actions of melatonin is not yet known.

In reindeer as in other species the effects of photoperiod and season on reproduction, changes in the voluntary food intake and metabolism are probably initiated through changes in the pattern of melatonin secretion, but the profiles of many other hormones, downstream from melatonin are also altered by photoperiod and availability of food and thus the changes in these compensatory signals may be required for the actions of melatonin (Fig. 3). These signals may include hormones, such as leptin, insulin and thyroid hormones. Leptin that is synthesized in the adipose tissue, affects the same physiological phenomena as melatonin, such as appetite, thermogenesis and activity of reproduction (Chilliard *et al.*, 2001; Morgan & Mercer, 2001; Friedman, 2002; Prentice *et al.*, 2002). In sheep the photoperiod may regulate the expression of leptin gene, but it is also inhibited by food deprivation (Chilliard *et al.*, 2001). In accordance to this a recent study by Soppela *et al.* (2003) shows that also in reindeer the serum concentration of leptin decreases during winter both in *ad libitum* fed and especially in undernourished reindeer calves. This finding is in accordance with the view that leptin plays a central role in the regulation of body energy homeostasis. Also concentration of insulin that is one of the key hormones to regulate metabolism, decreases during winter (Larsen *et al.*, 1985a; Soppela *et al.*, 2003). Decreases in insulin and leptin concentrations may be interconnected, because *in vitro* data suggests that pharmacological doses of insulin may promote the expression of leptin gene (Harris, 2000).

Thyroid hormones have a central role in the regulation of basal metabolic rate and their release increases at low ambient temperatures. In reindeer controversial results have been reported on the seasonal changes in T3 and T4 concentrations with a nadir occurring either in winter or summer while others have found no seasonal variation (Ryg & Jacobsen, 1982; Nilssen *et al.*, 1985; Timisjärvi *et al.*, 1994; Bubenik *et al.*, 1998). Thus it has been concluded that changes in the concentrations of thy-

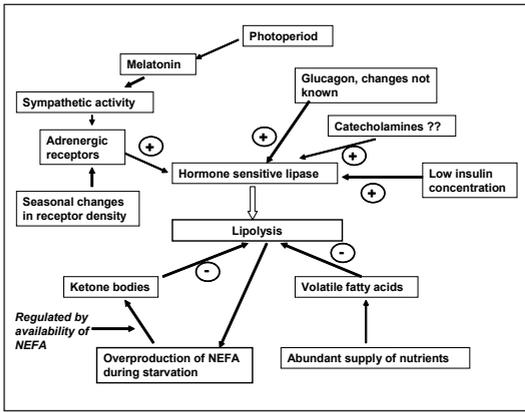


Fig. 4. Regulation of hormone sensitive lipase (HSL) and lipolysis in adipose tissue. + indicates a factor that increases the activity of HSL and – indicates inhibition.

roid hormones do not indicate variations in basal metabolic rate, but they rather fluctuate according to feeding (Ryg & Jacobsen, 1982; Ryg, 1984; Nilssen *et al.*, 1985).

Seasonal changes in energy balance

During winter energy balance of reindeer is negative. Appetite is reduced due to changes in concentrations of melatonin and leptin (Rhind *et al.*, 1998; Bartness *et al.*, 2002; Prentice *et al.*, 2002; Thiéry *et al.*, 2002), but also the availability and quality of food may contribute. The balance is also affected by the low temperatures that increase the demand of energy for heat production. To survive the reindeer is dependent on the energy stores that were deposited during the summer season, when the availability of good quality forage is abundant (Larsen *et al.*, 1985c; Suttie & Webster, 1995; Gerhart *et al.*, 1996). The strategies the reindeer uses to survive include good insulation, with the lower critical temperature as low as -30°C (Nilssen *et al.*, 1984b), and the decrease in resting metabolic rate which is accompanied by less time spent moving (Nilssen *et al.*, 1984a, 1984b; Cuyler & Øritsland, 1993).

One of the most pronounced changes is the marked decrease in the voluntary feed intake during winter, a finding that is apparent also when the reindeer are fed high quality feed all year round (McEwan & Whitehead, 1970; Ryg & Jacobsen, 1982; Nilssen *et al.*, 1984b; Larsen *et al.*, 1985c; Mesteig *et al.*, 2000). Although it is known that hormones such as melatonin and leptin affect appetite, correlations

between feed intake and hormone concentrations are generally low (Rhind *et al.*, 2000). This has been taken as an indication that single samples taken at interval of several days cannot adequately describe the relationship (Rhind *et al.*, 2000). Likewise the question whether the decrease in appetite precedes that in metabolism or vice versa is still an open. There is evidence to suggest that the adaptations of voluntary feed intake are initiated by the changes in the secretion of melatonin, with many other hormones downstream from melatonin probably contributing as well (Rhind *et al.*, 1998), but also data to suggest that metabolic changes precede those of appetite has been reported (Thiéry *et al.*, 2002).

Because the availability of food cannot be predicted in the early winter the survival strategy has to be based on economic and controlled use of energy stores. About 85% of energy is stored in the body fat deposits under the skin, around internal organs, such as heart and kidneys, and also in the bone marrow. The other major form of energy is body protein, which accounts for almost 15% of energy in the body. Carbohydrate, mainly glycogen in the liver and muscles, although important during acute stress situations, does not play any major role in the survival.

Circannual changes in lipid metabolism

The use of lipids during winter has been demonstrated in several studies. Usually the stores are at maximum in October and reach a nadir in April – June (Larsen & Blix, 1985; Gerhart *et al.*, 1996). The amount of lipid stored or the decrease in fat stores is determined by the balance between the rates of lipolysis and lipogenesis. Studies on Norwegian reindeer have shown that adaptive changes occur in both of these (Larsen *et al.*, 1985c). In adipose tissue lipolysis is catalyzed by hormone sensitive lipase (HSL), the activity of which is under hormonal control by insulin, catecholamines and glucagon (Fig. 4). Insulin is a very potent inhibitor of HSL, while catecholamines and glucagon activate it. As stated above, the concentration of insulin is low during winter (Larsen *et al.*, 1985a; Soppela *et al.*, 2003), a condition that favours lipolysis. Of the other hormones that regulate lipolysis, adrenaline and noradrenaline show no significant seasonal changes (Larsen *et al.*, 1985a), and nothing is known about the annual changes in the concentrations of

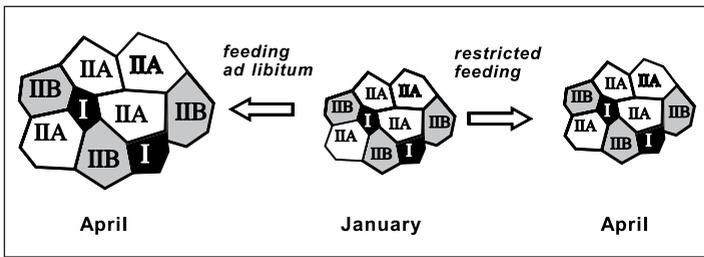


Fig. 5. Changes in cross sectional area in the middle gluteal muscle in reindeer calves. One group of calves was fed a pelleted feed *ad libitum* and the other group was fed lichens at 60% level of *ad libitum* intake.

glucagon. Thus it has been suggested that serum concentrations of catecholamines do not explain the elevated rate of lipolysis, although the stress caused by sampling may partially mask the changes in their concentrations. The activation of lipolysis may also be regulated via sympathetic activity, possibly by melatonin (Bartness *et al.*, 2002), and the subsequent release of noradrenalin from neurons. Because the observed rate of any physiological event regulated by several hormones is a sum effect of all hormones in question, it can be suggested that the low concentration of insulin and concentrations of catabolic hormones together with the neuronal activation result in increased rate of lipolysis. In reindeer lipolysis is increased in a controlled manner. This is indicated by the stable serum concentrations of nonesterified fatty acids over the main part of the winter (Larsen *et al.*, 1985a; Soveri *et al.*, 1992; Bubenik *et al.*, 1998; Soppela *et al.*, 2000) with increases in ketone bodies that would be an indication of massive increase in lipolysis occurring only in early spring (Soveri *et al.*, 1992; Soppela *et al.*, 2000). The increase in ketone body concentrations is apparent also in reindeer that are fed *ad libitum* high quality feed throughout the winter (Pösö *et al.*, 1994; Soppela *et al.*, 2000).

What controls lipolysis during winter? The regulation of lipolysis and lipogenesis are regulated in such a manner that they are not active simultaneously and thus during winter the rate of lipogenesis is low, while during summer, when the availability of high quality feed is abundant, lipogenesis is the predominant pathway (Larsen *et al.*, 1985c). The data on isolated adipocytes suggest that in winter the enzymes of the lipogenic pathway are downregulated (Larsen *et al.*, 1985c). On the other hand the activity of hormone sensitive lipase, the

key enzyme in lipolysis, is higher in winter in comparison to values measured in summer (Larsen *et al.*, 1985b). However, in isolated adipocytes the stimulation of lipolysis by adrenalin is less in winter than in summer, which suggests that lipolytic capacity is regulated also at receptor/post-receptor level (Larsen *et al.*, 1985c). In addition volatile fatty acids and ketone bodies have been found to

regulate lipolysis in isolated adipocytes (Larsen *et al.*, 1983). In summer, when the feed intake and the production of volatile fatty acids in the rumen are high and there is no need for mobilization of lipids, volatile fatty may control lipolysis. If the rate of lipolysis during winter increases above the level needed for energy, the oversupply of free fatty acids will increase the production of ketone bodies that in turn slow down lipolysis (Fig. 4). Furthermore reduced activity of 3-hydroxyacyl-CoA dehydrogenase in muscles during winter suggests that their capacity to use of fatty acids may be decreased (Kiessling *et al.*, 1986; Pösö *et al.*, 1996).

Seasonal changes in protein metabolism

In comparison to our knowledge on lipid metabolism very few studies have been performed on annual changes in protein metabolism. Protein as an energy source differs from carbohydrates and lipids, because there is no special storage protein, such as triglycerides for lipids or glycogen for carbohydrates. Thus when protein is broken down at a rate that is higher than the synthesis of proteins there will be loss of structural elements or enzymes that are needed to catalyze the metabolism. Thus only during extreme starvation does protein degradation occur to any greater extent.

A special feature of protein metabolism in reindeer is that lichen, which is the main winter feed, is low in nitrogen (Nieminen, 1980). This together with reduced feed intake results in strongly negative nitrogen balance during winter (McEwan & Whitehead, 1970; Gerhart *et al.*, 1996). This is demanding for the reindeer, especially to pregnant females that have to use their own tissues to produce amino acids for the growing fetus and later in spring for milk proteins. Reindeer are extremely well adapted

to large variations in the nitrogen content and may have a greater potential to recycle urea than domestic ruminants (Wales *et al.*, 1972). Thus a decrease in urea concentration is frequently seen in winter (Soveri *et al.*, 1992; Pösö *et al.*, 1994), a finding that has been taken as an indication that the recycling of urea to rumen is more effective during the winter. Increases in urea concentrations during winter may indicate severe starvation and greatly increased utilization of protein as an energy source (Valtonen, 1979).

The body protein mass is greatest in October and lowest in late spring (Gerhart *et al.*, 1996) and the loss of protein over winter may be up to 29%. It has been suggested that Svalbard reindeer that live in extremely harsh conditions, may use IIB fibres in their muscles as a protein source during winter (Kiessling & Kiessling, 1984). This was indicated by the decrease in the cross sectional area of these fibres. To study whether moderate undernutrition also causes reduction in the IIB fibre area Finnish reindeer calves were fed lichens for 6 weeks at a level that was 60% of their *ad libitum* intake of lichens (Pösö *et al.*, 2001). Other calves fed *ad libitum* with commercial feed served as controls. Although the calves in the lichen group lost about 8.8 kg of weight, the cross sectional area of all muscle fibre types remained unchanged during the starvation period (Fig. 5). In the control group there was an increase in the fibre area indicating that the rate of protein synthesis was greater than that of protein degradation. Interestingly the activity of cathepsin B, one of the proteolytic enzymes in the lysosomes, measured as an indicator of lysosomal protein degradation, was also decreased indicating that a similar control of protein catabolism prevails as seen in the controlled lipolysis over the period of low availability of food (Pösö *et al.*, 2001).

In summary, the seasonal changes in the growth, energy metabolism and reproduction of reindeer show that the reindeer are well adapted to the arctic climate. Our understanding on the physiology of these changes is increasing, but still very little is known about the molecular mechanisms. The role of photoperiod and thus melatonin as the major regulator is accepted, but the role of other hormones, such as leptin, insulin, glucagons and thyroid hormones, is less clear and even less is known about the interactions of the hormonal effects.

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Abstract in Finnish / Tiivistelmä:

Valaistus, lämpötila ja ravinnon saatavuus vaihtelevat vuodenajan mukaan. Jotta nämä muutokset voisivat saada aikaan adaptiivisia muutoksia porossa, ne täytyy muuttaa hormonisignaaleiksi. Luotettavin näistä edellä mainituista ympäristön vuodenaikaismuutoksista on valo, joka vaikuttaa poron elintoimintoihin käpylisäkkeen ja sen erittämän hormonin, melatoniinin, välityksellä. Melatoniinin plasmapitoisuuksissa on havaittavissa selkeä vuorokausirytmä, joka porolla häviää kesällä ja alkaa uudestaan syksyllä. Melatoniini-hormonin vuodenaikaisvaihtelut ovat mukana säätelemässä lisääntymistä, talvikarvan kasvua, lämmöntuottoa, elopainoa ja immuunitoimintoja. Melatoniini vaikuttaa geeniaktivaation kautta mekanismeilla, joita ei vielä tarkkaan tunneta. Muita hormoneja, joiden erityksessä on havaittu vuodenaikaisvaihtelua, ovat kilpirauhashormonit, insuliini ja leptiini. Havaitut muutokset ovat ilmeisesti usean hormonin yhteisvaikutuksen aiheuttamia. Ruokahalu sekä energian- että lämmöntuotto ovat keskeisiä hengissä säilymisen kannalta. Talvella poron energiatase on negatiivinen ja se käyttää lähinnä varastoimiaan rasvoja energian tuottoon. Rasvojen käyttö on ekonomista, sillä rasvojen hajoaminen, lipolyysi, on säädeltyä ja rasvahappojen käyttö lihaksissa vähenee talvella. Vasta vakavasti nälkiintyneissä poroissa lipolyysi aktivoituu siten, että myös ketoaineita alkaa kertyä vereen. Valkuaisainemäärä vähenee vähemmän kuin rasvojen ja ainoastaan nälkiintyneet porot käyttävät lihasten valkuaisaineita energiantuottoon. Poron talviravinnossa, jäkälässä, on vain vähän tyyppä, joten talvisin tyyppitasapaino on voimakkaasti negatiivinen. Poro reagoi tähän vähäiseen tyyppimäärään lisäämällä urean kierrätystä pötsiin. Kokonaisuudessaan poron elintoimintojen sopeutuminen auttaa poroa selviytymään talven yli. Vaikka adaptaatiosta on joiltakin osin kertynyt runsaasti tietoa, on siinä myös paljon selvitettävää.

Domestication of ruminant livestock and the impact of nematode parasites: possible implications for the reindeer industry

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Abstract: In a balanced ecological system, both host and nematode parasite populations are firmly controlled by a complex array of interacting factors. However domestication of livestock has tipped the balance in favour of the parasites. This is due to increasing the proportion of susceptible animals in the herd or flock (lactating females and weaned young animals), increasing stocking rate, increasing productivity demands and decreasing the movement of the animals. In contrast with microbial infections, where multiplication takes place entirely within the host, metazoan parasites have both a parasitic phase and a free-living phase. Every worm present has been separately acquired by the ingestion of free-living stages on pasture. Immunity to nematodes develops slowly, it is labile, and its maintenance is dependent upon a good nutritional state of the animal. Consequently, worm parasites are ubiquitous wherever livestock are kept and they impose a constant and often a high infectious pressure on grazing animals. Nematode infections in grazing livestock are almost always a mixture of species. All have deleterious effects and collectively lead to chronic ill thrift. Economic evaluations repeatedly show that the major losses due to parasites are on animal production, rather than on mortality. This paper focuses on the problems of nematode parasites; problems associated with drug use (anthelmintic resistance, environmental impact) and costs of nematode infections for the common ruminant livestock industries (cattle, sheep, goats), with possible analogies for the semi-domesticated reindeer industry.

Key words: domestication, losses, nematodes, parasites.

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Introduction

Few people realise that there are far more kinds of parasitic, than non-parasitic, organisms in the world. Even if viruses and rickettsias, which are all parasitic, as well as the many kinds of parasitic bacteria and fungi are excluded, the parasites are still in the majority (Schmidt & Roberts, 1981). In general, the parasitic way of life has proven to be highly successful, since it has evolved independently in nearly every phylum of animals, ranging from protozoa, to multicellular invertebrates, and even to chordates.

Parasites are organisms that live at the expense of their host and, in doing so, have undergone

some degree of evolutionary change, or adaptation, to survive within their hosts (Ebert & Herre, 1996). This is based on immunological phenomena (Maizels *et al.*, 2001). In contrast to the unicellular parasitic organisms (bacteria, protozoa), which are capable of very rapid replication within the host (hours), the metazoan parasites (helminths: nematodes, trematodes, cestodes) must remain in their hosts for a much longer period of time before they can successfully complete their life cycle, which generally takes several weeks. These long-lived helminth parasites are highly accomplished practitio-

ners of immune evasion and manipulation, using strategies honed during their long co-evolutionary interaction with the immune system of their mammalian hosts (Behnke *et al.*, 1992; Allen & Maizels, 1996). Thus, multicellular helminths present very different infection dynamics from the micro-parasites (viruses, bacteria and protozoa) as they do not replicate within the host, and parasite loads increase only as a result of accumulated exposure to infection (Barger *et al.*, 1985; Dobson *et al.*, 1990; Maizels *et al.*, 2001).

Helminth parasites do not outpace the immune system of the host by faster cell division, or rapid antigenic variation (Maizels *et al.*, 1993). Rather, their strategy seems to be one of stealth by defusing aggressive immune reactions and inducing forms of immunological tolerance to permit their long-term survival within their hosts (Dineen, 1963; 1978; Maizels & Lawrence, 1991). Therefore in contrast to the microbial infections where the host recognises their "foreign-ness" and very quickly induces a strong immune response to infection, or following vaccination with efficacies approaching 100% (Emery, 1996), host immunity to worm parasites is slow to develop, is labile and easily destroyed by any form of stress (Cox, 1997). Much research has been done, and is still being conducted, into the mechanisms of naturally acquired immunity to helminth parasites of ruminant livestock, but the final effector mechanisms are not known. Unfortunately from the standpoint of attempting to develop successful helminth vaccines for ruminant livestock, the situation seems complex, involving a combination of local hypersensitivity, cell mediated, antibody and inflammatory responses and is complicated further by the natural unresponsiveness which exists in the young animal and the dam around parturition (Smith, 1999). As a consequence, nematode parasites are ubiquitous wherever livestock are kept and they impose a more-or-less constant infectious pressure on grazing animals.

Effect of domestication on livestock

In a balanced ecological system both host and parasite populations are firmly controlled by a complex array of interacting forces. However domestication of livestock has tipped the balance in favour of the parasites. This is because of the following factors:

Restriction in livestock movement

Reduction in livestock movement to sedentary forms of management is an almost invariable consequence of domestication. Apart from the time taken to complete their life-cycle, another important difference between the microbes and nematodes is the pattern of their life cycles. For microbes, reproduction occurs within the host, whereas for all economically important nematode parasites, their life cycle involves both an obligatory free-living phase on pasture as well as a parasitic phase within the host. Thus every worm present in an animal is derived from its ingestion by the animal through grazing on pasture. In wild ruminant populations (*eg.* African ungulates) movement is primarily dictated by food supply, and characteristically they migrate over considerable geographic ranges. Likewise in nomadic and transhumance herding, animals are typically moved over long distances. Thus in many instances in the above situations, animals leave their faeces, containing the free-living stages of potentially future worm generations, behind them on pasture (Macpherson, 1994; Eckert & Hertzberg, 1994). They return often at a much later date, when these free-living stages are likely to have declined to very low numbers.

Restricting the movement of animals from this otherwise natural migration, or transhumance herding, to more sedentary systems of management, greatly increases the chances of animals being exposed to infection by grazing contaminated pastures. The environmental factors that determine the speed and success of the translation of nematode eggs to infective larvae are temperature and humidity. In the humid tropics and sub/tropics where both of these factors are invariably high, auto-infection (animals being infected by parasites derived from their own contamination) can occur within a few days (Banks *et al.*, 1990). However in milder locations and those where there can be seasonal discontinuities in rainfall, the development of worm eggs to infective larvae tends to be more protracted (Stromberg, 1997), although survival on pasture is also longer (Barger, 1999).

In addition, domestication often forces animals that have a natural tendency to browse on shrubs to a greater-or-lesser extent (*eg.* camels and goats), to graze on pasture as generally this represents the only available food supply. Such browsing animals

have not evolved to be highly resistant to nematode parasite infection (Pomroy *et al.*, 1986), as is the case with some indigenous or “unimproved” breeds of sheep, where the formidable combination of malnutrition, environmental stress and long-term and often massive larval challenge on pasture have imposed the harshest conditions for selection, resulting in survival of the fittest (Baker, 1996).

Although, in general, the semi-domesticated reindeer industries of Fennoscandia still practice herding over extensive areas, these are now often restricted by fencing to lands managed as co-operatives, made up generally of a large number of individual owners who communally graze their animals (Oksanen, 1999). In addition, natural grazing areas for reindeer are progressively diminishing, due to alienation to other priorities for land use. This artificially imposed restriction would mean that animals remain longer, and return sooner, to particular areas of land, thus potentially exposing the herd to greater parasite challenge. Also with the decline in browse available for reindeer, there is a tendency for co-operatives to provide more cultivated pastures as a feed substitute (Kumpula, 2001). Potentially this would also expose the animals to greater parasite pick-up.

Increasing stocking rate

Increasing stocking rate must of course be accompanied by providing more feed to the animals for them to remain productive. In the conventional ruminant livestock systems, such as cattle, sheep and goat production, this is generally achieved by improving pasture production (better pasture plants), often providing fertilizer and additional watering (irrigation) to improve pasture growth. However, enhanced productivity of pasture following application of fertilizer often fails to improve overall animal production (Speedy, 1980), and a commonly held view is that increasing stocking rate leads to increasing levels of parasitism in grazing livestock. This has prompted a number of studies to investigate such a relationship, particularly with studies on sheep in the temperate countries of the world, with mixed results. Although there was no positive correlation between stocking rate and parasitism in a number of studies (Spedding *et al.*, 1964; Cameron & Gibbs, 1966; Downey & Conway, 1968; Waller *et al.*, 1987), these were based on assessments of

performance in young lambs up to weaning or marketing at around 3 – 4 months of age when the effects of parasites would have been too early to have any marked effect. However equally a number of studies have shown a direct relationship between increasing stocking rate and increasing parasitism of livestock (Zimmerman, 1965; Downey, 1969; Southcott *et al.*, 1967; 1970; Beveridge *et al.*, 1985; Brown *et al.*, 1985; Thamsborg *et al.*, 1996).

The impact of increasing stocking rates in relation to increasing risk of internal parasitism does not necessarily translate to the reindeer industry, but certainly more feed is now being provided at times of nutritional stress (generally winter) to keep the increasing numbers of animals alive. Within the last several decades, the increasing numbers of reindeer has clearly exceeded carrying capacity in parts of Norway and Finland (Kojola & Helle, 1993; Kumpula *et al.*, 2002; Moen & Danell, 2003). In attempts to offset this feed shortage, increased supplementary feeding is being practiced (Helle & Kojola, 1993). However, increasing numbers of animals naturally puts greater grazing pressure on pastures and in turn potentially results in greater parasite pickup of the animals.

Increasing number of susceptible animals

Profitability of any grazing livestock industry is largely driven by product output. This translates into raising more animals on any given area to produce more meat, fibre and hides. Thus man-made changes to herd, or flock structure result in more reproducing females and their progeny. For ruminant livestock, both the lactating female and the young animal (< 1 year of age) are the most susceptible to nematode infections (Dineen & Outteridge, 1984). The so called “periparturient relaxation of resistance” to worm infection is well known in sheep, goats and cattle (Connan, 1976; Barger, 1993). There is no maternal transfer of immunity (via placenta, or milk) to nematodes in the young ruminant (Meeusen, 1996). So actively growing, but worm naïve, young animals are particularly susceptible to infection in their first year of life (Stear & Murray, 1994). For example, the age at which young sheep acquire natural resistance to nematode infections is usually 7-10 months (Gibson & Parfitt, 1972, Dobson *et al.*, 1990), but this can be delayed by insufficient exposure to infection (Stewart &

Gordon, 1953; Gibson *et al.*, 1970), or by poor nutrition (Abbott *et al.*, 1985a; 1985b).

Increasing productivity demands

Coupled with the pressure of increasing reproductive rate, livestock producers also strive for increasing the amount of animal product, such as meat, milk and wool from their herds or flocks. Depending on the age and metabolic condition of animals, they allocate food resources (*i.e.* energy and/or various nutrients) among their body functions (Coop & Kyriazakis, 1999). Such body functions include the usual ones such as maintenance, growth and reproduction, but also additional functions that are a direct consequence of parasite infection. Studies on the patho-physiology of internal parasite infection show a metabolic drain caused by increasing endogenous loss of protein (Symons & Jones, 1975) and a reduced efficiency in the utilization of metabolisable energy due to parasite infection (Sykes & Coop, 1976). Clearly the increase in parasite challenge associated with contemporary livestock production systems must come at a price with regards to animal productivity, particularly at times of sub-optimal nutrient supply, when the animal has to prioritise the allocation of scarce nutritional resources.

Nematode host specificity

Alternate grazing between sheep and cattle can be a very effective form of parasite control for both livestock species, provided that the grazing alternations are linked with the seasonal troughs in larval availability on pasture. From a practical standpoint, cross-transmission of parasites from one host to the other is of little consequence. In the temperate regions of the world, excellent control of parasites from both species of livestock can occur from very infrequent pasture interchange (Barger & Southcott, 1978) and if the timing is epidemiologically precise, pasture changes need not be accompanied by anthelmintic treatment (Donald *et al.*, 1987). However, care must be exercised in simply transferring such schemes to the tropics and subtropics, without first conducting ecological studies on the free-living stages of parasites in these environments. Similar benefits may result from interchange grazing, but the grazing intervals will, almost certainly, need to be shorter. Also control of *Haemonchus contortus* may prove difficult. In the more temperate regions this

species can cycle in calves but they rapidly acquire natural immunity to become refractory to infection by 12 months of age (Southcott & Barger, 1975). In the tropics this age resistance is slower to, or may never, develop. For example, in Paraguay there was no indication that cattle had acquired significant immunity after two years of grazing (Benitez-Usher *et al.*, 1984).

With domestication, it is inevitable that reindeer have come into closer contact with other species of domestic livestock. This is quite evident in the distribution range of reindeer in Fennoscandia, particularly so with sheep and goats in the Norwegian reindeer herding regions. A number of parasite species, considered to have domestic ruminants as their definitive hosts, have been reported in reindeer, particularly *Teladorsagia (Ostertagia) circumcincta* of sheep. It has been suggested that *T. circumcincta* represents a cryptic species complex, which may also be the case for *Ostertagia gruehneri*, which has been reported in roe deer (Dallas *et al.*, 2000; O. Halvorsen, pers.comm.).

The only reasonably comprehensive assessment of cross-transmission between parasites of reindeer and other livestock species has been done with the brain-worm *Elaphostrongylus* spp., which is also found in moose. This parasite is responsible for severe outbreaks of meningo-encephalitis after warm and moist summers (Handeland & Slettback, 1994). However, it has been established that different species of this parasite are found in reindeer and moose and these parasites are specific to their hosts (Steen *et al.*, 1997).

Also with domestication comes the opportunity for greater contact with the companion animals (dogs, cats) of man. In this regard, reindeer can play an important role with parasite zoonotic disease; that is, parasites of animals that can infect man. The two most significant are the dog tapeworm, *Echinococcus granulosus*, where the intermediate (cystic) phase, referred to as “hydatids”, has been a major problem in the reindeer herding communities (Skjenneberg, 1959; Huldt *et al.*, 1973) and toxoplasmosis caused by the protozoan *Toxoplasma gondii* of cats. Human infections of *T. gondii* are particularly serious if they occur during pregnancy and may result in abortion or congenitally acquired disorders, which primarily affect the central nervous system. Toxoplasmosis has recently emerged as a potentially serious

disease in reindeer (Oksanen *et al.*, 1996) and has been associated with increased corral feeding of reindeer and by implication, increased contact with cat faeces (Oksanen *et al.*, 1997).

Chemotherapy

There has been a continual battle by livestock owners to control worm parasites in their flocks, or herds, that have come with the changes associated with domestication. This battle has relied almost entirely on the use of chemotherapy, namely anthelmintics, or known colloquially as “de-worming” compounds. Over the last 50 years there have been some remarkable developments in anthelmintic discovery and development. Now there exists a seemingly formidable array of very highly effective, very safe compounds with a very wide spectrum of activity to control internal parasites of livestock (McKellar, 1997), but the broad spectrum drugs fall into just 3 groups or classes, namely:

- *Group 1:* the benzimidazoles / probenzimidazoles
- *Group 2:* the imidazothiazoles / tetrahydropyrimidines
- *Group 3:* the avermectins / milbemycins (or macrocyclic lactones)

Anthelmintic resistance

For anthelmintics used to control nematode parasites of small ruminants (sheep and goats), high levels of resistance now exist to two (Group 1 and 2) of the three main broad-spectrum anthelmintic groups (Waller, 1994; 1997a). However resistance to the only remaining group, the macrocyclic lactones, is now rapidly increasing in the most economically important nematodes of sheep and goats (Sangster, 1999). There are now instances, such as in Malaysia, southern Brazil, Paraguay and South Africa, where farmers abandoned farming of sheep and goats because of uncontrolled parasitic disease with annual mortalities exceeding 20%, due to total anthelmintic failure (van Wyk, 1990; Maciel *et al.*, 1996; Chandrawathani *et al.*, 2004).

Resistance in cattle nematodes appears to be spreading, but the reports are localised isolations. Most concern surrounds ivermectin resistance that has now been reported in *Cooperia* spp. in several countries in the southern Hemisphere (Coles,

2002). The macrocyclic lactone anthelmintics are so widely used for parasite control in cattle that the treatment failure because of resistance would be serious indeed.

The macrocyclic lactone drugs are exceedingly potent and their spectrum of activity, which includes not only nematode parasites but also arthropod pests, thus they are commonly referred to as endectocides. With the additional advantage of being administered by injection, these drugs (particularly the forerunner, ivermectin) have been a great boon to the semi-domesticated reindeer industry of Fennoscandia. The use of injectable ivermectin in this region is widespread. For example in Finland, estimates show that approximately two-thirds of the total overwintering reindeer population are treated with this drug (Nieminen, 1984; 1989). Concerns have been expressed that because of the almost exclusive use of ivermectin by reindeer owners, resistance may emerge in any of the target parasite species (Waller, 1990). Although the frequency of ivermectin treatment of reindeer is low, with the majority of animals treated with ivermectin only once per year (Oksanen *et al.*, 1992), this is more-or-less synchronous with the gathering of animals in early winter at the time when free-range grazing ceases and the larval stages of the warble fly (*Hypoderma tarandi*) have not penetrated the hide of the animals. Such strategic use of anthelmintics, even when the frequency of treatment is very low, can impose a powerful selection for resistance as the timing is chosen to coincide with a very high proportion of the parasite population being present in the animals. Field evidence to this effect comes from the very rapid selection for ivermectin resistance in the nematode parasite of sheep, *T. circumcincta*, following just two treatments / year (during summer) in the Mediterranean climatic conditions of Western Australia (Besier, 1997).

Drug resistance in any organism, including worms, is genetically determined and every time a drug is used there is the possibility to select for those individuals in the targeted pest population that are resistant. If the proportion of the population that escapes exposure to drug selection (refugia) is very small, then those individual parasites that survive treatment will have an enormous survival advantage to pass on resistance genes to their progeny (Dobson *et al.*, 2001). Although the chanc-

es of this occurring within parasite populations of reindeer might seem remote, the threat will always be present, particularly if ivermectin alone remains the drug of choice.

New anthelmintics classes?

It is unlikely that an entirely novel anthelmintic class, or group, will become commercially available in the foreseeable future. This is because of the high development costs, high risks and the expected poor return on investment to the pharmaceutical industry (Waller, 1997b). Irrespective of this, resistance is mainly a problem in the Developing World and with sheep and goat industries, which account for a relatively small share of the parasiticide market (Waller, 1997c). Thus there is little commercial incentive for drug companies to search for new active anthelmintic compounds for the ruminant livestock industry, let alone proceed with these down the development track towards marketing a new commercial product.

Anthelmintics and the effects on the environment

Apart from the avermectins, there has been very little published information on the impact of excreted anthelmintics, or their metabolites, on the environment (Waller, 1993). However, the effect of ivermectin excreted in the dung of treated animals still remains an issue of continued controversy (Herd *et al.*, 1993; Wiktelius, 1996; Edwards *et al.*, 2001). There is no doubt that this drug has profound effects on the larval stages of certain coprophilic arthropods (Steel, 1997), but limited information is available on the effects of this drug on either micro-organisms, or saprophytic nematodes in the external environment. To address this latter issue, recent environmental impact studies on the use of ivermectin bolus in young cattle in Sweden have focused on soil nematode dynamics (Yeates *et al.*, 2002; 2003). Additionally, the influence of ivermectin on cattle dung pat disintegration over three grazing years was studied (Dimander *et al.*, 2003). The results of all these Swedish investigations showed that there was no effect on total numbers, diversity, or functional groups of soil nematodes. Also there was no delayed breakdown of dung pats from ivermectin bolus treated cattle.

Arthropods are only part of the diverse array of organisms that play a role in dung breakdown. It

is also important to note that these arthropods are highly sensitive to the prevailing weather conditions (ideally suited to warm moist conditions) and are only attracted to freshly deposited dung. On this basis, it can be assumed that dung beetles and coprophilic flies play an insignificant role in the destruction of dung of reindeer treated with ivermectin in early winter. Breakdown of such dung has been observed to be slow and does not occur until the thaw of the following spring (Nilssen *et al.*, 1999). In addition to abiotic factors (eg. sun, rain, frost and wind), soil nematodes and micro-organisms are primarily responsible for this activity (Stark *et al.*, 2000). No long-term studies have been conducted on the effect of ivermectin residues in dung and surrounding soil on these latter organisms. Species diversity has been shown to be much less in extreme environments, such as in the arctic region, than in more temperate climates. This makes these former environments particularly sensitive to any man-induced changes. On this basis, it is of fundamental importance to conduct environmental impact studies on the effect of any chemical use that would ultimately end up in the arctic environment. This particularly applies to any chemical, such as ivermectin, that has been shown to have detrimental effects on non-target organisms in more equitable environments.

Costs of worm parasites

There are instances where livestock production systems are so ecologically out-of-balance that parasites have the potential to overwhelm their hosts unless they are kept in check by frequent drug treatment. Such systems are unsustainable. The inevitable penalty for suppressive anthelmintic treatment is the development of very high levels of resistance across the entire range of available anthelmintics, with the ultimate consequence that farmers are forced into abandoning their livestock enterprises (van Wyk, 1990; Maciel *et al.*, 1996). The costs of parasites to such livestock producers are obvious.

Although the vast majority of livestock production enterprises never reach the above extremes, worm infections occur in all grazing livestock, are almost always mixtures of species and collectively may lead to chronic ill thrift. In many cases this is not obvious to the livestock owner. However, these sub-clinical, or hidden costs of nematode parasite

infection, particularly in young ruminants, can be substantial (Perry & Randolph, 1999; McLeod, 1995).

Recently an exhaustive review was conducted (Perry *et al.*, 2002) to prioritise animal health research for poverty reduction in the Developing World on behalf of the major donors and international partners in improving animal health in these regions, such as the Food and Agriculture Organisation (FAO), the World Organisation for Animal Health (OIE) and the World Health Organisation (WHO). The report concluded that nematode parasite infections had the highest ranking in the global index of animal health constraints confronting the poor owners of livestock. *H. contortus*, the highly pathogenic nematode parasite of sheep and goats, was singled out as being of overwhelming importance.

Attempts to estimate the costs of parasites in reindeer have been made. For example, infestations by the larval stages of warble flies (*H. tarandi*) and throat bots (*Cephenemyia trompe*) were estimated to cause in the order of 15-30% lost production to the Swedish (Nordkvist, 1967) and Soviet (Saval'ev, 1968) reindeer industries. Notwithstanding the fact that these estimates were made more than 30 years ago, before the advent of the macrocyclic lactones, it is difficult to understand how these workers could partition the costs of larval stages of arthropods from concurrent nematode infections. Irrespective of whether or not one considers these estimates to be no more than wild guesses, it is probable that worm infections in semi-domesticated reindeer have increased in their prevalence and intensity since this time. Therefore by analogy with other livestock industries the costs of parasite infections to the reindeer industry would be very significant.

Conclusion

Domestication of ruminant livestock has disturbed the ecological balance, which has evolved between the animals and their parasites. As a consequence of imposing sedentary grazing systems, increasing stocking rate, modifying the age distribution, increasing productivity demands within livestock populations, parasites now have much greater opportunities. These man-made changes have increased the exposure pressure of parasites on their livestock hosts. As a consequence, parasite-induced productivity losses, and in certain circumstances mortalities, can be enormous (Chandrawathani *et al.*, 2004). For those livestock owners who can afford it, the use of anthelmintic drugs has been the mainstay for control. But the development of resistance by nematode parasites to these drugs, concerns about the effect of drug residues in animal products and the environment have necessitated a complete re-evaluation of parasite control in contemporary livestock grazing systems (Waller, 1997b; 1999). Coinciding with this have been economic evaluations and these show that internal parasitic infections are the greatest infectious disease problems that currently face the domestic livestock industries.

By analogy, the same is likely to apply to the semi-domesticated reindeer industry. Most of the parasitological studies on reindeer have been restricted to the wild populations on Svalbard and in South Norway (Halvorsen & Bye, 1999), which of course differ considerably from the management and environment of the semi-domesticated reindeer of Fennoscandia. Current studies on parasite population dynamics, control options and their environmental impact (Hrabok *et al.*, 2003) will provide answers to some of these issues of concern regarding the management of reindeer in semi-domesticated situations.

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Number of wild and domestic reindeer in Russia in the late 20th century

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Abstract: The dynamics of wild and tame reindeer populations in Russia during 1991-99 are described. Causes of declining numbers during this period are suggested and comparison is made with population fluctuations in the past.

Key words: population status, *Rangifer tarandus*.

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Introduction

During 1991–99, there was a crisis in management of wild and tame reindeer in Russia and wide spread over-exploitation of their populations. This was connected with a general breakdown of socio-economics conditions following the dissolution of the Soviet Union. Both hunting harvest from wild reindeer and from reindeer husbandry lost state financial support for management. Humans of the Russian North suffered from malnutrition and practiced unrestricted hunting of wild reindeer as well as uncontrolled slaughtering of tame reindeer.

After 1991, the system of collecting information on wild and domestic reindeer was discontinued for lack of funds. In some areas, however, due to the enthusiasm of a few scientists, expert estimations, at least, were provided. Not until 2000, did the state provide significant funding to enable aerial surveys of reindeer to be conducted.

The aim of this paper is to present information on dynamics of numbers of wild and domestic reindeer in Russia during the last decade of the 20th

century. A comparison of these data is made with the wild and domestic reindeer population peaks in 1970s and 80s, as well as with the situation in recent years. Suggested causes of the changes in numbers are discussed.

Methods

Winter counting of reindeer tracks is a regular practice in Russia. Officers of each regional hunting management district conduct counts of tracks on snow and send reports to regional and Russian National authorities. Using a formula for collating these data (Baskin & Lebedeva, 1987; Lomanov, 2002), reindeer density and general numbers are calculated in each region. This method has shortcomings because of inadequate coverage of all areas and non-uniform distribution of reindeer. However the data are useful for following general trends of numbers.

Aerial surveys are the main source of data on reindeer numbers in Russia. Three aerial survey methods have been used. The first involves animal

counting on routes with use of fixed-wing aircraft when small groups of reindeer are sparsely distributed but plainly visible in a large region. It has been used in the surveys conducted by the National authority (Tsentrokhokontrol) that is responsible for game animal counting (Novikov, 1996a; Paponov, 2000; Lomanov, 2002). The second method was used to count reindeer gathered in wintering grounds. This method was used mostly in mountain areas of Evenki Okrug, Khabarovsk Kray, and other regions where winter gatherings are in elevated forestless mountain valleys. This method is only suitable for following general trends of reindeer populations.

The third method was developed in Taymyr (Pavlov *et al.*, 1976; Kolpashchikov, 2000). These aerial survey or censuses take place in the hottest period of summer (in the last days of July – the first days of August) when reindeer under insect harassment gather in herds of hundreds and thousands. The scientists attempt to enlarge reindeer concentrations by circling around the herds in airplanes. In 1970–80s, they photographed these gatherings and later counted animals on the photos. When the animals were in the very large aggregations significant mistakes could occur. It was often not possible to determine whether the same reindeer had been photographed more than once. The scientists used fixed-wing aircraft having a turning radius of about 1.5 km. Prior to 2003, the scientists had no GPS and determined the position of gatherings by eye. During the 1990s, the size of herds was determined only by visual estimation from the aircraft, which could lead to serious errors in the estimates.

During 2000–03, two methods (survey along a route and photographing of reindeer gatherings) were used in Taymyr. In the extremely hot summer of 2000, Yakushkin and Kolpashchikov found extremely large reindeer aggregations of 85 000 to 450 000 (Yakushkin *et al.*, 2001; Kolpashchikov *et al.*, 2003). Total number of reindeer in Taymyr was estimated as 1 050 000 reindeer. The scientists determined the gathering sizes by eye; they flew only 28 hours (7 hours directly for the survey and 21 hours to locate the animals); they did not photograph the gatherings. In 2001, Lomanov and his collaborators (Tikhonov *et al.*, 2003) conducted a new survey. Summer in that year was cold and maximum aggregations did not exceed 3000 animals. Lomanov's

team counted reindeer along flight routes, used GPS, and flew 150 hours. They estimated the total number of reindeer as 354 000. In the summer of 2003, Lomanov, Kolpashchikov, and Yakushkin jointly conducted the survey. They attempted to compare visual estimations with counting on photos of the same reindeer groups (I. Lomanov, pers. comm.). They found that Lomanov overestimated the size of groups by 1.3 times, Yakushkin by 2.5 times, and Kolpashchikov by 3–5 times. According to Lomanov and Yakushkin (pers. comm.), in 2003 the total number of reindeer in Taymyr was estimated at not more than 400 000. Therefore, the previous estimate of 1 000 000 reindeer in Taymyr (Yakushkin *et al.*, 2001; Kolpashchikov *et al.*, 2003) is not considered acceptable.

Data on tame reindeer is based on information from state, cooperative and private farms. In the past, twice a year all animals were counted through corraling, and these data were considered correct. However, during 1991–2000 counting of tame reindeer took place irregularly. Numerous private farms have not had the incentive to present accurate information. More recently, increased reporting of numbers of tame reindeer numbers is occurring. However, during the last few years farms and private herders received money on the basis of the number of their reindeer, thus they benefit financially from providing inflated numbers in their herds.

Island populations

In the 1990s, the personnel numbers of military, border and meteorological stations, and geological parties in the arctic zone of Russia have decreased. Accordingly, hunting pressure on the arctic populations of reindeer also decreased. In the Novaya Zemlya Archipelago the reindeer population increased from about 10 thousand to 15 thousand. Reindeer were found in both the northern and southern islands. Population density fluctuated from 1.1 to 3.4 animals per km², up to 18.7 animals per km² (Tikhonov & Khakhin, 2003).

In the Novosibirskie Islands, surveys have not been conducted since 1981. There is information on migrations of the reindeer from the islands to the mainland in late autumn for wintering that has provided evidence of significantly large size of the island population. During population lows the migrations ceased.

Feral reindeer on Wrangel Island have maintained stable numbers during the last 20 years, and there are about 3000 reindeer there. Harvest from this population was stopped in 1993. There is no apparent management plan for regulation of the population (Baskin & Danell, 2003). There are 900 feral reindeer on the Komandorskie Archipelago. This population died out twice (in 1917 and 1955) and was reestablished in 1927, and again in 1984 when a hundred tame animals were released (Abolitz, 1987; Voropanov *et al.*, 2003).

On Sakhalin Island there are 3500 wild reindeer compared with 6000 in 1992, and 4400 in 1986 (Ermin, 2003). Industrial development of the island is progressing as well as human impact on reindeer pastures. However, the northern part of the island continues to be of limited accessibility by hunters because of the absence of roads, the rugged relief, and extensive area of swamps.

European part of Russia

In all regions of European Russia, with the exclusion of the Kola Peninsula, the distributional range and numbers of wild reindeer have declined (Fig. 1). In the Kola Peninsula, tame reindeer, being less alert and more available than the wild reindeer, have been the target for hunters, reducing hunting pressure on wild reindeer (Makarova & Khokhlov, 1985). In all regions of the European Russian

North, the former extensive range of wild reindeer has been fractured into smaller segments. Reindeer survived in areas more remote from human populated localities. Migrations of Arkhangelsk reindeer from the taiga to the tundra have ceased. The forest-tundra population (2000 animals) that existed to the south of the Nenets reindeer husbandry area has almost become extinct (Ermolaev *et al.*, 2003; Korepanov *et al.*, 2003).

Taiga regions of Siberia

In Western Siberia (Khanty-Mansi Okrug, Tyumen oblast, Tomsk oblast) causes of the strong decline of wild reindeer populations are particularly obvious. These areas include the main centers of the oil and gas industry of the Russian North. They are full of workers, oil drill rigs, and thousands of snow machines that are used to travel in the area by the seismic geologists (Novikov, 1996b; Fertikov *et al.*, 2003). In other parts of Siberia hunting pressure is not significant. Reported decline in numbers of wild reindeer in the taiga of Evenki Okrug and Yakut Republic (Fig. 2) can be explained by mistakes in the aerial survey estimates. There are no suitable localities (as, for example, river-crossings) for effective commercial reindeer hunting, and transportation of reindeer meat over the distances involved is too expensive. The limited harvest of animals is by the few local hunters present in the region.

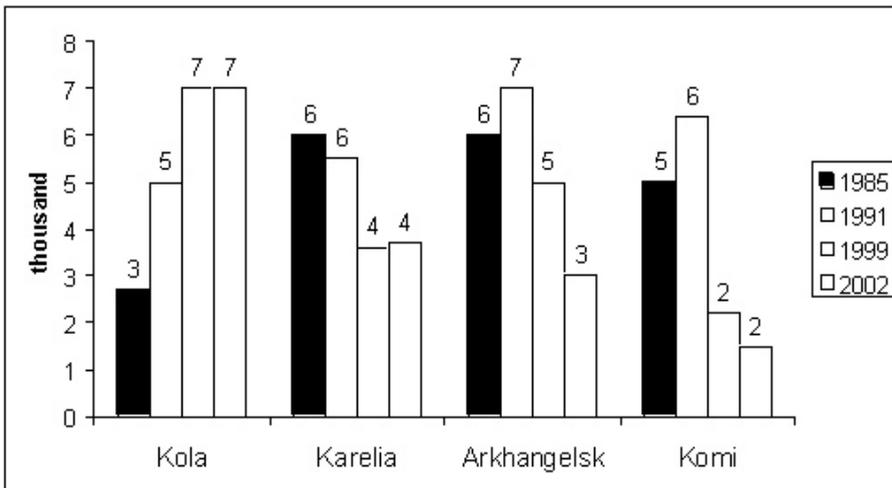


Fig. 1. Wild reindeer numbers in European Russia regions (Makarova & Khokhlov, 1985; Novikov, 1996a; Paponov, 2000; Ermolaev *et al.*, 2003; Korepanov *et al.*, 2003).

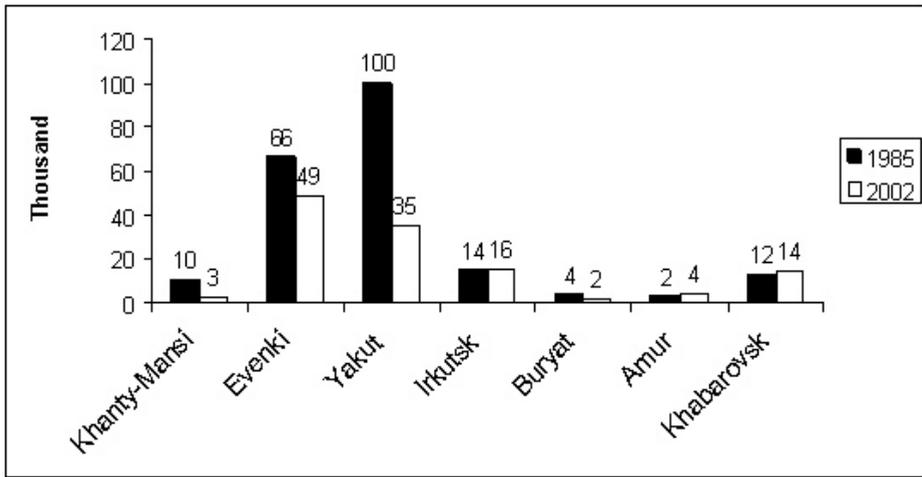


Fig. 2. Wild reindeer numbers in taiga regions (Syroechkovsky, 1986; Novikov, 1996b; Paponov, 2000; Fertikov *et al.*, 2003).

Tundra regions of Siberia

According to the last aerial survey, in Taymyr there are about 350 000 wild reindeer. The controversy over the accuracy of the survey methods (see above) required reconsideration of all statistics on the dynamics of the Taymyr reindeer populations since the 1970s (Syroechkovsky, 1986; Pavlov *et al.*, 1996). Data on the reindeer harvest in Taymyr Pronyaev (2003) demonstrated that the maximum numbers of the Taymyr reindeer (470 000-550 000) occurred in 1976-80. The commercial slaughtering on river-crossings on the Pyasina River and its tributaries (Baskin, 2003) essentially eliminated the largest segment of the Taymyr population that had migrated from Western Putorany Mountains to the tundra of Western Taymyr.

In Yakutia the Lena – Olenek population increased from 77 000 in 1990 to 90 000 in 2000. The probable cause of the increase was the cessation of commercial hunting on the Olenekskaya Protoka channel that is a western branch of the Lena River delta. The Yana – Indigirka population declined from 130 000 in 1987, to 101 000 in 1991, and to 42 000 in 2000. The main cause of decline was unlimited hunting of migrating females in spring. The Sudrun population declined from 39 000 in 1993 to 30 000 in 2000 (Safronov *et al.*, 1999; Popov, 2003). In the mid-1990s harvest of tundra reindeer reached 45 000, which was about 25% of total numbers.

Chukotka, Kamchatka

Numbers of Chukotka reindeer changed from about 15 000 in 1987 to 159 000 in 1999, and to 120 000 in 2002 (Paponov, 2000; Fertikov *et al.*, 2003). The increase of wild reindeer numbers is connected with a precipitous decline of tame reindeer from about 490 000 in 1991 to 121 000 in 1999. Observations of migrations of wild reindeer were begun during the latter part of the decline, showing that the migratory reindeer at times took with them the tame reindeer. An interview by the author with S. Shcherbakov, a leader of the Evens community, characterizes the situation. He explained that the community occupies the Pezhenka River basin in Chukotka. Seven men and their families, totaling 30 humans roam within the river basin. While two-three men herd tame reindeer on the mountains above tree line, others are fishing, trapping fur-bearing animals, and hunting moose, snow sheep, and brown bear. On one day in April, 2002 wild reindeer appeared in large numbers in the mountains. During three days large herds of wild reindeer moved through the Pezhenka basin, taking with them tame animals. Of the 3200 tame reindeer belonging to the community only 292 remained.

In Kamchatka the number of wild reindeer has remained stable at about 5000 since 1991 (Novikov, 1996a; Paponov, 2000). These are, however, “expert” estimations, since aerial surveys in the complex environment of Kamchatka are not possible.

Southern Siberian Mountains

In the Altai and Sayany Mountains only remnants of wild reindeer populations have survived, with 700 in Altai and 350 in Sayany. These reindeer have survived only in the high mountains or in nature reserves (Paponov, 2000; Fertikov *et al.*, 2003).

Reindeer husbandry

During 1991-99, the numbers of animals in tame reindeer husbandry were stable or increasing in Nenetsk Okrug and Yamal (Fig. 3). The large gas and oil companies in these areas provided sufficient financial support for transport, fuel for snow machines, and other goods. The staff of the companies utilized meat from the production of reindeer husbandry. In Yamal, numbers of reindeer increased so much that over-exploitation of pastures occurred.

lost significance since the 1960s. In the 1970s and 1980s, meat production developed in only a few areas of Yakutia (Baskin, 1989). In the Buryat Republic, Evenki Okrug, and Tuva Republic reindeer husbandry declined and almost ceased after 1991. Modern aims of taiga reindeer husbandry emphasize skin production, transport, sport, and tourism. The state and industrial companies support reindeer husbandry to conserve national cultures. They brought 600 tame reindeer from Yamal and moved them to Evenki Okrug. Similar translocations of reindeer are planned for Yakutia and Chukotka.

Conclusion

According to official data, in the 1990s the numbers of wild reindeer in Russia fluctuated around 1 million, with 1 005 000 in 1990, 972 000 in 1995, 1 232

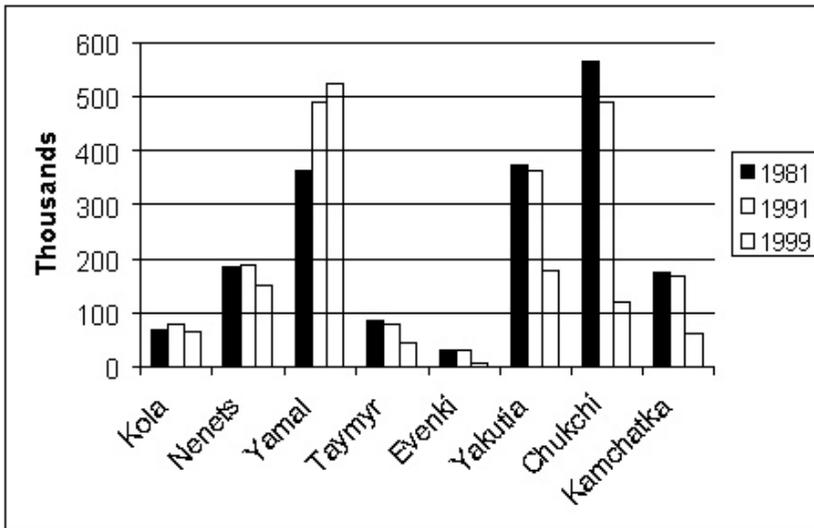


Fig. 3. Tame reindeer numbers in regions of the Russian Federation (Baskin, 1989; Syroechkovsky, 2001).

Tame reindeer numbers in Yamal increased twice to approach carrying capacity of pastures (Jernsletten & Klovok, 2002).

Reindeer husbandry in Yakutia and Chukotka has declined markedly in recent decades. Only after financial support was received in 1998 did recovery of the reindeer begin. Authorities not only delivered goods and arranged transport and communication, they started to pay about 500-600 rubles per reindeer (about 17-20 USD).

In the taiga areas, reindeer husbandry almost ceased. Traditional transport use of tame reindeer

000 in 1999, and 881 000 in 2002 (Novikov, 1996a; Paponov, 2000; Fertikov *et al.*, 2003). Fluctuations of total reindeer numbers depend to a large extent on the different estimations of the size of the Taymyr population. They, therefore, do not reflect real status changes in different regions. The total numbers of tame reindeer declined from 2.5 million in 1969 to 2.3 million in 1991, and to 1.2 million in 2001 (Jernsletten & Klovok, 2002).

In Russia, the period of 1991-99 included major socio-economic transformations. In many regions, the impact of these changes on reindeer husbandry

was destructive. Only since 1999 has stabilization and even improvement of the situation become apparent. Wild reindeer populations, however, were found to be less sensitive to human influence, mostly because of the vast territory of pasture grounds they occupy, the sparse human population in these regions, and the poorly equipped hunters there with inadequate transport and restricted availability of fuel.

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Reindeer husbandry in Finland

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Abstract: Reindeer are herded in the northernmost Finland over an area of 114 000 km², about 35% of the area of the country. Herding is carried out both by Sami and Finns. The paper gives some statistics on the reindeer industry and underlines the importance of reindeer husbandry in Finland.

Key words: *Rangifer tarandus*, reindeer industry, statistics.

Rangifer, 25 (1): 59-62

Reindeer area

In Finland, reindeer husbandry is practised in a region that comprises the Province of Lapland and parts of the Province of Oulu, and its surface covers 114 000 km² which is more than one third of Finland's total area. The herding year begins 1 June and ends 31 May next year. During this period of time there are two peak seasons: calf marking from June to July and round-ups from September to January. Reindeer husbandry has significant importance in maintaining the marginal regions inhabited. It is one of the cornerstones of Sami culture and it is of vital importance for the tourism in northern Finland.

Administration

Reindeer husbandry is governed by a herding co-operative system consisting of 56 reindeer herding co-operatives (Fig. 1). Each herding co-operative

has its own administration, defined borders and area. The number of reindeer and the size of the area vary. All reindeer owners are members of the herding co-operative and their respective rights and responsibilities are determined on the basis of the number of reindeer owned by them. The chief who is appointed by the General Meeting of the herding co-operative heads the herding co-operative. All co-operatives are members of the Reindeer Herders' Association that is the central body for them. In the meetings of the Association each chief can vote in accordance with the number of reindeer in "his" co-operative.

The number of reindeer and other statistics¹

The number of reindeer is determined by the Ministry of Agriculture and Forestry through the maximum number of reindeer that each herding

¹ The lecture referred to the herding year 2001/2002 but newer statistics are included in the article. Statistics of Finnish reindeer husbandry are published every year in issue no. 2 of the journal *Poromies*.

MARKING DISTRICTS
and
co-operatives

Max. number
of reindeer
allowed

Actual
number
of reindeer

UTSJOKI

1. Paistunturi 6 300 6 328

2. Kaldoaivi 5 300 5 252

INARI

3. Näätämö 3 600 3 457

4. Muddusjärvi 5 200 4 836

5. Vätsäri 3 000 2 527

6. Paatsjoki 1 600 1 336

7. Ivalo 6 000 5 297

8. Hammastunturi 5 500 4 889

9. Sallivaara 7 500 7 275

10. Muotkatunturi 6 800 7 257

ENONTEKIÖ

11. Näkkälä 8 300 8 242

12. Käsivarsi 10 000 9 962

PALLASTUNTURI

13. Muonio 6 000 5 702

14. Kyrö 3 500 3 276

KITTILÄ

15. Kuivasalmi 6 000 5 062

16. Alakylä 5 300 4 932

SODANKYLÄ

17. Sattasniemi 5 300 5 108

18. Oraniemi 6 000 5 876

19. Syväjärvi 5 500 5 277

21. Lappi 8 000 7 176

KEMINKYLÄ

22. Kemin Sompio 12 000 12 736

23. Pohjois-Salla 4 800 4 666

SALLA

24. Salla 5 300 5 417

25. Hirvasniemi 2 300 2 376

RAUDANJOKI

26. Pyhä-Kallio 6 500 6 328

27. Vanttaus 1 200 1 182

28. Poikajärvi 4 600 4 523

LÄNTINEN

29. Lohijärvi 1 400 1 386

30. Palojärvi 5 000 4 803

31. Orajärvi 1 500 1 700

32. Kolari 2 600 2 565

33. Jääskö 1 000 1 011

ITÄKEMIJOKI

34. Narkaus 2 000 1 902

35. Niemelä 1 400 1 360

36. Timisjärvi 1 900 1 880

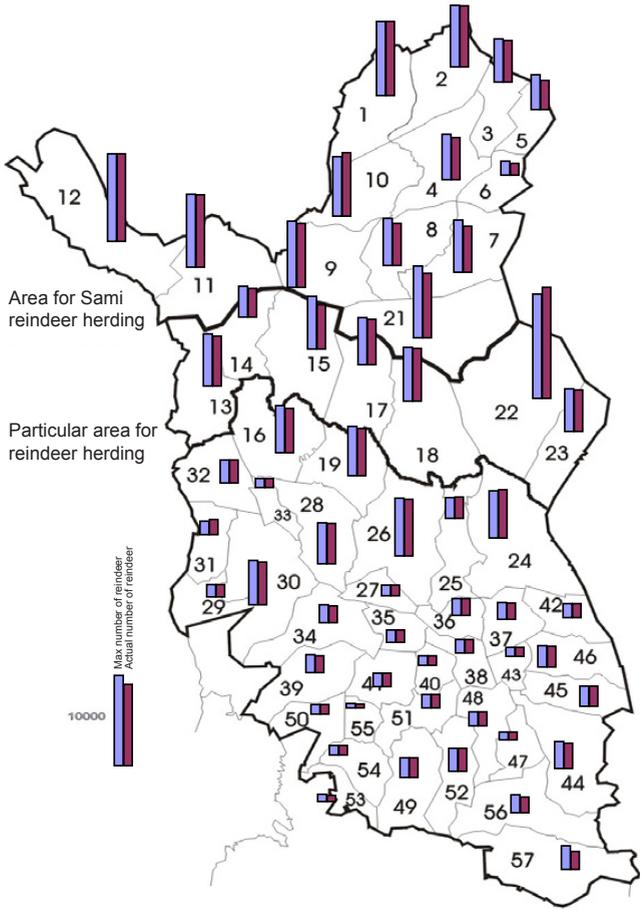
37. Tolva 1 900 1 833

38. Posion Livo 1 500 1 507

39. Isosydänmaa 2 000 1 908

40. Mäntyjärvi 1 100 1 094

41. Kuukas 1 500 1 518



KUUSAMO

42. Alakitka 1 600 1 605

43. Akanlahti 1 000 986

44. Hossa-Irni 3 000 2 826

45. Kallioluoma 2 300 2 247

46. Oivanki 2 400 2 346

PUDASJÄRVI

47. Jokijärvi 900 878

48. Taivalkoski 1 600 1 584

49. Pudasjärvi 2 200 2 213

50. Oijärvi 1 300 1 181

51. Pudasjärven Livo 1 500 1 493

52. Pintamo 2 600 2 588

53. Kiiminki 800 693

54. Kollaja 1 100 1 061

55. Ikonen 500 470

KAINUU

56. Näljänkä 2 000 1 752

57. Halla 2 700 2 042

203 700 196 727

Fig. 1. Areas of reindeer husbandry in Finland 2002/03.

Table 1. Statistics of reindeer husbandry in Finland 1980/81 to 2003/04.

Reindeer herding year	1980/81	1985/86	1990/91	1995/96	2000/01	2003/04
Reindeer owners	7 086	7 483	7 556	6 960	5 682	5 243
Highest allowed number of reindeer	187 700	187 700	228 900	228 900	203 700	203 700
Slaughtered reindeer	58 554	102 965	169 023	120 702	87 397	106 318
Living reindeer over winter	177 676	229 843	259 611	212 851	185 731	201 058
Calves	70 669	106 210	142 686	112 865	89 581	115 075
Production milloin kg	1,44	2,42	4,01	2,73	2,02	2,55
Medium weight kg	24,65	23,47	23,80	23,11	23,38	-
EURO/kg	3,70 €	5,00 €	4,25 €	4,43 €	5,49 €	4,15 €
Income of reindeer herding (million EURO)	-	13,62 €	20,83 €	19,10 €	17,89 €	18,51 €
Costs of reindeer herding (million EURO)	-	11,32 €	16,92 €	15,51 €	14,70 €	16,74 €

co-operative can own; a number regulated each decade (Table 1). During the current decade maximum revised number of reindeer is 203 700. The permitted number of reindeer owned by a herding co-operative member is likewise restricted; in the southern part of the reindeer husbandry region the maximum number is 300 while the corresponding number is 500 in the northern reindeer husbandry area.

There was in 2002/2003 5344 reindeer owners in Finland of which 800-1000 are Sami. During that reindeer herding year the total number of reindeer living over winter was 196 727. Reindeer husbandry produced about 2.5 million kilograms of meat, 90 000-110 000 skins and 100 tons of antler material. The total income of meat production was 13.2 million € in 2001/2002. One third of the slaughtered reindeer and the slaughtering income come from the Sami region. The economical turnover of reindeer husbandry amounts to 55-60 million € annually when foodstuffs, souvenirs and reindeer travel services are included in the calculations. About 690 families live from full-time reindeer husbandry and about 850 families practises reindeer husbandry as a secondary occupation.

Damages caused by predators have shown a growing trend but are now decreasing. The present number of predators and eagles should be reduced because the compensation systems do not cover all the losses for the herders. Either conservation ar-

eas should not be made as predator reservations. Losses from traffic are also substantial.

EU and Finnish reindeer husbandry

Finland joined the EU in 1995. The membership brought heavy investments into the reindeer husbandry caused by renewing the network of slaughterhouses. The previously existed >200 field-abattoirs had to be fully renewed to bring meat hygiene up to a uniform standard. Today there are about 14 reindeer abattoirs network meeting the EU directives. In addition to construction costs (6,7 million €), permanent costs have also increased for the fact that almost all reindeer must be transported by trucks to the abattoirs. Reindeer husbandry became also liable to VAT (Value Added Tax). The respective advantages from the reindeer herders' point of view are limited. The import restrictions from the third countries to Finland have not been completed. Reindeer meat is still imported from the low-cost countries, mainly from the east. The competing raw materials and various meat products have likewise been imported from third countries. Some of these products have even been marketed as reindeer meat because of a higher price level.

EU legislation should have special adaptations for reindeer husbandry in many cases. EU has approved Finland Northern Aid Funds for the reindeer industry based on the number of reindeer. The maximum aid is 27 € per head but the Ministry

of Agriculture and Forestry paid 22 € per reindeer in 2001/2002. Considering the raising production costs the aid is needed. But the Finnish herders have also challenged themselves to consider time-saving ways of organizing herding for example by using fences to control reindeer movements, and they take part in tourist services and small scale meat processing. By offering reindeer services to the tourists and high quality local products to consumers, the herders can attain a supplementary income source.

Information of the Finnish reindeer husbandry
The Reindeer Herders' Association created their own website in 1999 to serve information dissemination better. It is developed continuously side by side with the projects which give new information and bring up new questions. You will find updated information about the Finnish reindeer husbandry in the website of Paliskuntain yhdistys (The Reindeer Herders' Association): www.paliskunnat.fi. The journal Poromies (in Finnish) published by Paliskuntain yhdistys gives annual information about reindeer husbandry in Finland.

First Announcement

Nordic Conference on Reindeer and Reindeer Husbandry Research in 2006

NOR's 14th conference is planned to be held in Helsinki, Finland in March 2006.

National co-organisers are the Finnish Game and Fisheries Research Institute (RKTL) and probably other institutions as well.

The conference is arranged in conjunction with the Annual Meeting of the national delegations of NOR and will also be a 25th anniversary celebration for NOR.

In due time you will find more information about the conference, the registration and the conference languages in NOR's web pages www.rangifer.no

Participants are invited to give oral or poster presentations on all relevant topics concerning reindeer and reindeer husbandry.

Contact persons are:

for the co-organisers Mauri Nieminen (mauri.nieminen@rktl.fi) and for NOR, secretary Rolf Egil Haugerud (nor.rangifer@sami.uit.no).



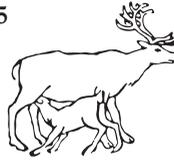
Survey Sami and indigenous research

Centre for Sami Studies at The University of Tromsø has by The Research Council of Norway been assigned to make a survey of sami and indigenous research going on in the Nordic countries. The survey will be a contribution to gain a comprehensive view of the situation regarding to sami and indigenous research going on within/inside the Nordic countries. The status for sami and indigenous research shall lead to recommendations on which areas it is needs for a bigger effort regarding to indigenous research. The survey shall also lead to advices which attempts and follow-ups that are required.

Centre for Sami Studies has composed an electronic tally sheet for sami research project located on our WebPages: www.sami.uit.no. We would be grateful if researchers take their time to register on going sami research projects. The registration will be an important contribution to the aim of making a comprehensive survey of sami and indigenous research within the Nordic countries. The received information is available on our WebPages:

www.sami.uit.no

Grants: Closing date 1st December 2005



NORDIC COUNCIL FOR REINDEER HUSBANDRY RESEARCH (NOR)

Grants 2006

Grants are allocated to researchers and students who study reindeer or reindeer husbandry. Applicants should belong to Nordic institutions or they should be students abroad having direct co-operation with Nordic institutions.

The NOR grants for 2006 will primarily be allocated for participation and presentation at the 14th NOR-conference (Nordic Conference on Reindeer and Reindeer Husbandry Research) in Helsinki, Finland, in March, 2006 (Exact dates not yet determined, see NOR's web pages later in 2005).

For idle means the applications will also be considered for:

- participation in other congresses, symposia, other scientific meetings about reindeer and reindeer husbandry or topics of relevance for the studies of reindeer and reindeer husbandry.
- contact-meetings for planning Nordic projects.

NORs working committee will decide upon further priorities as required.

The grants are paid retrospectively and will only be paid through the applicant's institution (university, research centre, etc.). Successful applicants must submit an expenses report to NOR not later than 15th October, 2006 before reimbursement will be made.

To be considered the application must include the following information:

- applicant's name, university/college address (Nordic institution), current position (student, researcher, other) and type of engagement (salaried, scholarship, no financial support),
- means of travel, budget (cheapest travel and accommodation),
- other grants applied for the same purpose,
- presentation in conference (oral/poster),
- if doctoral student, approval from institute/supervisor,
- if masters student, confirmation of supervisor/researcher who is also attending the conference.

The application should also report:

- title of presentation(s),
- all authors involved,
- a short summary or synopsis of content,
- whether the content is new or published/previously presented information.

Contact NOR's secretary Rolf Egil Haugerud for more information or visit web site www.rangifer.no

Submit applications in postal mail or e-mail to the Nordic Council for Reindeer Husbandry Research (NOR), Centre for Sami Studies, University of Tromsø, N-9037 Tromsø, Norway;
nor.rangifer@sami.uit.no

Closing date for applications 1st December 2005.

INFORMATION FOR CONTRIBUTORS TO **Rangifer**

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- NOR has the exclusive rights to publish a manuscript that is reviewed and accepted for publication in Rangifer.
- Authors transfer copy rights automatically to NOR when the article is printed in Rangifer.
- Manuscripts will be in English. It is the authors' responsibility to submit manuscripts in as complete and perfect condition as possible. Use linguistic consultant(s).

Typing

- Use body text in 12 points size and double spacing with 4 cm margins on both left and right sides. Do not hyphenate at the right margin.
- State name and complete address, fax number, telephone number and e-mail address of the person who is to receive editorial correspondence.
- Submit 3 good hardcopies and also submit manuscript in e-mail attachment. When accepted, the manuscript will be submitted in e-mail attachment and/or on a 3,5" diskette containing no other files (use ordinary programs and versions).

Main text, summary and key words

- The frame of a manuscript will depend on field and subject but it usually consists of the following main chapters; introduction, material and methods, results, discussion and references.
- Give comprehensive abstract and relevant key words, placed before the main chapters. Key words in alphabetical order should not include any words that occur in the title of the paper.
- Nordic authors should also prepare an abstract in their own language.

Tables, graphs and other illustrations

- These shall be numbered with Arabic numbers (1, 2, 3 etc.) and provided with a short text, such that they can be understood independently of the article text. Indicate in the margin of the manuscript where tables and illustrations will be placed. Figures and tables with texts can be put directly in the manuscript. Long tables shall be avoided.
- Illustrations must be ready for printing (repro quality). Most photos are accepted, including slides. Authors have to pay extra for printing photos in colour.
- If using electronic programmes, save figures as ai-file (Adobe Illustrator) or eps-files (Encapsulated PostScript). Figures shall additionally be exported as JPG-file.
- Graphs and tables should be made in Microsoft Excel.

References

- Sources given in the text shall be written: Smith (1994), (Smith, 1994), (Smith & Jones, 1994) or (Smith et al., 1994). Use semicolon between references: (Smith, 1994; Smith & Jones, 1995; Smith et al., 1996) and put references in chronological order.
- The list of references shall be placed at the end of the manuscript and listed alphabetically according to the author: **Holleman, D. F., Luick, J. R. & White, R. G.** 1979. Lichen estimates for reindeer and caribou during winter. – *J. Wildl. Manage.* 43 (1): 192-201. (43 volume number, (1) number in volume series (can be omitted) and: 192-201 page numbers). You can also give full journal names (NB: – dash before the journal name).

Measurements and units

- Use metric units. Follow the accepted nomenclature of the International Symbol of Units. Numbers shall be given as: 739 847.34. Use the CBE Manual for Authors, Editors and Publishers. Numbers 10 000 and more have thin spaces to group the digits.

Italics

- Italics shall be typed. Taxonomic names in Latin (genus and species; *Rangifer tarandus tarandus*), book titles and journal names shall be written in italics.

Proofs and offprints

- First correction of proofs is the responsibility of the author. Authors are fully responsible for checking all material for accuracy.
- Pdf-file will be available for the author for scientific and personal use; the journal and copy right holder must be mentioned when used (also in personal home page). Any offprints must be ordered at cost when page proofs are returned after correction.

Referees

- The journal covers many different scientific research fields. The author is expected to submit suggestions on actual referees in their special field (name, address, e-mail).

Rangifer

Rangifer is the international Journal of the Nordic Council for Reindeer Husbandry Research. It was first published in 1981. Since then the Journal has appeared in two to four ordinary issues per year with occasional Special Issues, including Proceedings, Monographs and Theses. The Journal is published biannually from 2002.

Rangifer is the world's only scientific Journal dealing exclusively with husbandry, management and biology of arctic and northern ungulates and publishes original, unpublished papers, review articles and brief communications.

Rangifer publishes quality papers on basic and applied research and is open for papers in both natural and social sciences on all themes relating to reindeer and reindeer husbandry (e.g. anthropology, biology, law, history of and modern practice in husbandry and management). The manuscripts are evaluated by at least two independent referees. The Journal offers the author pdf-file of printed article.

Rangifer is registered in international databases for scientific papers, including Biosis, Biological Abstracts, CAB, and Agris.