Key note presentations
10th Arctic Ungulate Conference
9–13 August 1999, Tromsø, Norway

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Editor: Rolf Egil Haugerud
Address: c/o NVH, Department of Arctic Veterinary Medicine
Stakkevollvn. 23 B
N-9292 Tromsø
Norway
e-mail: Nor.Rangifer@veths.no

Web address: www.rangifer.no

Telephone: +47 77 69 48 10 *Telefax:* +47 77 69 49 11 *Mobile telephone:* +47 414 16 833

Bank account: 4760 56 92776 *Postal account:* 0801 2116358
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RANGIFER

Key note presentations

10th Arctic Ungulate Conference

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Information

10th Arctic Ungulate Conference

The 10th Arctic Ungulate Conference was organised by the Department of Arctic Biology and held at the University of Tromsø, Norway, 9-13 August 1999. The conference continued a series of nine conferences devoted to Arctic ungulates, including five International Reindeer/Caribou Symposia, two International Muskox Symposia and two Arctic Ungulate Conferences.

Two hundred delegates from 14 countries attended and presented more than 150 scientific papers, making it one of the biggest Arctic Ungulate Conferences ever. The scientific and social programme as well as the abstracts have been published in *Rangifer* Report No. 4, 1999.

In an important break with normal practice, keynote speakers included scientists of international reputation who do not normally work with Arctic ungulates. They were asked to review recent work in northern species/ecosystems thus providing the conference with novel criticism and new perpectives. Their papers are published in this volume. Delegates' papers will be published in later issues of *Rangifer.*

The Conference also included a Circumpolar PhD-Network in Arctic Environmental Studies (CAES) workshop: "Reindeer 2000", attended by 47 participants presenting 25 student contributions, 5 keynote lectures and 3 introductory speeches. A *Rangifer* Special Issue with workshop papers is planned for publication later in 2000.

The Conference was sponsored by the Norwegian Reindeer Husbandry Development Fund, the Norwegian Reindeer Husbandry Research Council, the Nordic Council for Reindeer Research, the Norwegian State Bank of Agriculture, the University of Tromsø and the Roald Amundsen Centre for Arctic Research at the University of Tromsø.

A meeting of representatives appointed by the different national delegations was held on 11 August 1999. A new Arctic Ungulate Society was inaugurated. The statutes of the Society are appended.

In its first meeting, the Executive committee of the Arctic Ungulate Society agreed that the next Conference will be held in Finland and the Finnish representative later informed that the venue for the next meeting is likely to be Saariselkä in northern Finland.

Arnoldus Schytte Blix, Chairman of the Organising Committee

10th Arctic Ungulate Conference
University of Tromsø, 9–13 August 1999

The Tenth Arctic Ungulate Conference,
9–13 August 1999, Tromsø, Norway.

Quantifying the free living energy exchanges of Arctic ungulates with stable isotopes

Paul Haggarty

The Rowett Research Institute, Greenburn Road, Bucksburn, Aberdeen AB21 9SB, Scotland, UK (ph@rri.sari.ac.uk).

Abstract: When natural diets meet an animal's requirement for energy, other essential nutrients will usually be supplied in amounts at least sufficient for survival. Knowledge of the energy requirements of free ranging species under typical conditions are important in assessing both their nutritional needs and their ecological impact. The doubly labelled water (DLW) method is currently the most promising objective field methodology for estimating free living energy expenditure but expenditure is only equal to the energy requirement when an animal is in energy balance. Reproduction and seasonal cycles of fat deposition and utilization represent significant components of the energy budget of arctic ungulates but the information gained in the course of a typical DLW study may be used to estimate processes such as milk output and fat storage and mobilization in order to predict requirements from expenditure.

The DLW method has been exhaustively validated under highly controlled conditions and the introduction of innovations such as faecal sampling for the estimation of body water isotopic enrichment, the availability of appropriate correction factors and stoichiometries for known sources of error, and iterative calculation of unknown parameters, have produced a methodology suitable for use in truly free ranging species. The few studies carried out so far in arctic ungulates indicate that previous predictions have generally underestimated the true level of expenditure, that there is considerable between animal variation in the level of expenditure and that this is largely determined by physical activity.

The disadvantages of the DLW methodology are that it remains expensive and the isotope analysis is technically demanding. Furthermore, although DLW can provide an accurate value for free living energy expenditure, it is often important to have information on the individual components of expenditure, for example the relative contribution of physical activity and thermoregulatory thermogenesis, in order to interpret the values for overall expenditure. For these reasons the most valuable use of the DLW method in the field may be to validate factorial models and other approaches so that they may be used with confidence. Additional important information on the energy exchanges of free ranging animals may be obtained from other stable isotope methodologies. In addition to the use of the isotopes ^{2}H and ^{18}O in the DLW method, natural variations in the abundance of ^{13}C and ^{15}N in the arctic environment may be exploited to study diet selection in truly free living arctic ungulates.

Rangifer, 20 (2–3): 59–69

Introduction

When natural diets meet an animal's requirement for energy, other essential nutrients such as protein, fats minerals and vitamins will usually be supplied in amounts at least sufficient for survival (Kay *et al.*, 1984). Consequently, energy is often the most important single factor in the nutrition of an animal and knowledge of energy expenditure under typical free-living conditions are important in assessing both energy requirements and the ecological impact of free-ranging animals. Arctic ungulates such as reindeer and caribou (*Rangifer tarandus*) may range over large areas therefore traditional methods of estimating energy expenditure such as chamber calorimetry are of limited use as they impose a significant degree of restriction on 'normal' activity which makes up a significant portion of the energy budget of free ranging species. Furthermore, the harshness of the arctic environment also influences expenditure in ways which are difficult to model; these include the effects of temperature and wind chill, and the additional energy expenditure which occurs as a consequence of foraging when the vegetation may be of poor quality or where access is made difficult by snow cover. In an effort to make more realistic estimates of energy expenditure, a number of workers have developed factorial models where values for the energy costs of metabolic processes, activities, and the time spent in those activities are used to calculate the overall energy budget of the animal (e.g. Boertje, 1985; Tyler, 1987). Such models have been invaluable in studying the energy exchanges of truly free living animals in their natural habitat but the assumptions underlying these models have yet to be tested by comparison with objective measures of expenditure. The most promising method of estimating energy expenditure in free-living animals is the doubly labelled water (DLW) technique (Lifson & McClintock, 1966). This technique, which utilizes water labeled with stable isotopes, provides an integrated value for energy expenditure, typically over 1 to 3 weeks, and therefore is ideal to estimate requirements.

Energy expenditure is only equal to the energy requirement when an animal is in energy balance yet in arctic species fat deposition can make up a large part of the energy requirement in summer whilst mobilisation of body fat can supplement the energy requirement in winter. Similarly, productive processes such as pregnancy and lactation represent a significant part of the energy requirement of arctic ungulates. Since the DLW method only provides an estimate of energy expenditure, information on the magnitude of these other processes is required in order to estimate the more practically useful parameter of the energy requirement. This paper reviews new insights into the energy exchanges of arctic ungulates provided by the use of stable isotope methodologies and proposes novel ways in which stable isotopes may be used to study the various components of the energy budget of arctic ungulates (Fig. 1). The results for arctic species (Eurasian mountain reindeer; *R. t. tarandus,* Alaska caribou; *R. t. granti* and muskoxen; *Ovibos moschatus*) are compared with a non-arctic species (red deer; *Cervus elaphus*).

Stable isotopes

Isotopes are atoms with the same number of protons (atomic number) but different numbers of neutrons (mass number). They may be classified as either radioactive or stable and isotopes are available for many of the elements found in living systems (e.g. hydrogen, carbon, oxygen, nitrogen, sulphur and

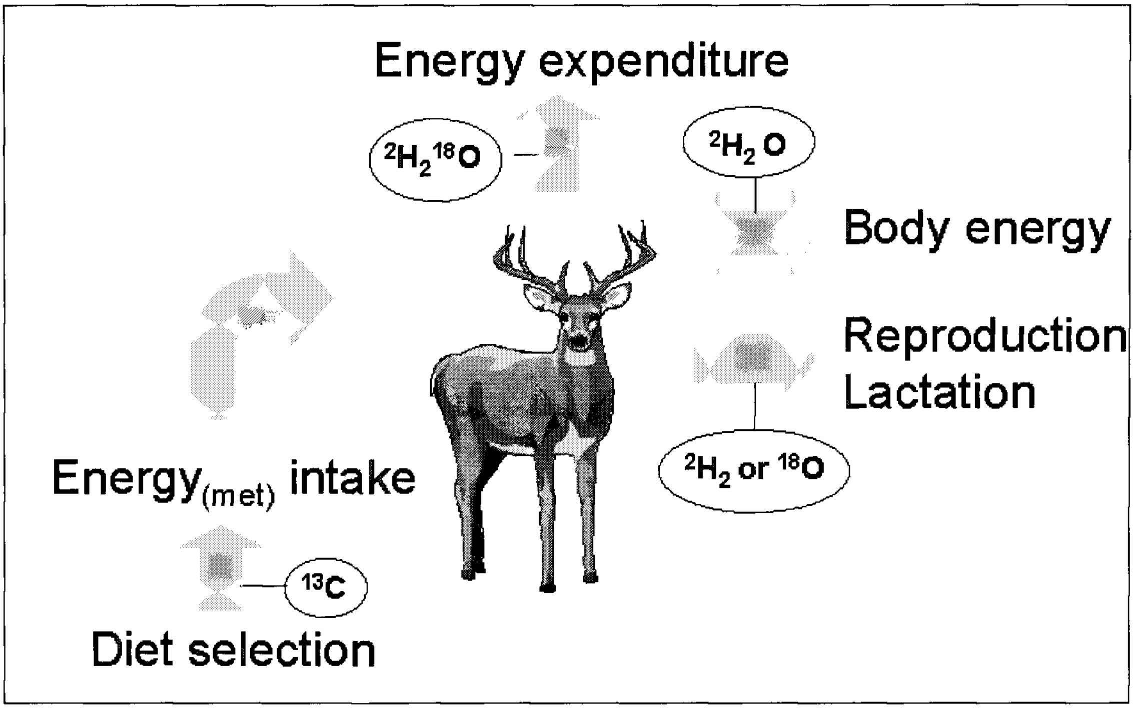


Fig. 1. The metabolisable $_{(met)}$ energy intake of an animal is equivalent to its requirement when this equals the energy expenditure plus the energy cost of reproduction/lactation, plus energy stored in the body or minus energy mobilised from body stores. All of these processes and the selection of diet can be measured in the field using a range of stable isotope methodologies.

many metals). The isotope concentration in biological samples is measured most precisely using gas isotope ratio mass spectrometry where the biological matrix is converted into a permanent gas (e.g. CO_2, H_2) prior to measurement. This conversion can be carried out 'off-line' or it can be automated and connected 'in-line' to standard laboratory techniques for isolation of individual molecules (e.g. gas chromatography-combustion-isotope ratio mass spectrometry). The isotopic results are presented as $\delta^{13}C_{PDB}$, the notation commonly used to report natural variations in ^{13}C abundance, or as parts per million (ppm) above background in tracer studies. Negative δ values indicate that the sample is depleted in ^{13}C relative to the standard (PDB: PeeDee Belemnite) and the numerical quantity expresses the depletion in parts per thousand or "per mil", designated by the symbol ‰.

In techniques such as the DLW method the only available tracer for oxygen is the stable isotope oxygen-18 (^{18}O) but the hydrogen of the body water could be labelled with either stable-isotopic deuterium (^2H) or radio-isotopic tritium (^3H). The latter has been used in the DLW validation studies of Fancy *et al.* (1986), presumably because ^3H is easier to measure using the widely available technique of scintillation counting. However, stable isotopes offer a number of advantages over radioactive isotopes: 1. Their use in free living animals studies does not result in the introduction of radioisotope contamination into the environment. 2. Stable isotopes can be measured more precisely than radioisotopes and in a comparison of water flux rate measurements in deer labelled with both ^2H_2O and ^3H_2O, the deuterium estimate of water flux was twice as precise as the tritium estimate (Haggarty *et al.*, 1998). Since the DLW method estimates CO_2 production from small differences between two isotopic flux rates which are dominated by water turnover, the improved precision offered by ^2H is an important consideration. 3. Stable isotopes are always present in the environment and natural variations in their concentration can be exploited to obtain information on the origin and inter-conversion of nutrients.

The doubly labelled water method

The DLW method is based on the observation that the hydrogen of body water is lost mainly as water whereas the oxygen of water is lost as water and CO_2. When the body water is labelled with ^2H and ^{18}O, the rate of dilution of ^2H gives a value for water flux and the rate of ^{18}O dilution gives a value for water flux plus CO_2 production and the production of CO_2 can be estimated from the difference between the two isotopic fluxes (Fig. 2).

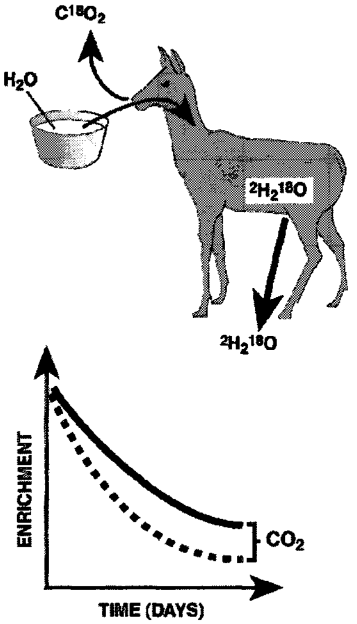


Fig. 2. Theoretical basis of estimating CO_2 production from the difference in washout rates of ^2H (—) and ^{18}O (....) from the body water.

This method (Lifson & McLintock, 1966) has now been successfully validated in ruminant (Fancy *et al.*, 1986; Midwood *et al.*, 1994) and monogastric (Haggarty *et al.*, 1994a) animals and may therefore be used with confidence in a wide variety of metabolic states if appropriate corrections are made for the processes which are known to introduce errors into the technique (Fancy *et al.*, 1986; Haggarty, 1991; Haggarty *et al*, 1994a; Midwood *et al*, 1989; 1993).

In order to calculate water flux and CO_2 production it is necessary to correct the isotope flux data for fractionated water loss (Haggarty *et al.*, 1988) and any change in pool size (Haggarty *et al.*, 1994a) during the course of the labelling period. There are, however, other processes which may introduce errors into the DLW estimate of CO_2 production; for example, loss of ^2H into products other than water will cause water flux to be overestimated and CO_2 production to be underestimated. This may occur during sequestration of ^2H into stable carbon-hydrogen bonds or by exchange of ^2H with labile positions on material which is subsequently export-

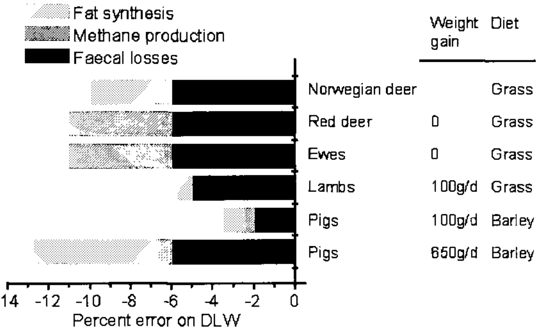


Fig. 3. The magnitude of errors which different sequestration/exchange processes introduce into the DLW method vary between species and between different physiological states.

ed from the body; faeces for example. The sequestration/exchange processes which have the potential to introduce substantial errors into the DLW method in production animals are fat synthesis, methane production, export of faecal dry matter and lactation (Haggarty, 1991; Midwood *et al.,* 1989; Haggarty *et al.,* 1994a). The magnitude of these processes must be estimated in order to make the necessary corrections to the isotope flux data (Haggarty, 1991). Some examples of actual effects (Fig. 3) illustrate that there are wide variations in the relative importance of each error in different physiological states. Also, the fact that all three processes result in an underestimate of energy expenditure mean that the errors are additive such that when they are combined they can have a significant impact on the accuracy of the DLW method. In addition, the DLW method only provides an estimate for CO_2 production, therefore furthet information on oxygen consumption, nitrogen loss and, in the case of ruminants, methane production, is required to calculate a value for energy expenditure. Under the highly controlled conditions of a validation study it is possible to make direct measurements of faecal losses, methane production and even fat synthesis, but the need to carry out such measurements in a typical DLW study would largely nullify the main advantage of the DLW method which is that it can be used in free-living animals in their natural environment. Although the DLW method was developed as a method of estimating free living energy expenditure, the necessity of correcting for these processes and the typical DLW dosing and body water sampling regime has severely resticted its use in truly free-living animals. To overcome the first limitation, an iterative method has been developed to correct for the above sources of error and provide estimates of oxygen consumption, methane production and nitrogen loss without the need to measure them directly, using only the data which is typically obtained in DLW studies in truly free-living animals (Haggarty *et al.,* 1998).

With respect to the second limitation, energy expenditure may be calculated from DLW data using the two-point or multi-point methods (Haggarty, 1991) but the two-point approach has the important advantage for studies in free-ranging animals that the samples of body fluids (typically blood) need only be taken on the first and last day of the labelling period and not each day as with the multi-point approach. Apart from the practical disadvantage of having to re-capture animals each day, daily capture and sampling could, in itself, significantly affect the energy expenditure of free-ranging animals. In such animals, the two-point methodology, where body fluids are sampled only at the beginning and end of an experiment, typically lasting between one and two weeks, would be a more feasible approach. A comparison of multi-point and two-point calculations has shown that there is no significant difference in the energy expenditute derived by these approaches in ungulates (Haggarty *et al.,* 1998) therefore the two-point method may be used with confidence. An ingenious way of further reducing interference with the normal activity of free ranging species during DLW measurements has been proposed by Gotaas *et al.* (1997) who have shown that faeces water can be used to estimate the isotopic composition of the body water. This method offers the possibility of carrying out a DLW study in free ranging ungulates requiring only one captute in order to give the dose, the wash out of isotope from the body can then be estimated by collection of fresh faeces in the field and Gotaas *et al.* (in press) have used this approach to estimate the energy expenditure of free living reindeer.

Free living expenditure

Until the advent of objective methods such as DLW the only way of estimating requirements under normal conditions was the factorial approach or, in a compromise between truly free living and fully confined, the measurement of food intake in penned animals. It is therefore useful to put the few existing DLW results in arctic ungulates in the context of data obtained using ttaditional methodologies.

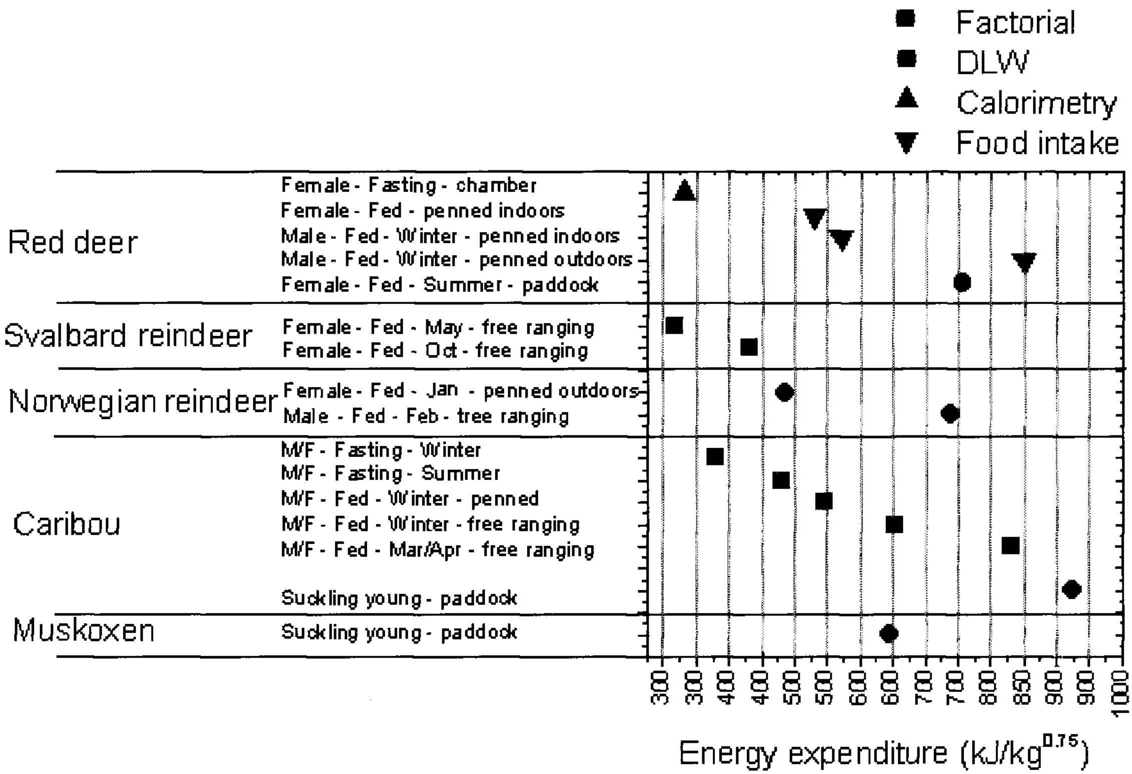


Fig. 4. Comparison of estimates of energy expenditure in three species of northern ungulates made using a range of methodologies: factorial, calorimetry, measured food intake and doubly labelled water (DLW).

To compare the metabolism of individuals within a species or to make between-species comparisons, the values for expenditure must be standardized in some way and the best method available is probably the Brody-Kleiber proportionality which suggests on empirical and theoretical grounds that expenditure should be expressed per kg$^{0.75}$ (Blaxter, 1989). When expressed in this way it can be seen from Fig. 4 that even within the factorial approach there is a very wide range in the estimated level of expenditure, both within and between species. Some of this variability will be due to differences between the studies in the sex of the animals, the season and the degree of restriction imposed but even after taking account of these effects the estimates are very variable. For example, factorial estimates of expenditure in free ranging Svalbard reindeer (*R. t. platyrhynchus*) in October (433 kJ/kg$^{0.75}$; Tyler, 1987) are considerably less than those for free ranging caribou in winter (652 kJ/kg$^{0.75}$; Boertje, 1985) and even studies within a species can be very variable with a second study in free living caribou in winter providing a value of (830 kJ/kg$^{0.75}$; Fancy, 1986). Some factorial estimates have been very low with free ranging female Svalbard reindeer in May having an estimated expenditure (319 kJ/kg$^{0.75}$; Tyler, 1987) which is similar to the resting metabolic rate (standing) in captive animals (348 kJ/kg$^{0.75}$; Nilssen *et al.,* 1984). The relatively small number of DLW studies which have been carried out in large ungulates indicate that, whilst there are some exceptions, the DLW method generally provides higher values than have been derived from feeding or factorial studies. For example, the DLW derived expenditure of female red deer kept in a group in a field covering 3300 m^2 was 757 kJ/kg$^{0.75}$ during the summer (Haggarty *et al.,* 1998), a value that was higher than previous estimates of requirements with the only higher estimate coming from a feeding trial in stags penned outdoors in winter (850 kJ/kg$^{0.75}$; Fennessy *et al.,* 1980). A comparison of the outdoor feeding results with similar studies in animals indoors in the same season (570 kJ/kg$^{0.75}$; Kay *et al.,* 1984) suggest that fully one third of the outdoor requirements in winter in red deer are due to the effect of outdoor temperature. This finding is reinforced by

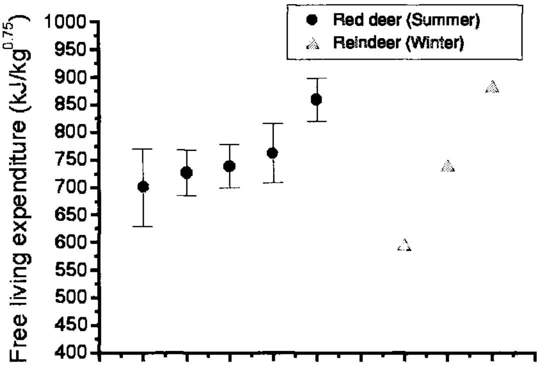


Fig. 5. Between animal variability in doubly labelled water (DLW) derived free-living energy expenditure for red deer (Haggarty *et al.*, 1998) and young male reindeer in winter (Gotaas *et al.*, in press).

the comparison of DLW derived free living energy expenditure in hinds in summer (757 kJ/kg$^{0.75}$) with the partially confined stags in winter (850 kJ/kg$^{0.75}$). Also included in Fig. 4 are some reports of DLW derived energy expenditure in caribou and muskoxen (Parker *et al.*, 1990) although the interpretation of these results is complicated by the fact that they were carried out during suckling.

Comparison of DLW results obtained in red deer with those from captive and free ranging reindeer are shown in Fig. 5. Given that the results for the red deer were obtained in summer where the thetmal stress was minimal, whilst reindeer have a level of thermal insulation which protects them from the effects of cold in winter (Tyler & Blix, 1990), the similarity in expenditure indicates that free living physical activity of both species is comparable since this will make up the largest proportion of heat production. This point is made clear in Fig. 6 where the DLW derived expenditure of free living reindeer (Gotaas *et al.*, in press) is compared with that of penned reindeer (Gotaas *et al.*, 1997). Whilst some of this difference may be explained by the fact that the free-living animals were male whilst the captive animals were female, it is striking that the non-fasting energy expenditure in the free living animals was up to 3 times that of the captive animals.

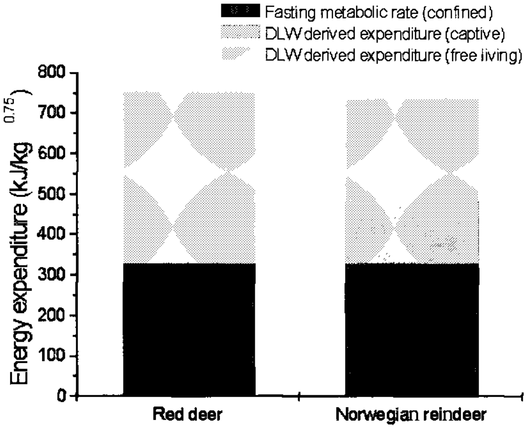


Fig. 6. Comparison of the components of free-living energy expenditure in ungulates from arctic (reindeer; Gotaas *et al.*, 1997; in press) and temperate (red deer; Haggarty *et al.*, 1998) regions.

When a new method suggests that old assumptions may be in error it is natural to question the validity of the method. However, all the processes which could result in errors have been exhaustively described and, in most cases they result in an underestimate of expenditure (Haggarty, 1991; Haggatty *et al*, 1994a; Midwood *et al.*, 1989; 1993; Gotaas *et al.*, 2000); the finding of generally higher than anticipated values for expenditure is thetefore robust.

The DLW method may provide information in addition to the estimation of energy requitements of groups if a value for the ptecision of energy expenditure is available. For example, it can be seen that one of the red deer had a significantly higher level of expenditure compared to the test of the group (Fig. 5). Since all the animals were exposed to the same climate and environment, this difference was presumably due to a higher physical activity, possibly reflecting the dominance of this hind within the social group. The equivalent values in free ranging reindeer shows that the mean level of expenditure was very similar to that in the red deer but that the range of values was much greater. No estimate of precision was available for these data but similar previous studies (Gotaas *et al*, 1997) indicated a similar level of precision to that found in red deer, suggesting that in truly free ranging animals the energy expenditure difference between individuals is much larger than is found in farmed species. This is not only important with tespect to the interactions between individuals within a herd but it also has implications for the number and type of individuals which have to be monitored (using DLW, the factorial method, or any other approach) in order to give a good estimate of the expenditute of the whole group. For example, Fancy & White (1985) have calculated that caribou breaking the trail at the head of the spring migration have an associated increment of minimal metabolism which is 2.5 times that in animals following the packed trail. Whilst the overall energetic effect of trail breaking would depend on the proportion of the day spent in this activity, such observations suggest that total energy expenditure measured by DLW could well be substantially different in these two groups of animals.

Cycles of fat deposition and mobilisation

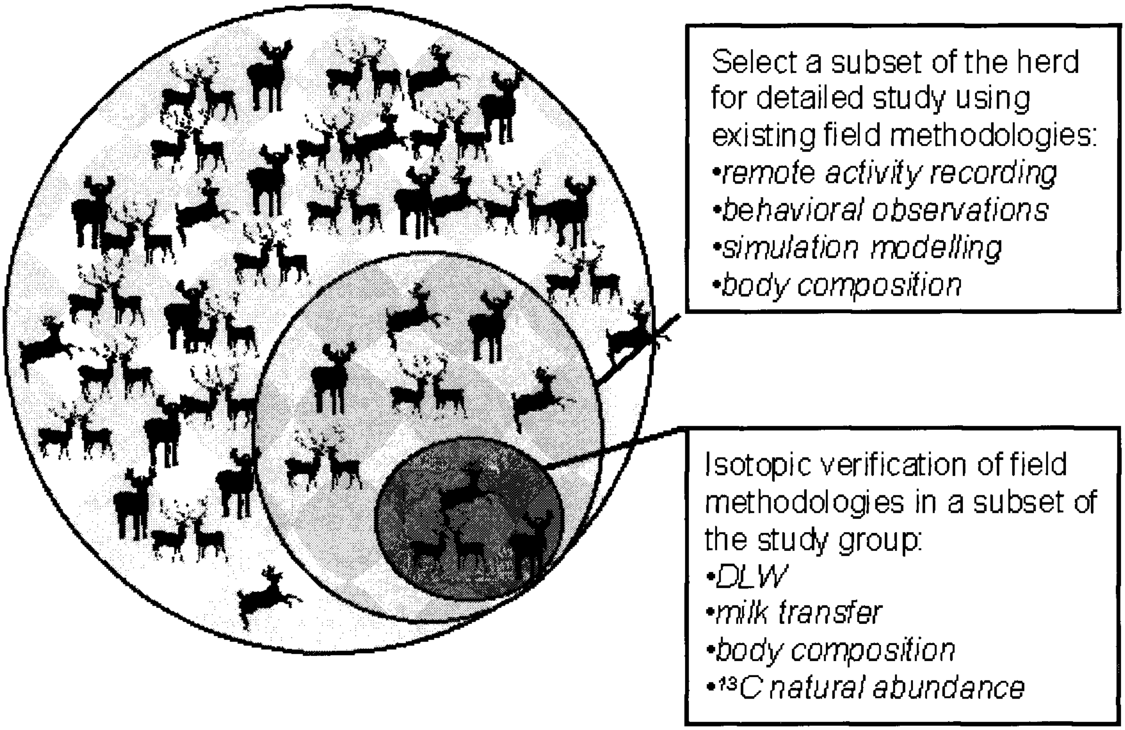
Arctic ungulates such as Svalbard reindeer store very large amounts of fat during the short arctic summer and lose most of it during the arctic winter when there is no daylight and restricted access to forage (Tyler, 1987). Boertje (1985) has calculated that utilisation of body fat can provide up to 10% of the energy requirement of caribou in winter whilst Tyler (1987) suggested a figure of up to 25% in non-pregnant Svalbard reindeer. Conversely, Boertje (1985) has calculated that in summer the energy cost of fat deposition accounts for around 17% of the total requirement. Body composition has traditionally been estimated from a variety of techniques including dissection and chemical analysis (Ringbetg *et al.*, 1981; Adamczewski *et al.*, 1987; 1995; Gerhart *et al.*, 1995) but in order to derive values for energy requirements in the different seasons in truly free living animals it is necessary to evaluate the magnitude of these processes in the field, preferably without recourse to serial slaughter. This can be done isotopically by estimating the body water from isotope dilution where the body fat content is estimated using information on the hydration of non-fat tissues (e.g. Larsen & Blix, 1985; Parker *et al.*, 1993). Measurement of the body water pool size is an integral part of the DLW method therefore a second measurement of body water using only a single isotope (most probably ^{2}H since this is much less expensive than ^{18}O) some weeks or months after the initial DLW measurement (the exact period over which the change is measured depends on the rate of fat loss) can provide an estimate of fat deposition/mobilisation (Haggarty *et al.*, 1994).

The rate of deposition of fat can also be measured in the same way during the summer months but it should be kept in mind when combining such measurements with a DLW study that the sequestration of ^{2}H into body fat during fat synthesis can be a major source of error in the DLW method (Fig. 3) and one which has to be corrected for (Haggarty, 1990; Haggarty *et al.*, 1990; 1994). Simple estimates of fat deposition cannot be used to estimate sequestration since ^{2}H incorporation into fat can occur during the normal process of fat turnover and fat synthesis has been detected in adult weight stable humans from the long term turnover of ^3H_2O (Snyder *et al.*, 1968) and the incorporation of ^{2}H into circulating fatty acid (Leitch & Jones, 1993). Since the resulting error on the DLW method is specific to each species and physiological state, it may be necessary to sample the adipose stores where the maximum rate of deposition is occurring in order to measure ^{2}H incorporation directly. The long term sequestration of hydrogen isotopes into body fat is a factor that may also be relevant to the choice of hydrogen isotope (stable ^{2}H or radioactive ^{3}H) in DLW or body composition studies in free ranging species as the biological half life of the ^{3}H will be increased in the presence of significant sequestration (Snyder *et al.*, 1968).

Lactation

Perhaps the biggest nutritional stress on female animals is reproduction and Boertje (1985) has calculated that the energy cost of lactation can account for up to 22% of the energy requirement of caribou. The best field method of measuring milk output is by isotopically labelling the body water of the mother and measuring the appearance of isotope in the body water of the suckling young (McFarlane *et al.*, 1969). This has typically been done in ruminants using radiolabelled ^3H_2O and the technique has been used in reindeer and caribou calves (McEwan & Whitehead, 1970) and caribou and muskoxen (Parker *et al.*, 1990; White *et al.*, 1989). The results of these studies produced estimates of milk intake of around 1.5-1.6 l/day on day 20 of lactation with very little difference between species.

The disadvantages of long term radioisotope contamination of the environment are even more important when carrying out studies involving young which may retain the ^{3}H for a long time and there have been some attempts to replace ^{3}H with ^{2}H, at least in domestic species (Odwongo *et al.*, 1985). However, as in the measurement of body composition, the normal use of the DLW method already provides much of the information required for this isotope transfer technique. Unfortunately, as with the estimation of body composition during fat deposition, the process of lactation can itself introduce significant errors into the DLW method. But



Select a subset of the herd for detailed study using existing field methodologies:
- *remote activity recording*
- *behavioral observations*
- *simulation modelling*
- *body composition*

Isotopic verification of field methodologies in a subset of the study group:
- *DLW*
- *milk transfer*
- *body composition*
- *^{13}C natural abundance*

Fig. 7. Isotopic methodologies are best used in combination with existing field techniques because of cost and because the field methodologies often provide additional information necessary to interpret the isotopic data.

the information collected in the process of estimating the transfer of nutrients in milk from the mother to the young is the same information needed to make the appropriate corrections to the DLW data (Haggatty *et al.*, 1990).

Diet selection and intake

The selection of forages which go to make up the intake of an animal can have a significant effect on expenditure since the quality of the forage will affect the energy cost of digestion and it will also have an effect via the energy cost of physical activity involved in the location and ingestion of the preferred grasses, shrubs, lichens and mosses. Some workers have attempted to estimate diet selection by observation and sampling (e.g. Boertje, 1990) but there is a stable isotope methodology which may also be useful in deriving this parameter. This approach is based on the fact that the ^{13}C concentration of biosynthetically derived organic compounds is determined by the ^{13}C abundance of the source material, the availability of the source material and kinetic isotopic fractionation effects during uptake, assimilation and incorporation into living organisms. In the case of marine organisms the autotrophic fixation of inorganic carbon dissolved in seawater (Conway *et al.*, 1994) results in an average difference in ^{13}C abundance between marine and terrestrial biomass reported by different groups have been relatively constant, with marine sources being enriched by 13‰ (Craig, 1952; 1953), 14‰ (Wickman, 1952) or 12‰ (Degens, 1970) relative to terrestrial biomass. This difference is large enough in relation to the precision of isotopic measurements on modern isotope ratio mass spectrometers (±0.4‰) to measure the contribution of marine and terrestrial foods to total intake in the human food chain (Haggarty *et al.*, 1999) which is surely the most diverse of any species. Furthermore, the simultaneous measurement of natural variations in other isotopes such as ^{15}N would provide further detail on the dietary origin of nutrients.

In less complex diets, such as those found in arctic ungulates, the task of determining the dietary origin of nutrients is simpler. It has been shown that plants such as lichens, which lack a vascular system, have a characteristic ^{13}C composition which is generally lower than that of plants with a vascular system; the ^{13}C abundance of lichen has been reported as -18‰ with that of annual grass growing only a few feet away as -28‰ (Park & Epstein, 1960; Craig, 1953; Wickman, 1952). This kind of difference should be large enough to provide an estimate of the relative contribution of these forages to nutrient intake therefore the approach of exploiting natural ^{13}C abundance variations may be useful in studying the diet selection and intake of free living arctic ungulates even when consuming mixed diets.

Conclusions

With the introduction of innovations such as faecal sampling for the estimation of isotopic enrichment, the availability of appropriate correction factors and stoichiometries for known sources of error and iterative calculation of unknown parameters, the DLW technique can now be considered to be a truly free living methodology suitable for use in wild, free ranging species. Providing the appropriate corrections are made, this field methodology provides accurate values fot free living energy expenditure in individual animals. The few studies carried out so far in arctic ungulates suggest that previous predictions have generally underestimated the true level of expenditure, that there is considerable between animal variation in the level of expenditure and that this is largely determined by physical activity.

Energy expenditure is only equal to the more useful parameter of the energy requirement when an animal is in energy balance. However, processes such fat deposition and utilisation and lactation represent a significant patt of the energy budget of arctic ungulates. Much of the information gained in the course of a DLW study can be used to estimate milk output and the change in body fat and the additional information required to make these estimates is ptecisely the same information required to correct the DLW method for any errors caused by such processes. In addition to the use of the isotopes ^{2}H and ^{18}O in the DLW method, it is possible that natural ^{13}C abundance variations in the arctic environment may be exploited to study diet selection in truly free living arctic ungulates.

Some disadvantages of the DLW methodology are that it remains expensive, the stable isotope analysis is technically demanding and it requires access to sophisticated mass spectrometry facilities. Therefore, the use of this technique is likely to be limited to relatively small numbets within each study. Furthermore, although DLW can provide an accurate value for free living energy expenditure, it is often important to have information on the individual components of expenditure, e.g. the relative contribution of physical activity and thermoregulatory thermogenesis, in order to interpret the values for overall expenditure. For these teasons it may be that one of the most valuable uses of the DLW method is to validate existing field methodologies and simulation models (Fig. 7) so that they may be used with confidence in truly free living arctic ungulates.

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Functional and comparative digestive system anatomy of Arctic ungulates

R. R. Hofmann

Institute for Zoo Biology and Wildlife Research Berlin, Alfred-Kowalke-Strasse 17, P.O.Box 601103, 10252 Berlin, Germany (Arndt-Hofmann@t-online.de).

Abstract: Dietary niche, feeding type classification and seasonal strategies of *Rangifer tarandus* and *Ovibos moschatus* are discussed in relation to the anatomy of their digestive system. Classification criteria for the flexible feeding type system, originally established in bovids and later adapted to cervids, are substantiated and critically discussed in the light of recent attempts to invalidate the system. Eurasian mountain reindeer, North American barren-ground caribou, Svalbard reindeer and Victoria Island caribou are seasonally adaptable, opportunistic ruminants of the intermediate feeding type but the long evolutionary separation of Svalbard reindeer has modified several morphological features for winter survival without lichen, resulting in better adaptation to fibrous forage. Muskoxen, despite their seasonal selectivity, are typical grass and roughage eaters with extremely long mean retention time. Detailed data on the entire digestive system from muzzle to anus on both species are still insufficient and extended studies are worthwhile for understanding their nutritional niche and feeding adaptations.

Key words: bovid, cervid, feeding strategy, *Ovibos, Rangifer,* ruminant.

Rangifer, 20 (2–3): 71–81

Introduction

There is general agreement that many populations of the highly variable suborder Ruminantia, a 'latecomer' in mammalian evolution, are limited by the availability and digestibility of their forage resources, by the extent of evolutionary variation of their digestive system and by body mass, in this order. The many variations of the digestive system within the suborder has permitted a flexible classification into morphophysiological feeding types which transcends phylogenetic classification and differences in body mass (Hofmann & Stewart, 1972; Hofmann, 1998). The situation is complicated, however, by the fact that the majority of species of bovids are found in tropical or subtropical habitats while most cervids are found in holarctic environments where minimal ruminant body size is about 20 kg compared to only 3-4 kg in the tropics. But there are fascinating ecological similarities among both large ruminants (>350 kg, e.g. Greater kudu, *Tragelaphus strepsiceros,* and moose, *Alces alces*) and small ruminants (<10 kg, e.g. muntjac, *Muntiacus* spp. and duikers, *Cephalophus* spp.). Within both groups there are many remarkable similarities in the characteristics of the digestive system, feeding behaviour and social system. Moose and roe deer, *Capreolus capreolus,* belong to the evolutionary older ruminant type of concentrate selectors (CS) and while several ecological, nutritional and morphophysiological factors make CS unsuited for life in the high Arctic, both moose and roe deer have extended their range well inside the subarctic. Two species of ruminants, however, the muskox (*Ovibos moschatus*) and the reindeer/caribou (*Rangifer tarandus*), are well adapted to and have survived for many millennia in potentially hostile arctic environments. Ninety years ago, Lönnberg (1901) presented anatomical data and descriptions of Swedish reindeer and half a century later Sablina (1961) presented data on reindeer and elk/moose from Russia. In the 1970s Finnish, Norwegian and Canadian workers expanded knowledge of these ruminants. The muskox was more or less unknown until the 1990s and still needs comprehensive study.

The link-up of digestive anatomy, physiology, nutritional behaviour, forage choice and evolutionary niche of wild ruminants had been stimulated by my own comparative work in East Africa (Hofmann

& Stewart, 1972; Hofmann, 1969; 1973). The importance of comparative work in the nutritional physiology of wild or free ranging species was emphasised in an early paper by Kay *et al.* (1980). Subsequently, comparative morphological and physiological studies of cervids resulted in a more differentiated approach to studying ruminant digestion and in adjusting the feeding regimes of wild ruminants in zoos - more so in Europe than in North America. Marholdt & Hofmann (1991) showed that most artificial feeds were too high in easily digestible components and frequently induced or maintained acidotic conditions in all three feeding types, resulting in the kind of alterations of the ruminal mucosa described in reindeer by Westerling (1975).

Robbins *et al.* (1995) attempted to invalidate the morphological basis and the functional deductions which permitted the differentiation of ruminants into a flexible system of three main feeding types. Nevertheless, Hofmann's (1989) classification has stimulated researchers world-wide including those dealing with arctic ruminants to arrive at a multitude of interesting and applicable results through comparative research. Our anatomy-based functional hypotheses are supported by sound experimental evidence (Hofmann, 1999).

In spite of the great adaptive range of all of 180 species of ruminants, the key to understanding ruminant biology and management is the recognition of the division into the evolutionary shaping as a result of co-evolution with forage plants of two extreme feeding types, the CS and the grazers (GR, i.e. grass and roughage eaters) with a range of intermediate feeders (IM) in between. The small roe deer, successful over the entire Eurasian land mass and the large moose, successful also in North America, can thrive without grass but will starve to emaciation and death if given only grass (not lucerne!) hay. These two species are CS and never GR in spite of their vast difference in body mass. Cattle are derived from the late-evolved aurochs (*Bos primigenius*) which adapted in the late Miocene to a nutritional staple of high cellulose content grass. Today they are loaded with industrial concentrates for milk or beef production but their digestive system will collapse if they are deprived completely of grass. The anatomy of CS and GR is diverse, be they large or small.

Ruminants gain energy from plants in two ways: (i) digestion of fibre (cellulose, hemicelluloses) through microbial digestion of carbohydrates in the rumen and/or in the distal fermentation chamber (DFC, formerly called 'caeco-colon'; Hofmann, 1985); (ii) direct utilisation of soluble plant cell contents (PCC), mainly sugars from dicotyledonous plants (either as 'ruminal escape' as a result of a short mean retention time (MRT), or of bypassing forestomach microbial digestion via the ventricular groove leading directly into the abomasum and the duodenum).

Three factors complicate these avenues: (i) the limited dynamics of the rumen microbial population which nevertheless represents a highly and rapidly adjustable system; (ii) the structure and the morphological dynamics of the ruminal and/or intestinal mucosa and (iii) the morphological dynamics of the salivary glands. Adaptive changes of the ruminal mucosa reach their limits under unphysiological conditions (e.g. acidosis) and become pathological. Fibre digestion, especially digestion of cellulose, is clearly linked to anatomical conditions because the MRT of forage must be long enough to exploit potential digestibility. Ingesta retention devices are poorly developed in CS and IM. Roe deer (CS) hardly ever select more than 20% of cellulose (Holand, 1994; Deutsch *et al.,* 1998). These animals are almost incapable of digesting cellulose in winter, when practically all plants are high in cellulose, because populations of cellulase-producing bacteria in their rumens are much reduced.

Rowell (1998) demonstrated the direct utilisation of sugars in the duodenum in roe deer and moose. While the energy gain from structural carbohydrate fermentation in the rumen is 26 mol ATP/mol glucose, direct oxidative utilisation following the transport of substrates along the rumen bypass yields 38 mol ATP/mol glucose. Rowell's experiments mimicked the oxidation of PCC diluted by copious saliva from large parotid glands. It remains to be seen to what extent the arctic ungulates can apply these alternatives. *Rangifer,* repeatedly classified as a selective IM ruminant with a considerable potential for seasonal adaptation between near-CS and near-GR strategies, is an obvious candidate. *Ovibos,* which is equipped with a very robust GR digestive system, falls into a different morphophysiological category and, consequently, these two species are not necessarily competitors for forage where they occur sympatrically.

Though still incomplete, our knowledge about the functional anatomy of these two arctic ruminant species has been considerably enriched over recent years. Most studies over the last 10 years have concentrated on the rumino-reticulum as the main fermentation chamber and especially its absorptive mucosa which is clearly influenced by seasonal changes in microbial activity, forage quality and availability. Fewer studies have focused on the intestine although the DFC certainly deserves more attention as suggested by Hofmann (1985) and, for Svalbard reindeer, by Mathiesen *et al.* (1985). Hemicelluloses generally escape ruminal fermentation and are broken down in the DFC after HCl hydrolysis in the abomasum. Digestion of cellulose, by contrast, is very slow in this organ, at least in roe deer (Deutsch *et al.*, 1998).

Only recently has the omasum, a somewhat enigmatic portion of the quadrilocular ruminant stomach, received attention in arctic ungulates and the physiologically important salivary glands, with their complex functions in selective CS and IM (Hofmann, 1989), have likewise only recently been studied in *Rangifer*. The importance of the forage prehension and mastication apparatus for diet selection has also received initial attention. All three last mentioned sections of the digestive system, much neglected in arctic ungulates, have been studied by the very active group of Svein Mathiesen in Tromsø, whose unpublished data I have kindly been allowed to include in this review (Mathiesen *et al.*, 1999; 2000 a; b; c).

On the following pages I review the physiology and functional anatomy of the digestive system of the two arctic ruminant species. A complete picture of adaptive strategies by both species can, in my opinion, be arrived at only when the entire system, including not only the classical tract but also the oesophagus, pharynx, tongue, palate, lips, teeth and the salivary glands, is considered.

I. Forage comprehension and mastication

Mathiesen *et al.* (2000 b) have studied the oral anatomy of arctic ruminants using a small CS, musk deer (*Moschus moschiferus*), for comparison. They confirmed Janis and Ehrhardt's (1988) conclusion that all three species have narrow muzzles and low crowned molariform teeth. They demonstrate how the cranial anatomy of reindeer has evolved to optimise utilisation of the high quality mixed forage available during the short arctic summer. Forage is abundant during this period and it pays to forage selectively avoiding lignified grasses as long as possible. Not surprisingly, musk deer had the narrowest muzzle and the lowest cheek teeth of all three species, reflecting their highly developed CS strategy, while the muskoxen had the typical broad-crowned incisor arcade typical of GR. I would accept the authors' conclusion that, at least in this cranial portion of the system, the main morphological development was an adaptation to summer conditions, because all the arctic species show reduced metabolic demands and forage intake in winter. There are similar observations on savanna grazers like hartebeest (*Alcephalus buselaphus*) and topi (*Damaliscus lunatus*) which can afford to use a narrow muzzle also during the dry season, when most forage is rich in lignin, in order to optimize selective grazing during the growing season. A broad muzzle (as found especially in the non-selective bovines) and hypsodont cheek teeth does not make a species a grazer. On the other hand, the reindeer muzzle has a comfortable intermediate width enabling it to cope with the contrasting foraging situations which occur on Svalbard and in mainland Norway. The authors' valuable detailed data for this species should, however, be complemented by a study of the tongue. The tongue of *Rangifer* is unusual, being apically broad-bilobular and with a short torus, i.e. a long freely mobile portion, and, thus, is quite different from the tongue of other IM cervids like red (*Cervus elaphus*) or fallow deer (*Dama dama*) (Hofmann, unpubl.).

II. Salivary glands

It is unfortunate, considering their great importance for digestion, how few studies deal with the salivary glands: the parotid and the ventral buccal and, with their feeding-type-related varying proportion of serous end-pieces, also the mandibular and the sublingual glands. It was again Mathiesen *et al.* (1999) who made the first attempt to fill this gap for European mountain reindeer and Svalbard reindeer. There are no published data for other subspecies of reindeer or for muskox salivary glands. We have, however, studied these organs in detail in a taxonomically close species, the takin (*Budorcas taxicolor*) (Frey & Hofmann, 1998). This northern montane species has relatively small parotid glands (0.07% of body mass) and total salivary gland weight amounts to 0.21% of live body mass, i.e. between the average values for GR (0.18%) and IM (0.26%; Hofmann, 1989). From initial observations, muskox salivary glands are similarly small, which is consistent with their predominantly fibrous forage choice (Staaland & Olesen, 1992;

Thing *et al.*, 1987; Forschhammer & Boomsma, 1995).

Ruminal cellulolysis, based on naturally selected feed in the wild, is a slow process but this does not obviate the danger of a lowered pH as is frequently seen when commercial concentrates are fed to GR species like muskox. A moderate flow of saliva buffer from small GR salivary glands is among the adaptive characteristics of such species. Mathiesen *et al.* (1999) compared the relative size of the salivary glands in Svalbard and Eurasian mountain reindeer in relation to feeding strategy, season and reproductive status. They provided a fine example of seasonal plasticity of the main buffer supplying gland, the parotid, which is also assumed to be prominently involved in bypassing soluble nutrients via the ventricular groove. They found little difference between the two sub-species in which the parotids, at 0.11-0.14% of live body mass, were within the range of IM ruminants (Hofmann, 1989).

The most striking feature, however, was that the relatively large parotids of the reindeer, amounting to 83-92 g late in the Arctic summer, atrophied in winter and were reduced to only 59-68 g by March/April. This reflects the functional response of the main buffering and diluting organ to high intake of easily digestible matter, high ruminal fermentation rates and reduced MRT (Kay, 1987). The authors ascribe these changes mainly to seasonal variation in food intake resulting from variation in appetite but it is difficult to quantify the obvious influence also of variation in fermentation rate. It may also be added that salivary gland mass corresponds to saliva output: the relative saliva flow is highest in CS (roe deer), intermediate in IM (fallow deer) and lowest in sheep which have salivary glands amounting to only 0.05% of live body mass. One important consequence of large CS and IM salivary glands with their high flow rate is their diluting effect on the ruminal fluid. Irrespective of live body mass, all CS from dikdik (*Madoqua* spp.) to giraffe (*Giraffa camelopardalis*) have dry matter retention times that are much closer to fluid retention than in GR. This is shown in Table. 1 in which the mean retention time of particles relative to fluids in the rumen, expressed as the ingesta selectivity factor (SF, Lechner-Doll *et al.*, 1990) where

$$SF = \frac{MRT\ particles < 2\ mm}{MRT\ fluids}$$

is compared in different feeding types. According to Illius & Gotdon's (1992) allometric equation for ruminant passage rates, the MRT of ingesta in giraffe should be 80-90 h; Claus (1998), however, measured MRTs of only 34-48 h in this species.

So far, no specific investigations have been carried out on the tannin binding capacity of reindeer or muskoxen saliva, as has been done using a new tannin binding assay and molecular biology techniques at IZW Berlin, for roe deer, red deer and moose saliva (Fickel *et al.*, 1998). These studies showed that the roe deer specific saliva protein binding capacity for tannins is almost twice that of red deer (IM) saliva. Presumably reindeer saliva is in a similar category while muskox saliva may well be without such capacities, as in most other GR.

III Rumen structure, capacity and mucosa

There are two early papers which deal with some important aspects:
Westerling's (1975) pioneering paper on the effect of diet on the ruminal mucosa and the paper by Staaland *et al.* (1979) comparing the digestive tracts of Svalbard and Norwegian reindeer. The latter paper provides no detailed description or measurements of stomach structure but only mean tissue weights from which the relative size of different portions of stomach were calculated. They confirm that rumen tissue in adult Svalbard reindeer in

Table 1. Mean retention time of particles relative to fluids in the rumen, expressed as the ingesta selectivity factor (SF, Lechner-Doll *et al.*, 1990) in ungulates representing three different feeding types: CS: concentrate selectors, IM: intermediate feeders, GR: grass and roughage eaters: *sensu* Hofmann (1989).

			SF	
CS	roe deer	natural forage	1.20	Deutsch, 1988
CS	giraffe	browser breeder pellets	1.29-1.47	Claus, 1998
CS	moose	aspen foliage and lucerne hay	1.69	Renecker & Hudson, 1990
GR	mouflon	natural forage	1.70	Deutsch, 1998
IM	wapiti	lucerne hay, winter	1.93	Renecket & Hudson, 1990
GR	cattle	thornbrush savanna pasture	2.79	Lechner-Doll *et al.*, 1990

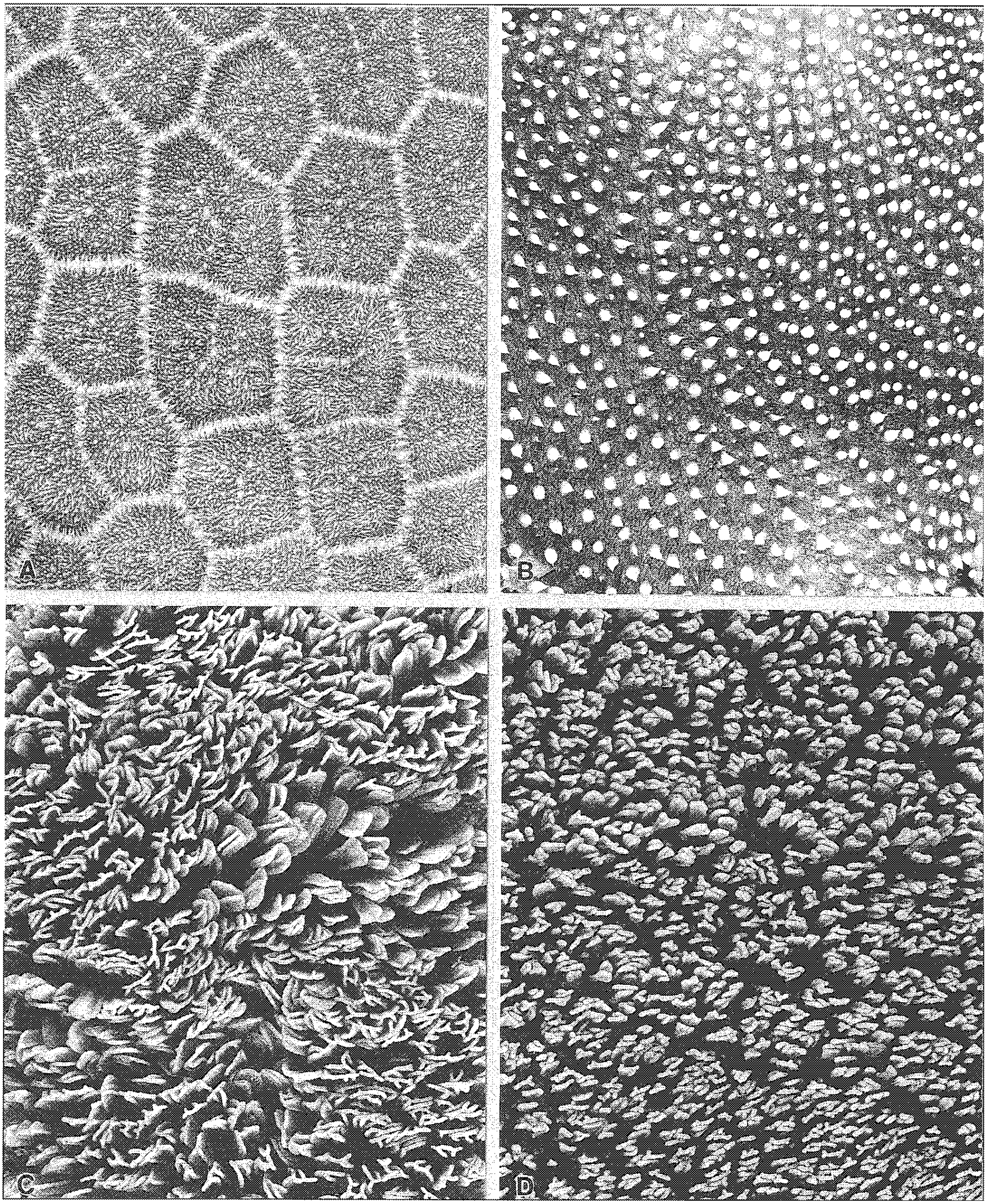


Fig. 1. Stomach mucosa of *Rangifer tarandus.* A: *Fundus reticuli* of a 5-6 year old female Yukon caribou. B: Central portion of a lamina omasi of 1st order of a 5-6 years old female Yukon caribou (Sept.). C: Ventral ruminal wall papillae of a 9-10 years old male Yukon caribou (Sept.). D: Ventral ruminal wall papillae of a 3 years old captive male reindeer (Whipsnade Park; August). Enlarged from natural size 2.2 x.

summer is about 48% of total digestive tract weight but only about 38% in winter. There is no such functional atrophy of rumen tissue in mainland reindeet in which rumen tissue remains about 48%. The omasum, approximately 5% by weight of the total digestive tract, was within the range of other IM while the abomasum, at approximately 6%, was slightly larger.

My own measurements of three adult caribou bulls show that these are similar to red deer, including the formation of thtee well-developed ruminal blindsacs and not two as in bovids. The ruminoreticulum in *Rangifer* is characterised by a capacious subdivided fermentation chamber with moderately strong muscular pillars and a thin walled, capacious reticulum. Its mucosa is furnished with low, mainly primary crests (Fig. 1). The most striking feature of the rumen is a very dense and evenly distributed papillation. This is strongly indicative of the absence of any ingesta stratification as in GR where, as a consequence, rumen papillae are absent or much reduced on the dotsal and ventral wall. The reindeer/caribou rumino-reticulum mucosa presents features similar to CS. With the exception of the thtee blind sacs the reindeer stomach anatomy resembles that of red deer and that of bovid IM such as impala (*Aepyceros melampus*).

Several papers deal with the question whether the different ecological situation and geographic isolation over evolutionary time of Svalbard reindeer has resulted in a change of feeding type from IM to GR (Staaland & White, 1991) or from IM to CS (Sørmo *et al.,* 1998). Staaland & White (1991) found support for classifying Svalbard reindeer as GR in winter though not in summer. This is simply confusing the issue. If one accepts the evolutionary developmental basis of a whole series of morphological criteria (i.e. typical variations of a hypothetical blueprint of the ruminant digestive system) and relates these to the principal choice of feeds of a species, it must be quite logical that all ruminants, irrespective of feeding type, still have to cope with seasonal changes in quality and quantity of forage. There is no intrinsic seasonality in any ruminant species and it is quite obvious that large species can better cope with low quality forage. One cannot, however, reduce all the complicated and interrelated morphophysiological adjustments, the result of very long evolutionary adaptation processes, to differences in body mass, seasonality or differences in one or two organ measurements. The basic digestive system structure of every ruminant species is specific and becomes, in the course of postnatal development, typical under the influence of behavioural traits (such as feeding habits), by acquiring or learning the typical forage choice which best suits its digestive tract. These can show species-specific variation which may also relate both to phylogeny or to biogeography, including adaptation to local forage plants such as the grasses and forbs which differ greatly in their nutritional value, digestibility and structure from season to season in the Arctic.

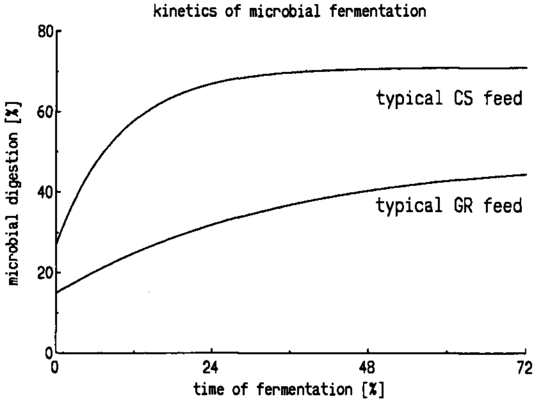
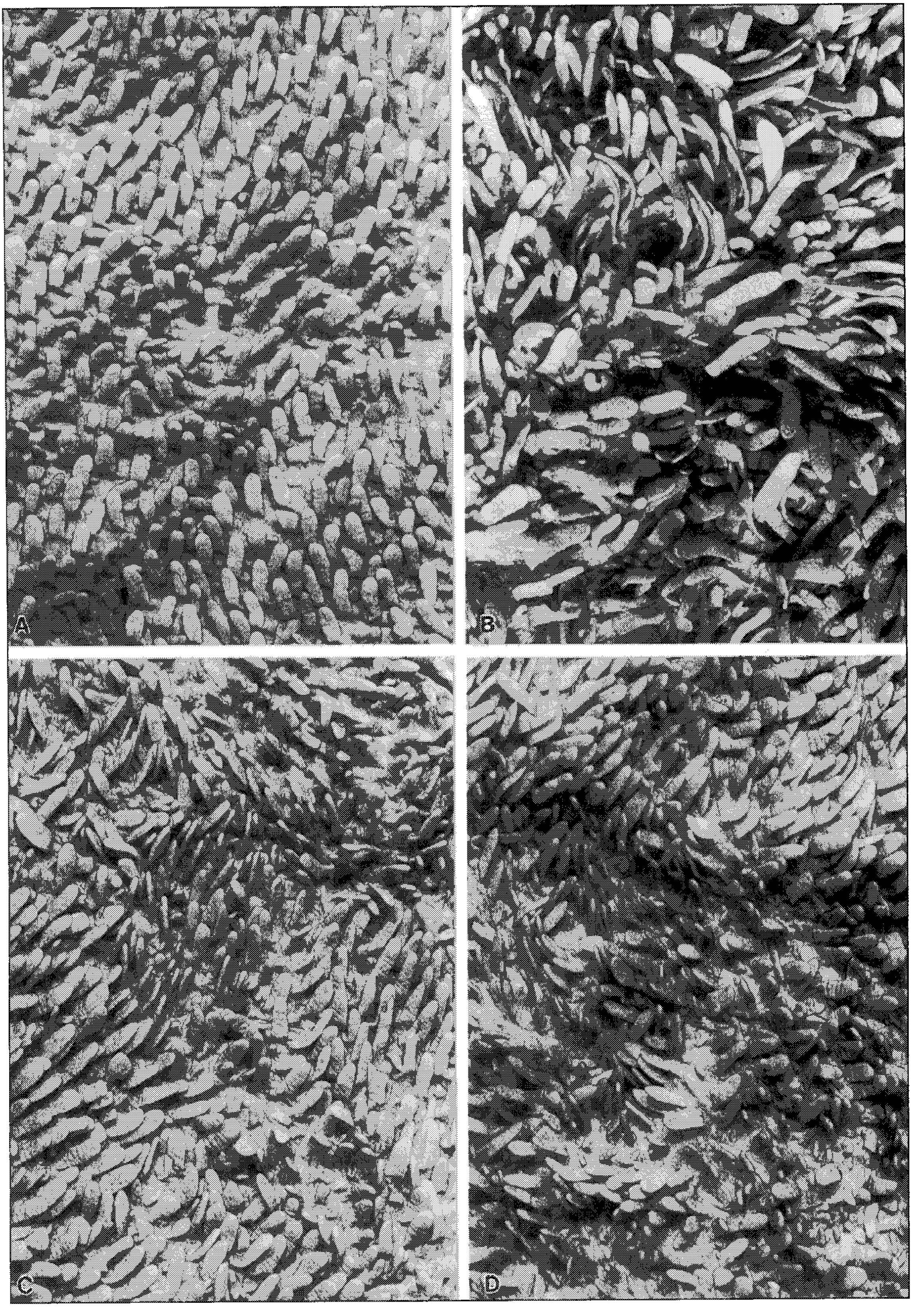


Fig. 2. Kinetics of microbial fermentation in ruminants of different feeding types. CS: concentrate selectors, GR: grass and roughage eaters, *sensu* Hofmann (1989). Data provided by M. Lechner-Doll.

Seasonal changes observed in basic structures are induced entirely by changes of the quality of specific forage plants and also, although to a lesser extent, by their reduced availability in winter. Here the sequence of events is clear. First, there is a rapid response from the rumen microbial population of cellulolytic, amylolytic and other organisms (Orpin *et al.,* 1985). These are dependent on a more or less steady ruminal pH which is regulated by buffering saliva and mucosal absorption and they are limited in their effects by the rate of flow of ingesta and the MRT. This is why the kinetics of microbial fermentation are necessarily different between feeding types (Fig. 2). Body size does not influence these inherent differences in microbial digestion. In CS,

Fig. 3. Ruminal mucosa of *Ovibos moschatus.* A: dorsal ruminal wall (mean Surface Enlargement Factor (SEF) 2.04). B: *atrium ruminis* (mean SEF 3.74). C: dorsal blindsac (mean SEF 3.23). D: ventral ruminal wall (mean SEF: 2.12). These samples from a muskox female collected by Jan Adamczewski in April 1990 on Victoria Island, NWT/Canada, reflect minimal papillary development in a low energy/high fibre winter forage situation at reduced intake. Surface enlargement increased threefold under optimal forage conditions later in the year. Enlarged from natural size 2.2 x.


A
B
C
D

and most likely also in IM feeding on comparable substtates in the Arctic summer, fermentation rate reaches its plateau and remains constant after 24 hours. From this it can be postulated that their anatomy does not provide better conditions for fibre digestion.

The second phase of seasonal adjustment takes place more slowly. The reactive adaptation period of the ruminal mucosa, induced by the microbial changes, is 2-3 weeks or even longer (Hofmann, 1985). This was first observed in reindeer by Westerling (1975) who demonstrated both the unusual shape of their rumen papillae which complicates the calculation of the papillary surface enlargement and makes comparison between species difficult. Soveri & Nieminen (1995) found distinct seasonal variation in the volume and absorptive surface of rumen papillae but not in papillar density, which is unusual. They suggested that the papillary structure of reindeer is better maintained on lichen winter diet than is the case with the fibrous, slowly fermenting winter diets of other IM species. But again, papillary distribution alone is no valid reason to reclassify reindeer as a CS. Mathiesen *et al.* (2000 a) have recently investigated this paradox again and postulate that increased lichen intake stimulates fermentation, increases the papillary surface enlargement factor and, thus, the utilisation of other winter forage plants.

Josefsen (1997) has presented a comprehensive study of the influence of diet on the forestomach mucosa of reindeer calves using morphometry, pathological studies and immunohistochemistry. However, most if not all studies of seasonal adaptive changes of the ruminal mucosa in other species have been conducted on adult, sometimes subadult, animals. As would be expected in animals gradually adjusting and expanding both their anatomy and the related physiological processes, Josefsen saw a wide range in papillary number and size in the calves. The SEF ranged from 5.8 to 18.6, with highest values in the *atrium ruminis* in summer. Low fibre silage produced effects similar to those observed in free ranging animals on food summer forage. He concluded that papillary morphology reflects ruminal function but he did not detect functional changes associated with epithelial lesions in artificially fed calves.

In a comparative feeding experiment, Aagnes *et al.* (1994) provided proof that starvation in ruminants, like seasonal adaptation, is mediated initially by the ruminal bacterial population. Starvation greatly reduced the bacterial population density and changed the bacterial species composition in the rumen. This is why CS and many IM which have had no such evolutionary pressure and adaptation period like Svalbard reindeer, are not able to exist entirely on fibrous forage, even if it is abundant, when they are deprived of suitable forage (Deutsch *et al.,* 1998). Reindeer have developed strategies for surviving periods of starvation to a greater extent than roe deer (Aagnes, 1998). As a ruminant species of the flexible opportunistic IM feeding type, reindeer can better adjust to fibrous forage than CS although not to roughage with high fibre content.

Studies of the structute of the omasum in 29 species of bovids showed that this organ was remarkably conservative in adults of a given feeding type and thus not prone to seasonal variation (Hofmann, 1973). A recent comparative study on Svalbard and mainland reindeer (Mathiesen *et al ,* 2000 c) revealed dramatic seasonal changes in total mass and absorptive surface of this organ in mainland reindeer in winter although this was not accompanied by any decline of body mass. On the other hand, Svalbard reindeer, with a distinct decline of body mass in winter, maintained omasal absorptive surface area throughout winter, possibly reflecting an adaptation to the marginal winter forage situation without lichen on Svalbard.

Very few structural data are available on the anatomy of the gastrointestinal tract of muskoxen. Staaland & Olesen (1991) suggest, though without any detailed description, that muskoxen have a typical GR digestive system (small DFC, large, cattle-like omasum) and that in West Greenland, monocotyledons dominate the diet. Staaland & Thing (1991) provide tissue and content weights and state that in north-east Greenland the muskox alimentary tract was developed in accordance with that of a typical grazer or roughage feeder. Adamczewski *et al.* (1991a) show in an excellent paper on intake, digestibility and passage rate, that muskoxen are well adapted to slow, thorough digestion of graminoid forage in winter. They recorded MRT in March among the longest recorded in any ruminant - and this is coupled, due to lowered metabolic rate in winter, with a temarkably low feed intake.

Following this and another fine study (Adamczewski *et al ,* 1992) on seasonal changes in weight, condition and nutrition of free-ranging and captive muskox females again in Canada, Jan Adamczewski sent me rumen samples from 24 muskoxen. We examined these (eight from four indicator regions in each animal); results are presented in Fig. 3. The muskox rumen has an uneven papillation (typical GR ingesta stratification) and obviously responds well, in all four regions, to increased or greatly reduced fermentation rates and low rates of production of volatile fatty acids. Papillary density shows little variation, from 51-77 cm^{-2}, but there is a remarkable range in papillary length. The longest papillae are found in the dorsal blind sac and in the *atrium ruminis;* they had a maximal length of 16.24 mm but on average papillary length ranged from 2.12-4.52 mm. In the main absorptive areas (atrium and blind sac), the surface enlargement had maxima between 18.48 and 21.77, while the average SEF had a lowest value of 2.78 and a maximum of 10.63. Thus, the SEF varied more than threefold between seasons. This obviously reflects changes in forage quality and availability which will have to be analysed further. Muskoxen, according to Adamczewski *et al.* (1992), lose 40% of their body mass from September to May related to a rapid decline in diet quality which has a maximum in July and its annual nadir in May. Ruminal mucosal enlargement obviously occurs most dramatically between May and July. It permits rapid and maximal absorption of nutrients, according to Staaland & Olesen (1991) in Greenland complemented by intake of *Salix arctica* which is rich in hemicellulose. This would also account for the relatively larger DFC in muskoxen (1:24) when compared to other GR (1:27-1:30). While the medium-sized omasum of *Rangifer* is 3.7-6.1% of GIT total weight, the advanced, multi-laminar omasum of *Ovibos* is 12% of GIT mass (Staaland & Thing, 1991).

IV Intestinal structure

Westerling (1975) provided the first classical description of the reindeer intestine with its very long spiral colon, more than half of large intestinal length and almost 18% of total intestinal length which can be explained mainly by complete absorption of any volatile fatty acids, minerals and most liquid still contained in the ingesta. At 25.6 m, the total intestinal length (TIL) is within the range of many other intermediate ruminants (Hofmann, 1985; 1989). Staaland & Thing (1991) measured a TIL of 36.5 ± 5.2 m in muskoxen (mean live body mass of 171 ± 60 kg (n=8)), a ratio of 68 : 32 for small and large intestine, a short (0.5 m) caecum and a shorter spiral colon (13-14% of TIL). This is considerably longer than in most other GR but compares well to oryx, *Oryx gazella,* a tropical dry-region grazer (Reissig, 1995; Hofmann, 1999). Staaland *et al.* (1995) corrected older gut measures upward for both arctic species (TIL 40.7 ± 5.1 in muskox and 26.6 ± 1.2 in caribou) and clearly separated *Rangifer* and *Ovibos* as IM and GR respectively with little potential interspecific competition.

Sørmo (1998) demonstrated that the size of the rumen is not affected much by changes in plant quality while the DFC increases in size with increasing amounts of hemicellulose in the diet. There is a pronounced seasonality of the DFC in Svalbard reindeer where the fermentation of cellulose seems to be inversely related to cellulose content, a process also observed in roe deer (Deutsch *et al.*, 1998). Sørmo *et al.* (1997) have also shown that production of volatile fatty acids in the DFC is of particular importance in reindeer when pastures show a low availability but high quality - a fact which clearly underlines the strong selectivity of the IM and CS ruminants for nutrient-rich plants low in fibre at any time of the year. Staaland & Thing (1991) remarked that, although the DFC is relatively small in muskoxen, it plays an important role in scavenging the digesta for important nutrients.

Staaland *et al.* (1997) have discussed, in the light of their comparative studies of digestive morphology in muskoxen and caribou, the papers of Gordon & Illius (1994) and of Robbins *et al.* (1995) who challenged the value of my comparative anatomical studies in 90 ruminant species world-wide and my morphophysiological feeding type system. Staaland *et al.* (1997) appear not convinced by the arguments of this challenge and, of course, neither am I. I expect soon to be able to evaluate this wealth of detail data statistically using a unique comparative material and test my own hypotheses regarding our feeding type-system. By then we will certainly also continue the discussion about Eurasian mountain and Svalbard reindeer, caribou and muskoxen and their admirable feeding strategies in a hostile environment. I am convinced, that morphological studies of the digestive system are and will continue to be an indispensable basis for increasing knowledge of the survival strategies of arctic ungulates, to which Tyler & Blix (1990) have supplied a wealth of physiological and bioenergetic data and which, I am sure, will be extended by including sound anatomical data.

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Viral diseases of northern ungulates

K. Frölich

Institute for Zoo Biology and Wildlife Research Berlin, Alfred-Kowalke-Strasse 17, P. O. Box 601103, 10252 Berlin, Germany (froelich@izw-berlin.de).

Abstract: This paper describes viral diseases reported in northern ungulates and those that are a potential threat to these species. The following diseases are discussed: bovine viral diarrhoea/mucosal disease (BVD/MD), alphaherpesvirus infections, malignant catarrhal fever (MCF), poxvirus infections, parainfluenza type 3 virus infection, Älvsborg disease, foot-and-mouth disease, epizootic haemorrhage disease of deer and bluetongue disease, rabies, respiratory syncytial virus infection, adenovirus infection, hog-cholera, Aujeszky's disease and equine herpesvirus infections. There are no significant differences in antibody prevalence to BVDV among deer in habitats with high, intermediate and low density of cattle. In addition, sequence analysis from the BVDV isolated from roe deer (*Capreolus capreolus*) showed that this strain was unique within BVDV group I. Distinct BVDV strains might circulate in free-ranging roe deer populations in Germany and virus transmission may be independent of domestic livestock. Similar results have been obtained in a serological survey of alpha-herpesviruses in deer in Germany. Malignant catarrhal fever was studied in fallow deer (*Cervus dama*) in Germany: the seroprevalence and positive PCR results detected in sheep originating from the same area as the antibody-positive deer might indicate that sheep are the main reservoir animals. Contagious ecthyma (CE) is a common disease in domestic sheep and goats caused by the orf virus. CE has been diagnosed in Rocky Mountain bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), Dall sheep (*Ovis dalli*), chamois (*Rupicapra rupicapra*), muskox (*Ovibos moschatus*) and reindeer (*Rangifer tarandus*). Most parainfluenza type 3 virus infections are mild or clinically undetectable. Serological surveys in wildlife have been successfully conducted in many species. In 1985, a new disease was identified in Swedish moose (*Alces alces*), designated as Älvsborg disease. This wasting syndrome probably has a multi-factorial etiology. Foot-and-mouth disease virus (FMDV) can infect deer and many other wild artiodactyls. Moose, roe deer and the saiga antelope (*Saiga tatarica*) are the main hosts of FMDV in the Russian Federation. In addition, serological evidence of a FMD infection without clinical disease was detected in red deer in France. Epizootic haemorrhage disease of deer (EHD) and bluetongue (BT) are acute non-contagious viral diseases of wild ruminants characterised by extensive haemorrhage. Culicoides insects are the main vectors. EHD and BT only play a minor role in Europe but both diseases are widespread in North America.

Key words: holarctic, cervid, moose, muskoxen, reindeer, viral disease.

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Introduction

This paper documents viral diseases in northern ungulates including those which are a potential threat to these species. The following species are discussed: reindeer/caribou (*Rangifer tarandus*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wapiti (*Cervus elaphus canadensis*), fallow deer (*Dama dama*), sika deer (*Cervus nippon*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), muskox (*Ovibos moschatus*), bison (*Bison bison*), chamois (*Rupicapra rupicapra*), ibex (*Capra ibex*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), Dall sheep (*Ovis dalli*), wild boar (*Sus scrofa*), pronghorn (*Antilocapra americana*) and Przewalski's wild horse (*Equus przewalskii*).

Bovine virus diarrhoea/mucosal disease (BVD/MD)

Bovine virus diarrhoea virus (BVDV) belongs to the genus *Pestivirus* within the family Flaviviridae.

There is a close antigenic relationship to classical swine fever and Border disease virus of sheep (Horzinek, 1991). BVDV is a major pathogen of cattle with world-wide economic impact (Thiel *et al.,* 1996). Signs in cattle include transient acute infections which may be inapparent or mild, or mucosal disease which is inevitably fatal. Transplacental infection leads to abortion, foetal malformations and development of persistently viremic calves depending on the state of development of the foetus and the biotype (cytopathogenic or non-cytopathogenic) of the virus (Moenning & Liess, 1995; Brownlie, 1990). It is unknown whether this applies to wild ruminants as well (Depner *et al.,* 1991) although viremic individuals in wild ungulates were demonstrated by experimental infection (Morton *et al.,* 1990; Hyera *et al.*, 1993; Van Campen *et al.,* 1997).

Primary clinical signs in wild ruminants are erosion and ulceration of the oral mucosa, haemorrhagic enteritis and general physical impairment. Clinical signs include weakness, lack of fear, impaired hearing and vision, dehydration and emaciation. Pyrexia, anorexia, salivation and nasal discharge usually also occur, while some cases have skin lesions and may be lame due to interdigital ulceration and inflammation of the coronary bands (Richards *et al.,* 1956; Romvary, 1965; Wiesner, 1987; Neumann *et al.,* 1980; Morton *et al.,* 1990; Nettleton, 1994).

Serological surveys in free-ranging populations have been successfully conducted in more than 40 species on several continents (Nettleton, 1990).

In the United Kingdom, serological evidence of BVDV was found in fallow deer by McDiarmid (1975) and by Lawman *et al.* (1978) (8%). Lawman *et al.* (1978) also described seropositive red deer (16%) and sika deer (9%). In France, Baradel *et al.* (1988) determined an antibody prevalence of 0.7% in roe deer, 5.5% in chamois and 7.5% in ibex. Seropositive reindeer were found by Stuen *et al.* (1993) in Norway (9%) and by Rehbinder *et al.* (1992) in Sweden (6%). In the fotmer West-Germany, antibodies against BVDV have been found in approximately 7% of red deer (Weber *et al.,* 1978, 6.6%; Frölich, 1993, 7.7%), and in roe deer (Weber *et al.,* 1978, 5.9 %; Frölich, 1993, 10%). However, in the former East-Germany, only 0.6 % of cervid sera were determined to be seropositive (Dedek *et al.,* 1988). Of wild species other than deer, Dahle *et al.* (1993) and Oslage (1993) found BVDV neutralizing antibodies in 0.8% and 1.2% of wild boar sera which were not identical to classical swine fever positive sera. Kahrs *et al.* (1964) and Friend & Haltermann (1967) reported white-tailed deer seropositive to BVDV. In several national parks in the US, the overall seroprevalence in mule deer was 59% (Aguirre *et al.,* 1995). High seroprevalence was also detected in wapiti (54%) in several national parks in the US by Aguirre *et al.* (1995) and in Alberta by Kingscote *et al.* (1987) (52%). 18% of moose in Canada (Thorsen & Henderson, 1971) and 12% in Alaska (Kocan *et al.,* 1986) have been reported to be seropositive. In Canada, 69% of caribou tested in 1978 and 60% tested in 1979 had specific antibodies against BVDV (Elazhary *et al.,* 1981), whereas Zarnke (1983) only found 3% seroprevalence in caribou in Alaska. In pronghorns, seropositive reactors were found in Canada (4%) (Barrett & Chalmers, 1975) and Idaho (Stauber et al., 1980). Seropositive reactors were reported in bighorn sheep by Clark *et al.* (1985) (10%) and Parks & England (1974).

Virus isolations: Romvary (1965) first isolated a noncytopathogenic BVDV from the spleen of a roe deer. Schellner (1977) isolated BVDV from spleen, intestinal lymph nodes, and abomasal mucosa of roe deer suffering from abomasitis and severe enteritis. Neumann *et al.* (1980) isolated the virus from farmed fallow deer. Weber *et al.* (1982) detected noncytopathogenic BVDV in three farmed fallow deer. Diaz *et al.* (1988) demonstrated BVDV in one fallow deer. Isolation of a noncytopathogenic BVDV from the spleen of a red deer was reported by Nettleton *et al.* (1980). A pestivirus differing from BVDV was isolated from red deer by Baradel *et al.* (1988). Cytopathogenic BVDV was isolated from two seronegative roe deer from northern Germany by Frölich & Hofmann (1995).

Clinical and pathological findings: Shope *et al.* (1955) described conditions which indicated the existence of a BVDV infection in a New Jersey deer herd. In several sick or dead white-tailed deer and mule deer from various parts of North Dakota, Richards *et al.* (1956) observed profuse salivation, nasal discharge, and in one case corneal opacity. Pathological changes included reddening and ulceration of the digestive tract. Romvary (1965) described lesions typical of BVD in six free-ranging roe deer in Hungary. In Sweden, histological changes and lesions characteristic of BVD were observed in captive fallow deer (Diaz *et al.,* 1988), as well as free-ranging moose and roe deer (Feinstein *et al.,* 1987).

Transmission: the role of pestiviruses in wild ruminant populations and the interactions between wild ungulates and domestic livestock are not well understood (Nettleton, 1990; Aguirre *et al.,* 1995; Frölich, 1995). Transmission in cattle may be either horizontal, mainly oronasal via direct contact between infected and susceptible animals, or vertical. The virus is shed in secretions or excretions including nasal discharge, saliva, semen, urine, tears and milk. Faeces are usually a poor source of virus (Brownlie *et al.,* 1987). Indirect transmission by vectors also occurs (Meyling *et al.,* 1990). Tarry *et al.* (1991) reported on the possibility of insect (*Stomoxys calcitrans, Haematopota pluvialis*) transmission. The natural mode of transmission of BVDV to wild ungulates and the question of whether wild ungulates can serve as a reservoir is not yet clear. Experimental infection with BVDV in wild ruminants was demonstrated by Richards *et al.* (1956), Morton *et al.* (1990), Hyera *et al.* (1993), and Van Campen *et al.* (1997). Whether persistent BVDV infections occur in wild ruminant species as in domestic ruminants is not yet proven but there is some indication that this might happen (Hyera *et al.,* 1993). Neumann *et al.* (1980) and Kocan *et al.* (1986) assumed a causal relationship between the spread of BVDV in cattle and its occurrence in deer. Romvary (1965) diagnosed BVD in roe deer living adjacent to a cow farm where BVD had pteviously caused severe losses. In contrast, Weber *et al.* (1982) and Liebermann *et al.* (1989) assumed an independent infection process in wild ruminants with BVDV. Pastoret *et al.* (1988) supposed that wild species do not play a major role in transmitting infection to domestic cattle. In free-ranging deer, the highest seroprevalence (60%-70%) was detected in Canadian caribou by Elazhary *et al.* (1981) although these caribou had had no direct contact with domestic ruminants for 25 years. Frölich (1995) found no significant difference in antibody prevalence among deer in habitats with high, intermediate and low densities of cattle. The sequence analysis of the BVDV isolated from roe deer (Frölich & Hofmann, 1995) showed a unique position of this roe deer strain within the BVDV group I (Fischer *et al.,* 1998). This study indicated that distinct BVDV strains might circulate in free-ranging roe deer populations in Germany and that virus transmission is independent of domestic livestock (Fischer *et al.,* 1998).

Alphaherpesvirus infections

Serological surveys performed in different species of deer revealed the presence of alphaherpesviruses related to bovine herpesvirus-1 (Nettleton *et al.,* 1988). Such viruses include BHV-1, which causes infectious bovine rhinotracheitis (IBR) and pustular vulvovaginitis (IPV) in cattle (Ludwig & Gregersen, 1986), the herpesvirus of red deer (HVC-1) (Inglis *et al.,* 1983; Reid *et al.,* 1986), the *Rangifer* herpesvirus (RanHV-1) isolated from reindeer (Ek-Kommonen *et al.,* 1986) and that from goats (caprine herpesvirus-1; CapHV-1) (Engels *et al.,* 1992). The clinical symptoms in deer associated with these herpesvirus infections include conjunctivitis, lacrimation and corneal lesions. Ulceration of the nostrils and a serous or purulent nasal discharge may also occur (Inglis *et al.,* 1983; Nettleton *et al.,* 1986; Reid *et al.,* 1986).

Serological surveys in free-ranging populations have been successfully conducted in many northern ungulates. Thiry *et al.* (1988) found a low seroprevalence in free-ranging populations of roe deer and red deer in France and Belgium: none of the roe deer in Belgium and less than 1% of those in France were seropositive for herpesviruses. In red deer, 1% were positive in France and 11% in Belgium. In Italy, 2% of fallow deer were seropositive for BHV-1 (Giovannini *et al.,* 1988). In the southern part of former West Germany, Weber *et al.* (1978) found antibodies against BHV-1 in 9% of fallow deer, 2.5% of red deer and 1.5% of roe deer samples. In the former German Democratic Republic, 13% of red deer, 1% to 3% of roe deer and 3% of fallow deer sera were seropositive for BHV-1 (Kokles, 1977; Kokles *et al.,* 1988). Higher antibody prevalence of alphaherpesviruses was found in Britain: antibodies against BHV-1 were detected in 16% (Lawmann *et al.,* 1978) and against HVC-1 in 29% (Nettleton *et al.,* 1986) of red deer. In Alaska, serological evidence of exposure was reported for reindeer (Dieterich, 1981) and caribou (Zarnke, 1992).

Alphaherpesvirus infections also commonly appear in ungulates from Scandinavia: In reindeer in Finland antibodies against BHV-1 were found by Ek-Kommonen *et al.* (1982) (18%) and Hyllseth *et al.* (1993) (10% to 46%). In Norwegian reindeer a seroprevalence of 9% to RanHV-1 was found by Stuen *et al.* (1993) and of 32% in studies by Hyllseth *et al.* (1993).

The mode of infection in free-ranging ungulates is not yet clear. Direct contact is normally required for the natural transmission of herpesviruses in

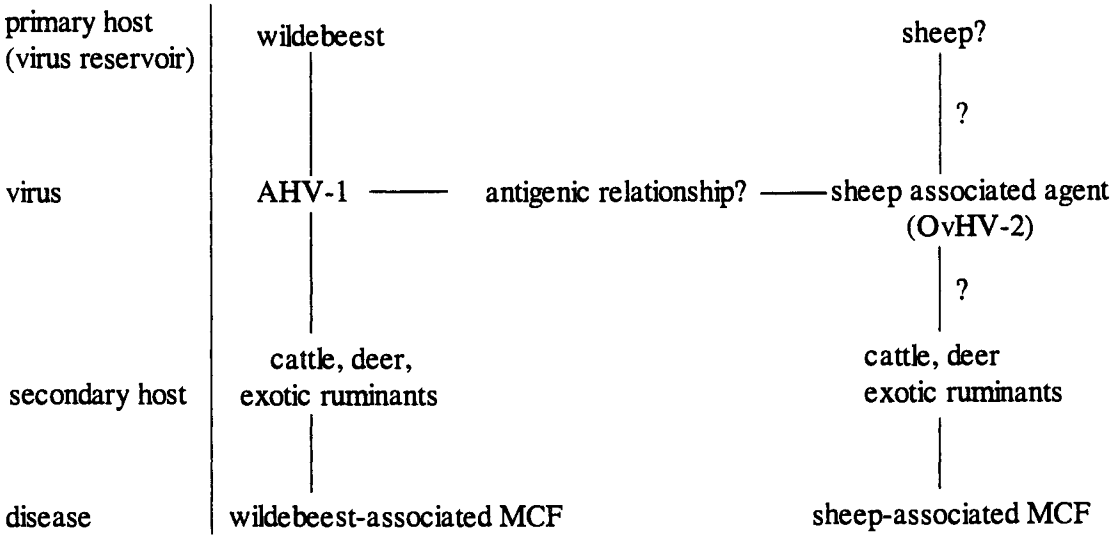

Fig. 1. Malignant Catarrhal Fever (MCF), modified after Rolle & Mayr (1993).

ungulates. In Germany, no association has been found between cattle density and antibody prevalence against alpha-herpesviruses in deer. In these deer populations, contact with cattle is obviously not essential (Frölich, 1996). This contrasts with the hypothesis of Weber *et al.* (1978) and Lawmann *et al.* (1978) who assume a transmission from a domestic to wild host and vice versa. Nettleton *et al.* (1988) and Kokles (1977) assume that herpesviruses of free-ranging deer have not so far posed a threat to other domestic livestock and that alphaherpesviruses from deer occur only in their natural hosts and do not cross to other species. Baradel *et al.* (1988) stated that there may have been a separate parallel evolution of viruses in wild and domestic ruminants. Likewise Ronsholt *et al.* (1987) showed that cattle are not susceptible to the topical HCV-1 isolate which would not, therefore, appear to represent a health hazard to cattle.

Malignant Catarrhal Fever (MCF)

MCF affects many species of ruminants. Howevet, there is great variation in susceptibility to infection (English, 1981; Hunter, 1981; Seal *et al.*, 1989; Reid, 1992; Mackintosh, 1993; Murphy *et al.*, 1994). Based on the reservoir ruminant species from which the causative viruses arise, the two major epizootiological entities of the disease that have been described are wildebeest-associated (WA) and sheep-associated (SA) MCF (Fig. 1). The etiologic agent for WA-MCF has been isolated, characterised as a gammaherpesvirus, and named alcelaphine herpesvirus 1 (AHV-1) (Plowright *et al.,* 1960; Bridgen *et al.*, 1989) whereas the putative SA-MCF agent has not yet been isolated (Reid, 1992). Based on its antigenic and base-sequence homology to AHV-1, the putative agent of the SA-MCF has been tentatively classified as ovine herpesvirus 2 (OvHV-2) (Roizman, 1992). MCF has been described in several species of deer (Westbury, 1984) and cervids are generally regarded as highly susceptible to MCF (Plowright, 1986; Buxton, 1988). The range of clinical signs observed in MCF affected ruminants has been diverse (Westbury, 1984; Blake *et al.*, 1990). The disease tends to be peracute or acute with animals succumbing before the more florid lesions, characteristic of protracted cases, develop (Reid & Buxton, 1989). However, MCF in ruminants can also be present as subacute or chronic disease with clinical signs becoming progressively more marked with duration of illness (Buxton, 1988).

In contrast to many reports in captive ruminants (e.g. Pierson *et al.*, 1974; Westbury, 1984, Krogh & Jensen, 1988) only single cases of MCF in free-ranging ruminants have been published. The disease was diagnosed in two free-ranging moose from Sweden showing CNS symptoms. Subsequently one was shot and the other one found dead and both were diagnosed as MCF based on histopathology (Warsame & Steen, 1989). Frölich *et al.* (1998)

Table 1. Family Poxviridae, modified after Rolle & Mayr (1993).

genus	host range
orthopoxvirus	e.g. humans, bovidae, various wild aminal species
avipoxvirus	birds
capripoxvirus	ruminants
leporipoxvirus	leporidae
suipoxvirus	pigs
molluscipoxvirus	humans
yatapoxvirus	primates
parapoxvirus	predominantly ruminants

investigated 329 samples from three species of free-ranging deer, including 253 roe deer, 22 red deer and 54 fallow deer, in which only fallow deer were antibody-positive. The few teports of the disease in free-ranging deer in Europe may reflect a lack of surveillance and awareness of the disease in wild cervids in Europe.

Few data are available on the transmissibility of SA-MCF agent in free-ranging ruminants. The cause of cervid MCF has not been determined in most cases (Buxton & Reid, 1980; Oliver *et al.*, 1983) although it is thought to be a virus carried by clinically normal sheep (Buxton, 1988). Recent studies have further implicated OvHV-2 or a similar virus (Tham, 1997; Tomkins *et al.*, 1997). Circumstantial evidence also suggests that there may be sources of virus other than sheep in SA-MCF as a number of outbreaks have been observed in which no contact with sheep was reported (Straver and van Bekkum, 1979). Domestic goats and rabbits (*Oryctolagus cuniculus*) have been mentioned as possible reservoirs (Blood *et al.*, 1979). In studies of Frölich *et al.* (1998) the seroprevalence and positive PCR results detected in sheep samples, which originate from the same area as the antibody-positive fallow deer, might indicate that in this case sheep are the main reservoir animals.

Poxvirus infections

Poxvirus infections in holarctic wild ungulates are mainly caused by species of the genus *Parapoxvirus* within the family of Poxviridae (Table 1). There are three accepted members of the parapoxvirus genus, orf virus (OV) papular stomatitis virus (PSV), and pseudocowpox virus (PCV).

Contagious ecthyma (CE), otherwise known as orf, is a common disease in domestic sheep and goats caused by the OV. CE can also affect several wild ungulates including Rocky Mountain bighorn sheep (Lance *et al.*, 1981), mountain goats (Blood, 1971), Dall sheep (Smith *et al.*, 1982), chamois and muskox (Falk, 1978; Kummeneje & Krogsrud, 1978), as well as reindeer (Kummeneje & Krogsrud, 1979). Lance *et al.* (1983) conducted experimental infections in mule deer, white-tailed deer, pronghorns, and wapiti. Parapoxvirus has also been isolated from red deer (Robinson & Mercer, 1995).

Clinical signs: OV enters its host through skin abrasions (Bruner & Gillespie, 1973). In bighorn sheep and Dall sheep the disease is characterised by lesions of the lips, mammary gland and teats, muzzle, legs, vulvae, and occasionally the eyes and hooves. Most lesions start as discrete reddened swellings, followed by pustules and ulcers in 3 or 4 days. Lesions usually disappear in 2 to 4 weeks. Most infections are seen in lambs but mild cases are observed in adult ewes and rams (Blood, 1971). Clinical signs appear to be more severe in hot weather and to improve in cold weather (Dieterich *et al.*, 1981). In reindeer CE is benign (Kummeneje, 1979). However, during an outbteak of CE in Finnish semi-domesticated reindeer in winter 1992-1993, 400 individuals died as a result of secondary bacterial infection and starvation (Tryland *et al.*, 1995). The clinical picture showed cauliflower-like papillomas mainly around the mouth and lips. Similar lesions on the lips, muzzles and nostrils and to a lesser extent on the neck, eye lids, chest and in the perianal region could be observed in CE affected muskox (Kummeneje & Krogsrud, 1978). The affected animals often suffered from dyspnoe and feeding problems as well as from secondary bacterial infections (Kummeneje & Krogsrud, 1978). During an outbreak of CE in a herd of captive muskox in Norway all members of the herd showed signs of infection. Five of eight males died while the 11 females only showed small warts. CE never reoccurred in the animals which survived this outbreak (Mathiesen *et al.*, 1985). In red deer the virus produced lesions similar to those seen with OV in sheep (Robinson & Mercer, 1995).

Pathological findings: The papilloma-like lesions of CE affected muskox in Greenland were grossly and histologically similar to common warts (Kummeneje & Krogsrud, 1978). Biopsy of lip nodules in a captive muskox in Alaska revealed proliferating tubes of keratinized epidermis projecting upward over a core of dermis. Many cells in these epithelial papillae had ballooning degeneration and papillae had partially necrotic patches of epithelium. Numerous inflammatory cells were seen throughout the biopsy with neutrophils predominating on the surface and in the epidermis. Bacterial colonies were seen in the necrotic areas. Lymphocytes and macrophages predominated in the dermal tissue (Dieterich *et al.,* 1981). Superficial dermatitis with eosinophilic intracytoplasmatic inclusion bodies were seen in biopsy material of teat lesions of an Alaskan Dall sheep (Smith *et al.,* 1982).

CE is very common in sheep and goats in Norway and transmission of parapoxvirus from these animals to reindeer or muskox seems highly likely. It is believed that the infection of a muskox herd in Greenland was of ovine or caprine origin (Kummeneje, 1979). However, the presence of a reindeer strain of the virus cannot be excluded (Kummeneje, 1979) and the identity and the host specificity of newly found parapoxvirus isolates still has to be investigated (Büttner *et al.,* 1995). Transmission occurs by contamination of abrasions of mucous membranes or skin, with exudate or scabs. The virus is very stable in dried scabs. Indirect transmission of the infection via objects such as knifes and barbed wire has been reported (Leavell *et al.,* 1968; Johannessen *et al.,* 1975). Lambs infected on the mouth may transmit the infection to their mothers during suckling. Regular use of salt blocks by bighorn sheep also appears to be important in maintaining the disease (Blood, 1971).

The genus *Orthopoxvirus* within the family Poxviridae causes diseases in a wide range of species. Little is known about the occurrence of orthopoxviruses in wildlife species (Tryland, 1998). Mayr *et al.* (1995) detected orthopoxvirus-specific antibodies in wild boar in Germany.

Parainfluenza type 3 virus (PIV-3) infection

PIV-3 commonly causes respiratory infection with little or no clinical manifestation. However, in association with othet viral and bacterial pathogens and stress-inducing situations, it causes a severe pneumonia in cattle called «shipping fever». Parainfluenza viruses are classified in the genus *Paramyxovirus* within the family Paramyxoviridae. Four serotypes of parainfluenza virus have been described but almost all infections in livestock are caused by serotype 3. The vitus is shed in nasal and ocular secretions. Persistently infected animals have not been reported (Woods, 1968; Frank & Marshall, 1973; Kingsbury *et al.,* 1978). Most parainfluenza infections are mild or clinically undetectable. Development of clinical disease is usually dependent on interaction with infectious and environmental factors. The virus, together with *Pasteurella* species, can lead to pneumonia and death. Fever is accompanied by lachrymation, serous to mucopurulent nasal discharge, depression and dyspnoea. Recovery is the general rule, but when secondary bacterial infection occurs, dyspnoea and depression may be severe or fatal (Lopez *et al.,* 1976; Lehmkuhl & Cutlip, 1982). Serological surveys have been conducted in many species: in white-tailed deer antibodies against PIV-3 were found in Minnesota (20 %; Ingebrigtsen *et al.,* 1986) and Canada (around 80%; Sadi *et al.,* 1991). A high seroprevalence also was detected in pronghorns (49%) in southeastern Alberta (Kingscote & Bohac, 1986) and in free-ranging bison (67%) in Alaska (Zarnke, 1983). In 8 national parks in western US, the overall prevalence in wapiti was 46% and for mule deer 32% (Aguirre *et al.,* 1995). Clark *et al.* (1993) detected that 10% of bighorn sheep had been exposed to PIV-3.

In Germany and Italy, Kokles *et al.* (1988), Giovannini *et al.* (1988) and Maglione *et al.,* (1992) determined antibodies against PIV-3 in fallow deer, red deer, and roe deer, with a prevalence of 9% to 20%. However, in a serological survey in reindeer in Norway all 326 sera tested for antibodies against PIV-3 were negative (Stuen *et al.,* 1993).

Virus isolates of PIV-3 were possible from nasal swabs or secretions from fallow deer, mule deer, and pronghorns in Alberta (Thorsen *et al.,* 1977).

Älvsborg disease

In 1985, a new disease was identified in Swedish moose and designated Älvsborg disease. The name 'Älvsborg' originates from a region in Southern Sweden, where the disease was first observed. Between 1985 and 1995, Älvsborg disease killed more than a thousand moose. The actual number of affected moose remains unknown (Rehbinder *et al.,* 1991; Steen *et al.,* 1993; Merza *et al.,* 1994). The disease affects all age classes of moose. The post mortem picture of Älvsborg disease is characterised by erosive, ulcerative and necrotic lesions in the mucous membranes of the digestive tract, atrophied lymphoid organs and emaciation (Merza *et al.,* 1994).

This wasting syndrome probably has a multifactorial etiology. The pathological changes, as well as serological findings, indicate the possible presence of BVDV (Cedersmyg, Steen, Ftank, Frölich and Rehbinder, unpubl. data). Moreover, a retrovirus (*Alces* leucotropic oncovirus, ALOV) has been isolated (Merza *et al.*, 1994). Retroviruses are known to cause wasting diseases and immunodepression in domestic ruminants. In addition, unusually low levels of copper, chromium and zinc had been observed in the livers of these moose. Undernutrition and malnutrition resulting in starvation and emaciation is considered an important factor having a profound and adverse effect on trace element levels (Cedersmyg, Steen, Frank, Frölich and Rehbinder, unpubl. data). In conclusion, Älvsbotg disease is regarded as a multifactorial disease but the etiology of this disease is not yet fully elucidated.

Foot-and-mouth disease (FMD)

FMD is a highly contagious acute viral infection almost exclusively of ruminants and pigs. It is characterised by high morbidity and low mortality. A variety of other wildlife species becomes infected periodically but there is little evidence that they are important for viral maintenance or transmission to cattle. FMDV belongs to the family Picornaviridae, and is the only member of the genus *Aphthovirus*. Seven serological types have been found: A, O, C, SAT-1, SAT-2, SAT-3 and Asia 1 (Thomson, 1994). The virus is resistant to external influences and may survive for many weeks. FMDV can be transmitted by the airborne route and may be transported over considerable distances (Hedger, 1981).

Clinical symptoms: In all species, foot lesions develop in the interdigital space. Secondary bacterial infections of foot lesions frequently occur, particulatly where animals are kept in muddy, unhygienic conditions. Moreover, FMD is characterised by the development of lesions in the mouth. The young of domestic species susceptible to FMD may die suddenly as a result of myocarditis. This is referred to as «tiger-heart disease» (Thomson, 1994). The respiratory tract is the usual route of infection. Virus is excreted not only during the clinical manifestations of disease. In some species infection may take place and virus may be excreted in the total absence of clinical signs (Hedger, 1981). An overview about the occurrence of FMDV in wild artiodactyl animals in the holarctic region was presented by Rea-Min *et al.* (1997). Moose, roe deer and saiga antelope are the main hosts of FMDV in the Russian Federation (Kruglikov *et al.*, 1985). In addition, serological evidence of FMD infection without clinical disease was detected in one of 88 free-ranging red deer in France by Barrat *et al.* (1988).

Epizootic haemorrhage disease of deer (EHD) and bluetongue disease (BT)

EHD is an acute non-contagious viral disease of wild ruminants characterised by extensive haemorrhage. EHD and BT are caused by antigenically related though distinct viruses and are clinically and pathologically rather similar. Culicoides insects are the main vector (Alexander & Buxton, 1994).

The clinical course is usually acute and rapidly fatal, while wapiti develop only a mild disease. The symptoms of EHD are characterised by extensive hemorrhages, progressive weakness, terminal coma and death. Animals develop a mucopurulent nasal discharge, conjunctivitis and coronitis. Widespread haemorrhages of the mucous membranes and intestinal serosa are typical at post-mortem examinations (Wallach & Boever, 1983; Alexander & Buxton, 1994; Rolle & Mayr, 1993).

The clinical signs for BT are similar to EHD; namely excessive salivation with a purple-blue discoloration of the tongue, caused by circulatory disorders. Hemorrhages in the pulmonary artery are pathognomic. Congenital malformations and abortion have been reported following exposure to BT in the first trimester of pregnancy (Wallach & Boever, 1983; Dedek & Steineck, 1994).

Although EHD and BT only play a subordinate role in Europe (BT only occurs in Spain and only a few reports of EHD exist for Great Britain), transmission to other parts of Europe may be possible (Dedek & Steineck, 1994). In North America, EHD was first recognised as a specific disease in white-tailed deer in the mid 1950s when die-offs occurred in New Jersey and Michigan. Since then, many outbreaks have occurred (e.g. Alberta, North and South Dakota, Missouri, Nebraska, Texas and Washington) and serological studies have been performed in various parts of the US (e.g. Chalmers *et al.*, 1964; Fay *et al.*, 1956; Fosberg *et al.*, 1977; Hoff *et al.*, 1973; Prestwood *et al.*, 1974; Ttainer & Karstad, 1970; Shapiro *et al.*, 1991; Nettles *et al.*, 1992; Fischer *et al.*, 1995; Stallknecht *et al.*, 1995; Stallknecht *et al.*, 1996; Farnell *et al.*, 1999).

In the US, BT was noted as a disease of white-tailed deer in 1955 (Fay *et al.*, 1956). In 1976, an extensive wildlife die-off due to bluetongue occurred in the Missouri River Basin. During that die-off, at least 4100 pronghorn antelopes and deer died in Wyoming (Thorne *et al.*, 1982). Since then, outbreaks have occurred and serological studies have been performed in various parts of the US (e.g. Kocan *et al.*, 1982; Dulac *et al.*, 1988; Stallknecht *et al.*, 1991; Pearson *et al.*, 1992).

Rabies

Rabies is an acute infectious disease of the centtal nervous system caused by a virus that generally persists in natural hosts as a salivary gland infection in carnivores. The virus is usually transmitted from animal to animal and from animal to man by biting. All warm-blooded animals are susceptible. An animal with clinical signs of rabies should be killed and its brain examined for Negri bodies. A Negri body is well differentiated by Sellers´s stain as a magenta (purplish red) round or oval body with blue to black, basophilic, internal bodies (Sikes, 1981).

The arctic fox (*Alopex lagopus*) serves as a reservoir and vector for rabies in most Arctic regions, and outbreaks of disease coincide with population peaks and migrations. Cases in othet species are only sporadic (Ødegaard & Krogsrud, 1981).

Deer are susceptible to infection with rabies if bitten by a rabid carnivore but are represent hosts incidental to the epizootiology of the virus (Ødegaard & Krogsrud, 1981). Sporadic cases of rabies have been diagnosed in reindeer (Ødegaard & Krogsrud, 1981; Prestrud *et al.*, 1992) and moose (Lis, 1991; Anonymous, 1996; 1997; Muller *et al.*, 1998). Rabies is also known to occur in fallow deer and red deer (Anonymous, 1992 a; b; Cac *et al.*, 1992). A relatively high number of cases of rabies, however, were reported in roe deer from several European countries (Schulz, 1986; Blancou & Barrat, 1988; Duricic *et al.*, 1988; Birlbauer *et al.*, 1990; Lis, 1991; 1996; Anonymous, 1991; 1992 b, 1994). A change in behaviour may suggest a rabies infection in free-ranging cervids but a clinical diagnosis cannot be carried out with certainty in a living herbivore. The terms «furious rabies» and «dumb rabies» which point to certain behavioural features are not appropriate for non-carnivorous animals. In addition, especially in tuminants, the inflammatory changes of the btainstem are often inconspicuous and may be confined to a few brain vessels with cuffing lymphocytes and a very small glial nodules, commonly called Babes' nodules (Jubb *et al.*, 1993).

Adenovirus infection

Adenovirus infections are probably widespread although most are subclinical. Bovine adenovirus infections have been associated with a variety of respiratory and alimentary tract diseases but their role in the causation of these diseases remains uncertain (Thomson, 1994). Antibodies to bovine adenovirus have been found in red deer, fallow deer, roe deer, and sika deer in Great Britain. The reaction rate was highest in fallow deer but no clinical disease associated with the infection has been noted. In Hungary, type 6 bovine adenovirus was responsible for an outbreak of respiratory disease in a group of captive fallow deer. One buck which died showed acute tracheitis and interstitial pneumonia (Alexander & Buxton, 1994). In France, Barrat *et al.* (1988) found antibodies against bovine adenovirus in 33 of 89 serum samples collected from wild red deer.

Thousands of mule deer were killed by a haemorrhage disease and an apparently novel adenovirus was associated with this epizootic in California (USA) during 1993-1994. A systematic vasculitis with pulmonary edema and haemorrhage enteropathy or a localised vasculitis associated with narcotising stomatitis/pharyngitis/glossitis or osteomyelitis of the jaw were common necropsy findings in the animals that died (Woods *et al.*, 1997). Artificially infected mule deer showed identical histological findings to free-ranging animals which died naturally (Woods *et al.*, 1997).

Respiratory syncytial virus (RSV) infection

The virus is classified as a member of the genus *Pneumovirus* in the family Paramyxoviridae. Infection with bovine respiratory syncytial (BRS) vitus is undetectable in the majority of animals but in some it does cause mild to sevete respiratory tract disease characterised by fever, coughing, serous nasal and ocular discharges and dyspnoea. It is one of several viruses which are primary pathogens in the bovine respiratory disease complex (Van Vuuren, 1994). However, RSV does not appear to be a problem in farmed, park, or free-living deer. Under experimental conditions, virus isolated from sheep was transmitted to white-tailed deer calves. Clinical disease was not recognised although lung lesions, similar to those found in lambs, developed. Virus was recovered from the lower respiratoty tract but transmission to deer did not occur (Alexander & Buxton, 1994). However, serological evidence of RSV in wildlife is available from different countries. In

North America, antibodies against BRS virus were found in free-ranging white-tailed deer, mule deer, bighorn sheep and mountain goats (Clark *et al.*, 1985; Dunbar *et al.*, 1985; Johnson *et al.*, 1986). In eight national parks in the western US, 54% of wapiti were seropositive (Aguirre *et al.*, 1995). However, Kingscote *et al.* (1987) and Hein *et al.* (1991) found no serological evidence in wapiti collected in Alberta and Central Washington, respectively. In Italy, six of 43 sera of free-ranging fallow deer (Giovannini *et al.*, 1988) and 7% of red deer were positive for antibodies against BRS virus (Maglione *et al.*, 1992).

Hog cholera

Hog cholera is an acute, highly fatal disease affecting wild boar of all ages. It is characterised by sudden onset, high morbidity and very high mortality. Transmission is accomplished by direct contact or by ingestion of virus-contaminated feed or water. Young animals which recover are permanently stunted. Clinical signs include anotexia, diarrhoea, neurological symptoms and high fever. The disease may last from 24 hours to 16 days. Wild hogs lose their shyness and develop polydipsia as a result of high fever. Post mortem lesions are characterised by petechial hemorrhages on serosal surfaces and in the renal cortex. Chronically infected individuals may show «button ulcers» 10 mm in diameter which are associated with the intestinal mucosa (Wallach & Boever, 1983; Loepelmann & Dedek, 1991; Dedek & Steineck, 1994). Presently, hog cholera officially occurs in wild boar in six European countries: Germany, Italy, Austria, France, Slowakia and Czechia.

Aujeszky's Disease

Although many species of domestic animals are susceptible to infections by pseudorabies virus (PrV), pigs are considered to represent the main host reservoir. Only limited data exist about natural infection in wildlife. During 1991-1994 European wild boar were serologically and virologically investigated for the occurrence of PrV-infections in Eastern Germany by Müllet *et al.* (1996). 281 (8.9%) of the tested sera were positive in ELISA. Reactivity was confirmed by presence of neutralizing antibodies in 220 sera and by immunoblotting. Based on epidemiological analysis the authors concluded that PrV-infections occurred in wild boar populations of the examined region for a number of years with increasing prevalence. Interestingly, pseudorabies had been eradicated in domestic pigs in this area in 1985. Four PrV could be isolated from epidemic areas. Molecular biological analysis using restriction length polymorphism showed considerable differences to PrV-strains occurring in domestic animals. Thus, the infections in the wild boar population appear to be endemic and persist completely separately and without affecting the domestic pig population (Müller *et al.*, 1996).

Clinical signs include a brief course of hyperexcitability, ataxia, coma, and progressive paralysis. The disease is relatively mild in adult animals, causing heavy mortality only in the young (Wallach & Boever, 1983). Aujeszky's disease has not been reported as causing natural disease of free-living deer (Alexander & Buxton, 1994).

Equine herpesvirus infections

The horse is natural host to five hetpesviruses of which three are classified as alphaherpesvirinae and two as gammaherpesvirinae (Roizman, 1996). The three equine alphaherpesviruses so far known are: equine herpesvirus type 1 (equine abortion virus, EHV-1), equine herpesvirus type 3 (equine coital exanthema virus, EHV-3) and equine herpesvirus type 4 (rhinopneumonitis virus, EHV-4). Equine herpesvirus type 2 (EHV-2) and the related equine herpesvirus type 5 (EHV-5) are gammaherpesviruses (Telford *et al.*, 1993). Until now, no literature is available about the occurrence of antibodies against EHV in reintroduced Przewalski´s wild horse or other free-ranging equids in the holarctic region.

Conclusions

For some diseases (e.g. BVD, EHD, BT, CE and alphaherpesvirus infections) serological studies as well as virus isolation in wildlife have been performed quite intensively in different countries. For other viral diseases antibodies could be detected only in a few cases but virus isolation or DNA detection was not possible in free-living ungulates (e.g. MCF). For some agents like EHV even antibody detection was not possible. However, the mode of transmission for most diseases remains unclear which may reflect a lack of surveillance of viral diseases in wild ungulates.

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Biological rhythms in Arctic vertebrates

B. E. H. van Oort[1], N. J. C. Tyler[2], E. Reierth[1] & K.-A. Stokkan[1]

[1] Department of Arctic Biology and Institute of Medical Biology, University of Tromsø, N-9037 Tromsø, Norway (bob@fagmed.uit.no).
[2] Department of Biology, University of Tromsø, Norway.

Abstract: Many biological processes show regular cyclical fluctuations that persist throughout an organism's life; these range from the transcription of DNA to patterns of behaviour. Persistent, cyclical phenomena of this kind are a fundamental feature of all organisms. They are governed primarily by endogenous rhythms generated by a 'biological clock' situated in the brain. Normally, however, the expression of the clock is modulated to a greater or lesser extent by environmental cues. This paper reviews the physiological control of the temporal organisation of cycles in vertebrates and, in particular, explores their regulation in arctic species like reindeer (*Rangifer tarandus* L.). We emphasise how exposure to the photoperiodic conditions that characterise polar regions places special demands on timing mechanisms and how arctic species, therefore, are of particular interest for the study of biological rhythms. Thus far, behavioural and physiological studies of these species show that arctic reindeer (and ptarmigan) appear to be truly opportunistic in summer and winrer, seemingly without any active biological clock and that they are, instead, driven directly by photoperiod. This situation, if confirmed, would be unique among vertebrates.

Key words: caribou, cervid, endogenous rhythm, melatonin, muskox, photoperiod, reindeer, ruminant, Svalbard.

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Introduction

Many biological processes show regular cyclical fluctuations that persist throughout an organism's life; these range from the transcription of DNA to patterns of behaviour. Persistent, cyclical phenomena of this kind are a fundamental feature of all organisms. They are governed primarily by endogenous rhythms generated by a 'biological clock' situated in the brain. Normally, however, the expression of the clock is modulated to a greater or lesser extent by environmental cues. This paper reviews the physiological control of the temporal organisation of cycles in vertebrates and, in particular, explores their regulation in arctic species, like reindeer (*Rangifer tarandus* L.), which are exposed to the photoperiodic conditions that characterise polar regions.

The basic problem

In many species, daily and annual cycles in physiological and behavioural parameters are closely correlated with daylength, usually referred to as 'photoperiod' (Table 1). Organisms can extract two kinds of infotmation by monitoring the duration of the daily photoperiod: the daily light/dark cycle provides them with a 24 hour clock and changes in daylength provide them with a calendar indicating the changing of the seasons. In these two ways photoperiod provides an absolutely secure, predictable signal for keeping track of time in what are otherwise often unpredictable environments. Plants and animals living at 30-60°N lat. in the northern temperate zone experience a strongly rhythmic and dynamic photoperiodic environment with clear daily light/dark cycles and pronounced seasonal changes in daylength (Fig. 1). Not surprisingly, therefore, photoperiod plays a major role in the regulation of temporal organisation in temperate species. Arctic species, such as reindeer and muskox (*Ovibos moschatus*), by contrast, live in regions where photoperiodic information is much reduced or even absent for considerable periods of the year. These animals are exposed to continuous daylight, the

Table 1. Glossary.

Terminology	Explanation
Circadian cycle	A cycle with a frequency ≈24 h., i.e. with a length of approximately (*circa-*) a day (*diem*).
Entrainment	Synchronisation of the phase of the biological clock with the correct phase of the environment. Entrainment ensures the proper phase-relationships between particular body rhythms and the appropriate rhythmic changes in the environment.
Free-running rhythm	Biological rhythm expressed under constant conditions.
Infradian cycle	A cycle with a frequency >>24 h., i.e. with less than (*infra-*) one cycle a day (*diem*).
Photoperiod	Duration of night and day.
Pineal gland	Endocrine gland in the brain. Innervated by sympathetic nerves from the SCN. Produces the hormone melatonin.
Polar day	Period of continuous light in summer when the sun is continuously above the horizon.
Polar night	Period of continuous darkness in winter when the sun is continuously below the horizon.
SCN	Suprachiasmatic nucleus. Structure in the hypothalamus where the mammalian biological clock is situated.
Temperature compensation	Independence of the frequency of a cycle from ambient temperature.
Ultradian cycle	A cycle with a frequency <<24 h., i.e. many (*ultra-*) cycles occur within a day (*diem*).
Zeitgeber	Time cue which signals the setting or resetting of the biological clock to the correct phase with respect to the time of the day or of the year. Light is the most important, but not the only, zeitgeber.

'polar day', in summer and continuous darkness, the 'polar night', in winter. Nevertheless, they display pronounced, highly predictable annual cycles of metabolism, growth and behaviour. This simple observation suggests that the regulation of cyclical phenomena may be different in Arctic compared to temperate species.

The role of self-sustained, clock-driven, endogenous rhythms in the regulation of annual cycles of growth and behaviour is well documented in temperate ungulates such as red deer (*Cervus elaphus:* Loudon & Jabbour, 1994), white-tailed deer (*Odocoileus virginianus:* Brown *et al.*, 1978) and sheep (*Ovis aries:* Lincoln, 1992; 1998). However, there is no convincing evidence for the role of a biological clock in the control of the corresponding cycles in reindeer and muskoxen. One way to identify the presence of an endogenous rhythm is to demonstrate that a cycle - the daily cycle of the production of melatonin or the annual cycle of coat growth, for instance - persists while the animals are maintained under constant daylight conditions. However, this has not been investigated for arctic ungulates.

In a sense, of course, the necessary experiments are performed twice a year every year, for these are exactly the conditions to which animals living in their natural environment are exposed in mid-winter and mid-summer. Thus, the clear daily rhythms of behaviour which Svalbard reindeer (*R. t. platyrhynchus*) display in February and March and September and October disappear under the continuous light conditions of May, June and July and December and January (van Oort *et al.*, 1998 and unpubl. data). A similar situation is observed in Svalbard ptarmigan (*Lagopus mutus hyperboreus:* Reierth & Stokkan, 1998). Both organisms fail to show persistent rhythms of behaviour when exposed to continuous light conditions. The possibility

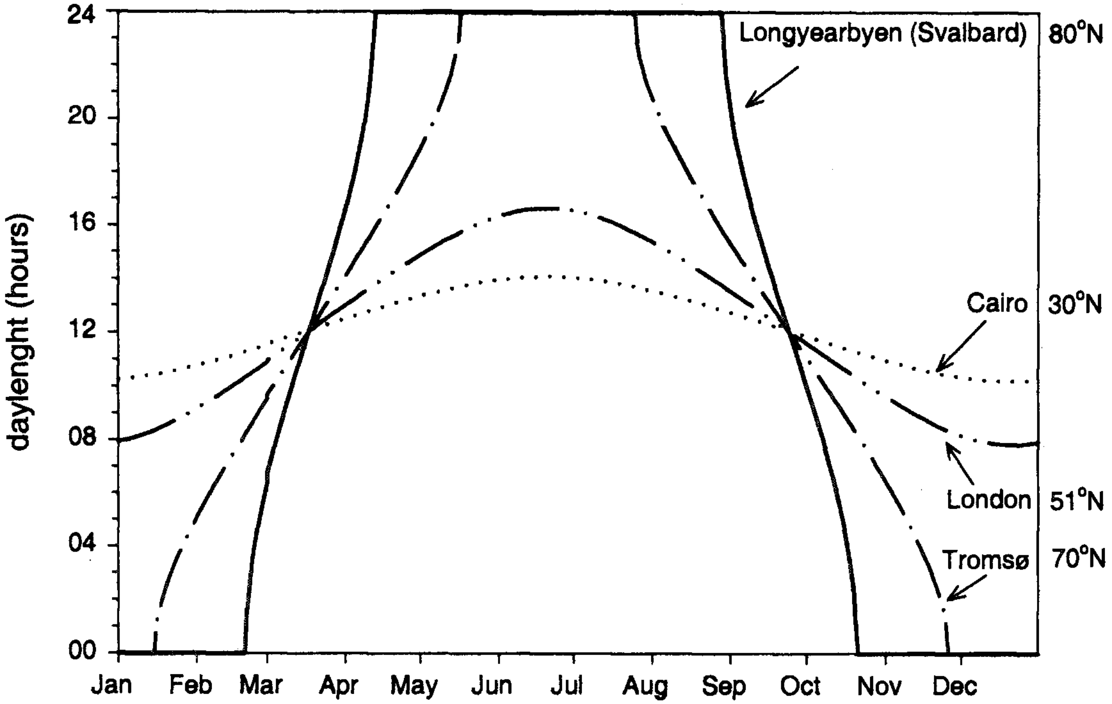

Fig. 1. Comparison of daylength at different latitudes. Note both the long period of continuous light and darkness at 80°N and also the much higher speed of changes here in daylength in spring and autumn compared to more sourherly latitudes.

exists, therefore, that the annual cycles of growth and metabolism of reindeer and muskoxen might be regulated directly by daily changes in photoperiod while the clock itself has become virtually vestigial. In support of this, there is evidence that the clock function which governs daily patterns of behaviour and the secretion of melatonin in reindeer is much reduced, if not completely absent, during the polar day and the polar night.

Characteristics and functions of rhythms

Biological rhythms are regular, cyclic events of any length of time which are under the control of endogenous oscillators. Such rhythms are generally recognised on three time scales: ultradian (<<24 h), circadian (~24 h) and infradian rhythms (>>24 h). The latter include rhythmical phenomena with frequencies of months or years.

Examples of ultradian rhythms include the spontaneous beating of the heart, breathing, the alternating bouts of REM and non REM sleep, the secretion of many hormones (e.g. Orth *et al.,* 1979; Moore-Ede & Sulzman, 1981), feeding bouts in ruminants (Squires, 1971) and in daily bouts of activity in animals living in the intertidal zone. Examples of circadian rhythms include the daily rhythms of body temperature, the secretion of melatonin and the sleep/wake and activity cycles (Akerstedt, 1979; Orth *et al.*, 1979). Infradian rhythms include arousal during hibernation (e.g. ground squirrels *Spermophilus lateralis:* Ruby *et al.,* 1996), menstruation, the annual cycle of growth and fattening in northern cervids (Leader-Williams & Ricketts, 1982; Suttie *et al.,* 1983; Tyler, 1987; 1995; Lincoln & Baker, 1995; Suttie & Webster, Hewison *et al.*, 1996), the antler cycle in reindeer (Lincoln & Tyler, 1994), the annual moult of hair and feathers (Meijer, 1989; Stokkan & Sharp, 1990), breeding and migration (e.g. Lundberg & Eriksson, 1984). All these cyclical fluctuations occur regularly and spontaneously. They are not prompted by exogenous environmental cues but are triggered, instead, by endogenous signals that arise independent of, but may become modified by, the animals' environment.

An important test of the endogenous basis for an overt rhythm is the persistence of cyclicity even when the environment is held constant. To identify the endogenous basis of a rhythm one should, in addition, be able to demonstrate (i) that its phase can be altered by the manipulation of light/dark signals (Aschoff, 1964a; 1999) and (ii) that it's expression is temperature compensated (Table 1). Golden hamsters' (*Masocricetus auratus*) daily cycle of wheel-running and the sleep/wake pattern of humans, for example, persist when the experimental subjects live in constant darkness (Jorgens, 1967; Aschoff, 1985). Had these cycles of activity been driven directly by the light/dark cycle, they would have been abolished immediately following the onset of constant light (or dark) conditions.

While the functional role of biological clocks has been demonstrated in a wide range of organisms, there is little direct experimental evidence of the adaptive significance of the circadian organisation which the clocks regulate. Nevertheless, it is generally accepted that organisms benefit from the temporal organisation of physiological functions and behaviour, chiefly because it enables them to anticipate daily and seasonal changes in their environment (Aschoff, 1964b). Thus, in plants, protein synthesis and the otientation of leaves anticipate the onset of daylight as well as the movement of the sun across the sky (Stayton *et al.*, 1989; Levy & Moore, 1993). Honey bees (*Apis mellifera*) have a sense of time which allows them to anticipate the peak of the daily production of floral nectar and even find their way back to previously detected food stores by means of time-compensated sun-compass orientation (Aschoff, 1986; Frish & Aschoff, 1987; Moore *et al.,* 1989). The immune function of deer mice (*Peromyscus maniculatus*) is enhanced (Demas & Nelson, 1998), reindeer fatten and grow a thick coat (Suttie & Webster, 1995) and Arctic waders migrate south all in advance of the onset of wintet. Accurate timing of estrus and mating in northern species of deer ensures that the burden of lactation many months later coincides with the period when the females have access to abundant high quality forage. When aberrations in timing result in conceptions outside the normal breeding season, the unusually early-born or late-born calves suffer heavy mortality (Clutton-Brock *et al.*, 1982).

The biological clock(s)

In mammals, the clock which generates circadian rhythmicity is situated in a region of the hypothalamus called the suprachiasmatic nucleus (SCN). The SCN consists of groups of neurons whose activity oscillates spontaneously with a frequency close to 24 hours. The oscillating frequency of the SCN as a whole is the mean of the activity of the individual cells. Neither the way in which the activity of the different cells is integrated, nor the way in which the net circadian rhythmicity of the SCN is translated into the regulation of the body's rhythmic functions is known, but the pineal hormone melatonin evidently plays an important role in this.

While the SCN plays a central role in generating endogenous circadian rhythms and, for this reason, is often referred to as *the* biological clock, it is not unique: there is a variety of oscillators in mammals which, singly or in combination, are involved in driving different behavioural and physiological rhythms. There are also different classes of oscillators, even within a single cell (Hoffmans-Hohn *et al.,* 1984). Some are normally entrained by the light/dark cycle while others are entrained by other stimuli, such as the cyclical presentation of food. One such is the oscillator which regulates feeding activity in rodents (Boulos & Terman, 1980), pigeons (*Columba livia:* Phillips *et al.*, 1993) and house sparrows (*Passer domesticus:* Hau & Gwinner, 1992). The existence of oscillators of this kind is easily overlooked because in nature the availability of food is often closely linked to the light/dark cycle (e.g. the abundance of insects eaten by insectivorous birds). Thus, while the activity of the birds, for example, is tightly correlated to light conditions, the relationship may be only indirect. The role of multiple or compound clocks in regulation of the temporal organisation of behaviour has been demonstrated by the experimental separation of rhythms that were apparently inextricably linked and by recording the subsequent independent persistence of each (Mrosovsky & Hallonquist, 1986). The mammalian SCN, therefore, is better considered not as *the* clock but as the *master clock,* the chief among many. This view represents a widely accepted model for the hierarchical regulation of rhythmic phenomena in many classes of organisms including plants, insects, amphibians and mammals (Hagemayet & Waisel, 1987; Turek & Losee-Olson, 1988; Grandin & Charbonneau, 1991; Reinberg & Touitou, 1996; Heintzen *et al.*, 1997; Turek, 1998; Weaver, 1998).

Control of rhythms in temperate species

Though biological rhythms are, by definition, driven by endogenous mechanisms, this in no way denies the role of the environment in modulating

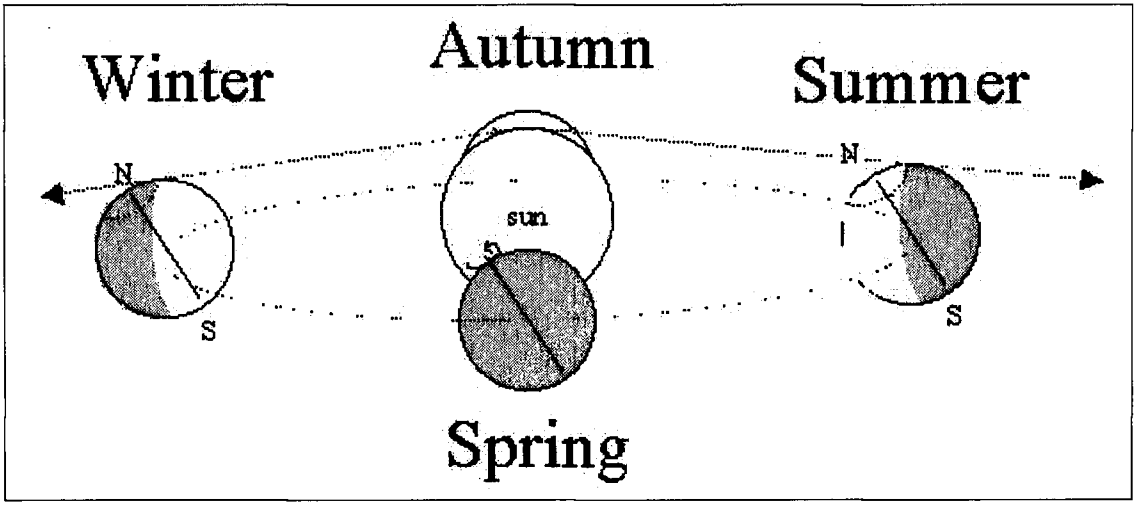

Fig. 2. The figure shows the revolution of the Earth around its axis and the consequential occurence of night and day. Seasons are a result of the tilting of the Earth's axis which causes different parts of the Earth, in turn, to face predominantly towards or away from the sun. The seasons are indicated for the northern hemisphere. The arrows show how sunlight is absent north of the Arctic circle in winrer, while there is conrinuous daylight there in summer.

their expression. Environmental input is essential: the rhythms evolved to synchronise the physiological and behavioural functions of the organism to its environment, not to isolate the organism from that environment. The indispensable role of environmental input is nicely illustrated by considering the function of the SCN itself. The master clock has an endogenous frequency of only *approximately* 24 hours. Most animals, however, live in an environment with a light/dark cycle of *exactly* 24 hours. The discrepancy is small but significant. To the extent that the role of the SCN is to synchronise the animal to its environment, the clock must be reset from time to time. The resetting of the phase of the clock is called 'entrainment' (Table 1) and the environmental cues which serve to entrain it are called 'zeitgebers' (Table 1). The best known zeitgeber is the daily light/dark cycle which, at any given latitude, varies in an entirely predictable manner throughout the year.

The light/dark cycle

The occurrence of day and night is due to the rotation of the planet around its axis as a result of which every point of the surface of the Earth moves alternatively into and out of direct view of the sun. The Earth completes one rotation every 24 hours. In addition, it revolves around the sun, completing one cycle approximately every 365 days. The occurrence of seasons, which so influence the life history of temperate and polar species, is a consequence of the fact that the axis of the Earth is tilted at 23.5° relative to the plane of its orbit. The poles, therefore, alternately face mainly towards or mainly away from the sun (Fig. 2). In the northern hemisphere, we enjoy the long days of summer when the North Pole is tilted towards the sun while in winter, when the situation is reversed, the days are short. Seasonal variation in daylength incteases with increasing latitude. At high latitudes, the daily light/dark cycle disappears both in mid-summer when the sun remains continually above the horizon (the 'polar day') and in mid-winter, when the sun remains continually below the horizon (the 'polar night'). At Tromsø, 70°N lat., the polar day lasts 69 days and the polar night lasts 51 days (Fig. 1). Information on daylength at different latitudes is available at *http://aa.usno.navy.mil/AA/data/*.

Receiving and conveying photoperiodic information to the rest of the body

No animal can be entrained by the light/dark cycle unless it posseses a supetficial photoreceptor (although see Campbell & Murphy, 1998; Yamazaki *et al.*, 1999). In mammals, photoperiodic information is transmitted to the SCN via neural relays from photoreceptors in the retina which, independent of the visual pathway, are concerned only with entrainment of the circadian clock (Miyamoto & Sancar, 1998). An animal can, therefore, be visually blind but still receptive to photoperiodic information. The retinohypothalamic tract - a projection with no visual function - is believed to be the major route along which photic information is fed into the circadian system although other inputs from the primary and accessory optic tracts also exist (Hofmann, 1981; Menaker & Binkley, 1981).

Adjusting the clock

Diurnal mammals seem to entrain to the daily light/dark cycle through dynamic adjustments in SCN function which result in alteration of the phase and the frequency of the clock (Pittendrigh, 1981; Beersma *et al.,* 1999). The phase of the clock may be advanced or delayed relative to the real (solar) time of day and its frequency may, likewise, be accelerated or decelerated. Adjustment of the phase of the clock appears to be a rapid response, while alteration of the clock's frequency seems to occur continually while the animal is awake (Beersma *et al.,* 1999).

The sensitivity of the clock to the different kinds of temporal information to which it can become entrained varies throughout the day and is described in so-called 'phase response curves' (e.g. Pittendrigh, 1981). Sensitivity to photoperiodic information is characteristically high at the beginning and the end of the daily period of activity and low, or even absent, during the middle. These responses are species specific: for example, golden hamstets are highly responsive to photic information while white-footed mice (*Peromyscus leucopus*) are much less responsive (Pittendrigh & Daan, 1976). The functional significance of these differences is unclear. It may be that low sensitivity to environmental zeitgebers enhances opportunistic behaviour. This might be highly beneficial, for example, in animals moving from one rhythmic environment into another. Birds appear to reduce their zeitgeber sensitivity while migrating across many degrees of longitude (Gwinner *et al.,* 1997); the pineal gland of lampreys (*Petromyzon marinus*) altogether ceases to synthesise melatonin while the animals are switching hosts (Menaker & Tosini, 1996). Whatevet the adaptive significance of these differences in zeitgeber sensitivity, they ate reflected in the amplitude of the daily cycle in the plasma concentration of the hormone melatonin (Hau & Gwinner, 1997).

The role of melatonin

The information represented by the output of the SCN, which integrates an endogenous component with photoperiodic modulation, is presumably transmitted to the rest of the body by the daily fluctuation in the plasma concentration of melatonin. This hormone appears to be a key intermediate between the biological clock - the SCN - and rhythms of behaviour and physiological function. Melatonin is secreted by the pineal gland which lies between the cerebral hemispheres above the third ventricle of the brain where it receives sympathetic innervation from the SCN (Lincoln, 1998; Fig. 3). Changes in the plasma concentration of melatonin convey two kinds of information. The daily fluctuation in concentration makes distinction between day (low melatonin) and night (high melatonin) while, in species living in the temperate zone, the duration of the night-time peak of melatonin indicates season, varying from summer (short dutation) to winter (long duration). Thus, the duration of the nighttime peak of melatonin shortens as the days grow longer in spring, reaches a minimum in summer, lengthens as the days grow shorter in autumn and teaches a maximum in wintet.

Melatonin is a hormone of darkness: it is secreted at night and its secretion is suppressed by light during the day. This can be misleading, because the secretion of melatonin is a response to the endogenous rhythm of the SCN, not to darkness itself. In most mammals, the rhythmic secretion of melatonin persists during exposure to several days of constant darkness (Scott *et al.,* 1995). Light does, however, play a role in the regulation of the secretion of melatonin by inhibiting the SCN from stimulating the pineal production of the hormone (Reiter, 1993).

The role of melatonin in the regulation of biological rhythms has been well demonstrated in ungulates, particularly with regard to the timing of reproduction in seasonal breeders. Photoperiod has clear inductive effects on reproduction in both red deer and sika deer (*Cervus nippon*). An artificial change from long to short days induced premature reactivation of the reproductive axis owing to its signalling the early onset of autumn (Goss, 1969). Treatment with melatonin in spring and summer gives the same signal and the same result. Artifically increasing the duration of exposure to the hormone induces autumnal (short-day) responses such as the premature reactivation of testicular activity and the early onset of ovulatory cycles in red deer (e.g. Lincoln *et al*, 1984; Webster & Barrell, 1985; Adam *et al.,* 1986).

There is one important caveat. The alteration of the timing of reproduction by the manipulation of photoperiod or of circulating levels of melatonin or in response to dietaty and social factors (Martin, 1984) demonstrates ways in which environmental cues can modulate the overt expression of an underlying, endogenous rhythm. None of these observations, however, preclude the central role of the clock in establishing the basic seasonal (or daily) rhythm. Clear evidence for this is provided by the persistence of physiological cycles in animals maintained under constant photoperiod, such as the seasonal rise in blood levels of luteinizing hormone in ovariectomised ewes kept on short days for 2.5 years (Bronson, 1989: 118), or the persistence of the antler, pelage and other cycles in deer (Goss, 1969; 1974; Loudon & Brinklow, 1992). Consistent with this, the characteristic seasonality of reproduction in different species of cervids remains unaltered despite major changes in their photoperiodic regime. Gerald Lincoln illustrated how tropical Axis deer (*Axis axis*), originating from 15°N lat. in India, continued to breed and calve throughout the year; mule deer (*Odocoileus hemionus*), originating from 40°N lat., calved from June to September; and reindeer, from 60-70°N, showed a restricted calving season lasting approximately four weeks at the beginning of summer, even though all these animals were maintained in captivity in London Zoological

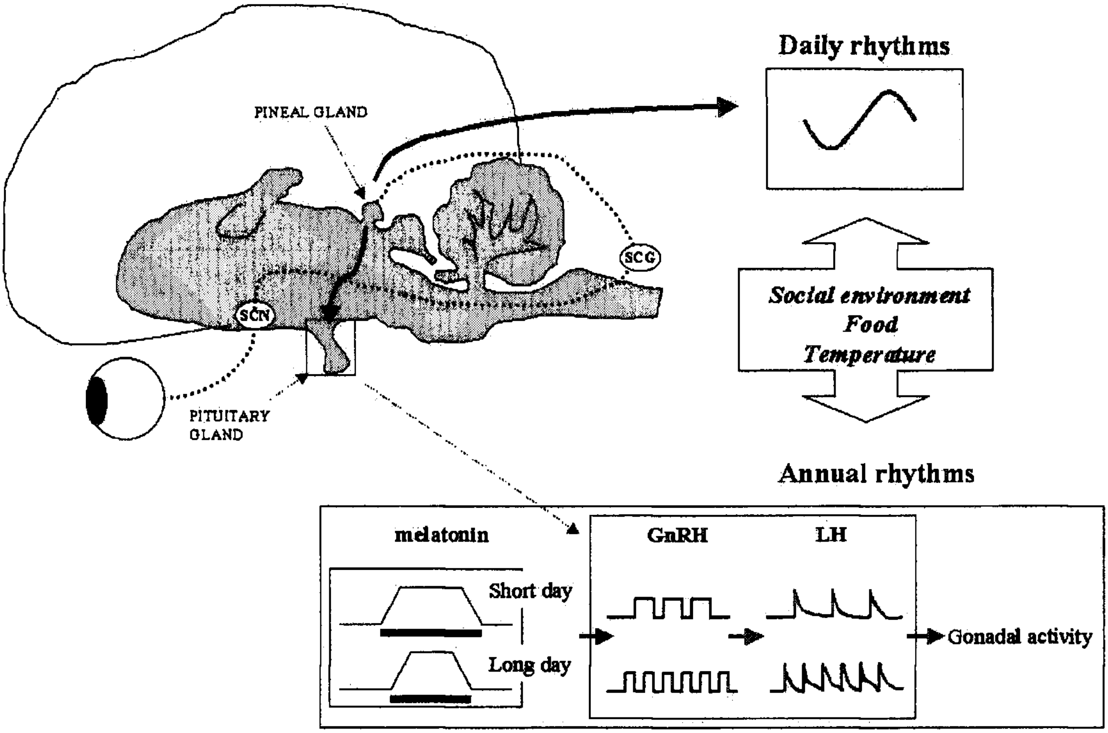

Fig. 3. Schematic plan of the brain illusrrating the circadian and circannual axis after a model for a remperate zone long-day breeding mammal. The dotted line shows the pathway along which photoperiodic information is transmirted to the pineal gland. Light acts both to entrain rhe phase of the daily endogenous rhythm of the SCN and to suppress melatonin secretion in the pineal gland. The two bold arrows show the pathways along which photoperiodic information, translated into a melatonin rhythm, is believed to influence daily and annual rhythms of physiological function and behaviour. The duration of melatonin secretion acts, for example, via the pituitary gland to modulate the pulsatile secretion of GnRH, thus regulating the activity of the reproductive axis. Daily and annual rhythms are also modulated by non-photic environmental input. (SCN = suprachiasmatic nucleus, SCG = supracervical ganglion, LH = Luteinising hormone, GnRH = Gonadotropin releasing hormone).

Gardens (51°30'N lat.: Lincoln, 1985). The expression of the endogenous rhythms which regulated the breeding season in these deer persisted and was not modified by the characteristics of the photoperiod to which they were latterly exposed.

Rhythms in the Arctic

The life-history of arctic animals exemplifies biological timing in an extreme form. Accurate timing of breeding, rearing young, moulting etc. is particularly important in the Arctic where the ambient temperature may rise above freezing for just a few weeks in summer. Consequently, the degree of synchrony of these and other life-history events within populations generally increases markedly with increasing latitude (e.g. Lincoln, 1998). How is this timing achieved at latitudes characterised by the absence of any marked light/dark rhythm in mid-summer and mid-winter which might regulate clock function? We can explore this question using two groups of animals: summer visitors and arctic residents. Visitors, such as migratory birds, are exposed to daily light/dark cycles throughout the year except in mid-summer when they breed and rear their young before departing south. Residents, on the other hand, are exposed to a daily light/dark cycle in late winter and late summer but live under continuous light conditions for the remainder of the year.

Activity rhythms in summer visitors

Snow buntings (*Plectrophenax nivalis*) visit Svalbard (74-81°N lat.) in summer to breed. Their daily rhythms of locomotor activity persist throughout the summer and appear to be entrained by the solar cycle (Krüll, 1976). The birds are evidently able to extract photoperiodic information from the continuous daylight conditions of the arctic summer. Similar observations have been made in a variety of birds and mammals exposed to summer light conditions near the Arctic circle (66°N lat.), including species which do not normally penetrate so far north (Daan & Aschoff, 1975). All species which perform in this manner must have a strong sensitivity to the zeitgeber, thereby being able to extract photoperiodic information even under the continuous daylight conditions of the polar day. The exact nature of the cue is unknown; it might be the changing azimuth of the sun or the changes in the spectral composition of light which occur during the course of the 24 hour day (Krüll, 1976).

Humans, by contrast, behave quite differently. Unlike snow buntings, the summer visitors to Svalbard studied by Johnsson *et al.* (1979) displayed free-running rhythms of body temperature and sleep-wake cycles which soon fell out of phase with the solar, 24 hour day. Humans, therefore, appear to be less sensitive to the photic zeitgeber than snow buntings and are unable to extract photoperiodic information during the continuous daylight conditions of the high arctic summer. Human subjects at 70°N lat. (Tromsø) have been shown to synchronise their melatonin rhythm to the 24 hour day both in summer and winter (Stokkan & Reiter, 1994) but the resultant rhythmicity of the sleep-wake cycle is not strong and sleep disturbances are frequently reported at this location (Lindgjærde *et al.*, 1985). Clearly, sensitivity to continuous light conditions is species specific.

Activity rhythms in arctic residents

High arctic residents respond quite differently to continuous light conditions. Two sub-species have been studied in considerable detail while living under natural light conditions: Svalbard ptarmigan, the only herbivorous bird permanently resident on the high arctic archipelago of Svalbard, and Svalbard reindeer. Both these sub-species behave similarly in response to changes in their photoperiodic environment. As expected, they display daily rhythms of activity while exposed to the daily light/dark cycles of late summer (September-October) and late winter (February-March). In mid-summer and mid-winter, by contrast, the animals become intermittently active around the clock (Stokkan *et al.*, 1986; Reierth & Stokkan, 1998; van Oort *et al.*, 1998; 1999a; b; van Oort, unpubl. data). These results indicate that Svalbard reindeer and Svalbard ptarmigan have weak circadian mechanisms: either weak endogenous pacemakers or low sensitivity to the subtle changes in photic conditions which entrain snow buntings in summer. Consequently, these animals are able to feed opportunistically around the clock during the polar night and the polar day as conditions permit, unconstrained by any endogenous control of the temporal pattern of their daily activity. Similar results have been observed in tundra voles (*Microtus oeconomus*) and red-backed voles (*Clethrionomys rutilus*) at 70°N (Swade & Pittendrigh, 1967). In every case, the animals failed to show any free-running or entrained rhythms of activity under continuous light conditions, indicating either loss of the normal coupling between clock function and behaviour or between the rhythm generating cells within the SCN or even a 'switching-off' of the clock.

In contrast to this, most, though not all, individual arctic ground squirrels (*Spermophilus undulatus*) and brown lemmings (*Lemmus trimucronatus*) maintained rhythmic cycles of activity when exposed to natutal summer light conditions at 70°N (Swade & Pittendrigh, 1967). The behaviour of these individuals, therefore, was governed endogenously as in snow buntings and humans (Krüll, 1976; Johnsson *et al.,* 1979). It is evident that considerable variation exists both within and between species in the ways in which the biological clock responds to the special photic conditions which characterise high latitudes.

Rhythms in arctic ungulates

Many cyclic phenomena have been described in Arctic ungulates. These include seasonal variation in activity rhythms (muskoxen: Jingfors, 1982; Oakes *et al.,* 1992; Schaefer & Messier, 1996; Côté *et al.*, 1997; reindeer: Eriksson *et al.,* 1981; Skogland, 1984; van Oort *et al.,* 1998; 1999b), growth (McEwan, 1968; Leader-Williams & Ricketts, 1982), appetite (McEwan & Whitehead, 1970; Ryg & Jacobsen, 1982; Larsen *et al.,* 1985; Tyler *et al.,* 1999), the antler cycle in reindeer (McEwan & Whitehead, 1980; Leader-Williams, 1979; Ryg, 1983; Lincoln & Tyler, 1991; 1994; Bubenik *et al.,* 1997), heart rate (Nilssen *et al.,* 1984; Fancy & White, 1986; Sokolov, 1990; Mesteig *et al.*, submitted), testis function (Leader-Williams, 1979) and a variety of reproductive and metabolic hormones (e.g. Whitehead & McEwan, 1973; Ringbetg *et al.,* 1978; Ryg & Jacobsen, 1982; Nilssen *et al.,* 1985; Suttie *et al.,* 1991; Bubenik *et al.,* 1997; 1998).

Notwithstanding the variety of phenomena which have been described, little is known about the regulation of these cycles. Recent work on two sub-species of reindeer, however, provides some intriguing clues. Like in Svalbard reindeer (above), the matked daily rhythms of activity which mainland reindeer (*R. t. tarandus*) living at 70°N lat. show in late winter also break down under the continuous light conditions of summer. Their daily bouts of activity become evenly distributed across the 24 hour day such that they are just as likely to be active at midnight as at noon (van Oort *et al.,* 1998; 1999b). Like Svalbard reindeer, therefore, mainland reindeer seem to have only weak circadian mechanisms in summer.

Interestingly, these two sub-species of reindeer seem to respond differently to the continuous darkness of winter in their respective natural evironments. While Svalbard reindeer become arrhythmic during the polar night, showing activity around the clock as in summer, mainland reindeer living freely at 70°N lat. remain synchronised with the 24 hour day. Their main bout of activity occurs in the middle of the day and the timing of the onset of activity early in the morning remains highly predictable throughout the winter (van Oort *et al.,* 1998; 1999b). In both situations where these studies were carried out (at 70° and 78°N lat.) the sun remains permanently below the horizon in the middle of winter: mainland reindeer, nevertheless, were capable of responding to the weak diurnal fluctuation in the level of twilight that occurs during December and January at 70°N lat. These results can be interpreted in one of two ways. Either mainland reindeer are entrained by the weak photic information which is available in winter, or their clock function is suppressed and activity is tegulated, instead, directly by changes in light intensity. The key difference between these alternatives may be the level of SCN activity and the functional significance of the clock in winter. This can be explored by studying the pattern of secretion of melatonin which lies closer to the clock than the rhythm of activity and which might, thetefore, more accurately reflect clock function.

Melatonin rhythms in arctic ungulates

Only three groups have investigated the roles of photoperiod and melatonin in the control of endogenous mechanisms in arctic ungulates (muskoxen: Tedesco *et al.,* 1992; reindeer: Eloranta *et al.,* 1992; 1995; Stokkan *et al.,* 1994). A null hypothesis in all these studies is that clock function is maintained throughout the year and, reflecting this, the circadian rhythm of the secretion of melatonin persists throughout the polar night and the polar day. Were this the case, the observed breakdown of the daily rhythms of locomotor activity in mid-summer and mid-winter in reindeer would be attributable to an uncoupling of the influence of the melatonin cycle from the regulation of activity. If the null hypothesis is rejected, i.e. if the circadian rhythm of the secretion of melatonin is lost in mid-summer and mid-winter, two alternative explanations fot the atrhythmicity of activity arise. Either clock function must be shut down or it persists while the link between the SCN and the pineal is somehow interrupted.

The daily cycle of the secretion of melatonin has been studied in reindeer living under natural light conditions at 70°N lat. Both Eloranta *et al.* (1992) and Stokkan *et al* (1994) demonstrated the presence of robust daily rhythms in the plasma concentration of melatonin in spring and autumn while in summer the cycle disappeared altogether and the daily production of melatonin fell to an annual minimum. The results from mid-winter trials diverged slightly. Eloranta *et al.* (1992) apparently detected a weak daytime reduction in the plasma concentration of melatonin. Stokkan *et al.* (1994), however, were unable to replicate this result and detected no daily rhythm in the secretion of melatonin in reindeer in December. Taken together, these studies suggest that the breakdown of the daily rhythmicity of activity in reindeer in summer is associated with the suppression of the daily rhythm of the secretion of melatonin, while leaving aside the question of the level of clock function at this time.

Eloranta *et al.* (1995) took a first step towards investigating clock function with an important experiment in which reindeer were put into a dark room in the middle of the day in mid-summer. The animals, which had been exposed to continuous, natural daylight for several weeks, responded with an immediate rise in the plasma concentration of melatonin. Clearly, the abrupt and unprecedented onset of darkness (i.e. 'night') triggered the SCN which was at once capable of stimulating the pineal gland to secret melatonin. This result offers strong evidence that the link between the SCN and the pineal gland remains uninterrupted in summer.

The outstanding question, therefore, is whether the SCN of reindeer sustains circadian rhythmicity in the absence of environmental (photoperiodic) input. Clearly, in mid-summer it cannot owing to the animals' exposure to continuous bright light, but what is the situation in late winter and late summer when the animals are exposed to a daily light/dark cycle? Is it the case that the SCN can sustain a daily rhythm at these times - just as in temperate species of mammals - and that this ability is lost in summer or, alternatively, is the SCN just a passive partner in the system, with its activity being triggered literally every day? Results from a recent series of trials conducted in Tromsø favour the latter model. No evidence has been found of any persistent daily cycle in the secretion of melatonin in reindeer exposed to several days continuous darkness in spring and autumn (K.-A. Stokkan, unpubl. data). Thus far, therefore, it seems possible that the daily rhythm of melatonin secretion in reindeer is generally driven by the daily light/dark cycle and not by an endogenous mechanism. This situation, if confirmed, would be unique among vertebrates.

Conclusion

Reindeer and muskoxen display a rich variety of daily and annual rhythms in their behaviour and their physiological function which, through accurate timing, ensure that the animals' requirements are adapted to the challenges imposed by the environment. The driving force behind this rhythmicity, however, has as yet not been identified. Remarkably, it is not even certain to what extent the rhythms are driven by endogenous mechanisms. The criteria for identifying circadian rhythmicity have not been met in reindeer. Neither their daily rhythms of activity nor their daily cycle of the secretion of melatonin persist under constant photoperiodic conditions. The rhythms quickly become reestablished on exposing the animals to a light/dark cycle but it is not clear whether this is a result of resetting the phase of an endogenous clock or, instead, merely a passive response to an exogenous rhythm. A few shreds of evidence indicate clock function. For example, the phase of the daily onset and end of activity of free-living reindeer deviates asynchronously from sunrise and sunset both in late-summer and late-winter (van Oort, unpubl. data). Nevertheless, in reindeer, which show a higher degree of synchrony in seasonal timing than probably any other cervid, clock function remains largely unknown.

Failure to demonstrate clock function begs many questions. The disappearance of an overt rhythm can be explained in several ways; either as a 'stopping' of the circadian pacemaker, or as an uncoupling of the rhythm from its pacemaker, or as a desynchronisation among the multiplicity of oscillators which control the rhythms (Aschoff, 1981; 1986). The endogenous basis of daily and annual rhythms has been clearly established in several species of temperate ungulates and for this reason alone we would expect to find it in reindeer. The most parsimonious interpretation of the evidence to date, therefore, is that the observed arrhythmicity is due to some kind of uncoupling of the clock rather than its 'stopping'.

The circadian timing mechanism shows great flexibility in vertebrates. We have already indicated in this review that subtle differences exist along a latitudinal gradient in the ways in which different sub-species of reindeer respond to changes in photoperiod. It is tempting to suggest that the strength of circadian mechanisms varies across a latitudinal gradient in different species of cervids with reindeer, the most northerly, showing the weakest mechanisms rather as Pittendrigh & Takamura (1989) suggested for different sub-species of *Drosophila* flies. We have emphasised how exposure to continuous photoperiodic conditions places special demands on timing mechanisms and how arctic species, therefore, are of particular interest for the study of biological rhythms. Reindeer, of course, are not the only mammals which live under a continuous photoperiod; subterranean blind mole rats (*Spalax ehrenbergi:* Goldman *et al.*, 1997) live in constant darkness. Unlike reindeer however, these animals have persistant rhythms, indicating the presence of strong oscillators. Rigid temporal organisation, therefore, remains, even in the absence of temporal information. High arctic reindeer and ptarmigan, however, appear to be released from the grip of the biological clock in summer and winter which enables them, instead, to become truly opportunistic at these times.

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Wild and semi-domesticated reindeer in Russia: status, population dynamics and trends under the present social and economic conditions

Eugene E. Syroechkovski

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, Moscow 117071, Russia (rgg@eesjr.msk.ru).

Abstract: At present (in 1999) there are approximately 1.5 million semi-domesticated and 1.3 million wild reindeer in Russia. The co-existence of these two forms remains a major problem. Reindeer herding has declined while the number of wild reindeer has increased during the last 10 years. The main causes of these changes are social and economic. The 1960s and 1970s were characterised by a deliberate attempt to eradicate the nomadic way of life of reindeer herders. It was relatively easy to introduce public (*kolkhoz* or *sovkhoz*) reindeer herding in the Nenets, Chukchi and Komi-Izhem areas where large-scale reindeer herding was typical and, as a result, there were almost 1 million reindeer in collectives in the extreme north-eastern part of the USSR. At the same time reindeer herding deteriorated among the Khanty, Mansi, Evenk, Even, Selkup peoples. *Perestroika* in the 1990s resulted in the formation of a market economy. Collective reindeer herding declined and the number of semi-domesticated reindeer decreased during a period of gradual return to private ownership of reindeer. The largest region of reindeer herding is now the Nenets region in the north-west of Russia. Successful symparric exisrence of wild and semi-domesticated reindeer is not possible. The Taimyr wild reindeer population numbers about 500-600 000 reindeer. From 1971 to 1981 not less than 700 000 reindeer in this population were shot. Ecological and economic control over them has now been lost. Thete are approximarely 200 000 animals in Yakutia. The number of wild reindeer here has grown following the decline of reindeer husbandry. Yakut and Even reindeer herders believe that the decline has been due to wild reindeer drawing semi-domesticated reindeer away. At present 13 aboriginal peoples in northern Russia engage in reindeer herding. Five former reindeer herding peoples have given up herding bur there are signs of improvement in the situation among those peoples which have rerained reindeer herding culrure following the gradual restoration of privare ownership of reindeer. In the 20 regions where only a few wild reindeer remain hunting should be prohibited and measures should be taken for protecting and restoring the populations. There are approximately 6000 reindeer on Novaya Zemlya; a further 6000 animals live on the Novosibirsk islands. The Red Data Book of Russia should include rare and disappearing populations both on the periphery of the species' distribution and inside it to preserve and restore the species and to conserve its genetic diversity.

Key words: Chukchi, Even, Evenk, herding, hunting, Khanty, *kolkhoz,* Komi, Mansi, Nenets, *Rangifer tarandus,* Selkup, *sovkhoz,* Taimyt, Yakutia.

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Note on terminology provided by David Andersen

A *kolkhoz* (*kollektivnoe khoziaistvo*) is an abbteviation for a common property institution common in Siberia from 1925 until the mid 1960s. It was characterised by common access to land, wages calculated according to the quantity produced by each member and local democratic institutions such as group meetings of members. It is often translated as 'collective farm'. A *sovkhoz* (*sovetskoe khoziaistvo*) was a much more centtalised version of the *kolkhoz* wherein producers fitted into a complex division of labour regulated by labour statues, trade unions and formal professional qualifications. Remuneration was made on the basis of official salary tables. Direction of the *sovkhoz* was not locally based but filtered through a long chain of authority culminating in the Ministry for Rural Economy in Moscow. Although *sovkhozes* were designed in the early 1930s they did not replace *kolkhozes* in most places in Siberia until the early 1960s. Some parts of Siberia retained the *kolkhoz* stucture right to the end of the Soviet period.

Table 1. The numbers (thousands of animals) of semi-domesticated reindeer in diffetent regions of Russia, 195

Regions	1951	1961	1965	1970	1971	1975	1976	1977	1978	19
Amur Region	6.3	12.6	15.0	17.3	17.3	16.1	14.7	14.9	15.0	15
Arkhangelsk Region	189.7	169.9	174.6	193.2	193.2	180.0	183.2	183.4	181.8	192
Buryatia Republic	2.3	3.9	4.2	5.0	5.0	4.8	4.2	4.3	2.6	1
Chitta region	10.3	11.6	14.1	18.3	18.3	17.3	15.9	15.2	15.6	14
Irkutsk region	5.5	7.0	7.5	5.4	5.4	4.5	4.1	4.0	4.1	1
Kamchatka Region	194.2	158.8	174.8	178.9	178.9	174.8	175.6	176.3	177.0	177
Karelia Republic	0.400	-	0.200	0.100	0.100	-	0.003	-	-	-
Khabarovsk Territory	38.0	42.3	52.4	50.3	50.3	51.5	51.6	49.3	41.9	48
Komi Republic	211.0	136.7	135.9	147.1	147.1	100.6	104.9	107.7	97.6	120
Krasnoyarsk Territory	137.0	136.8	188.1	164.8	164.8	142.9	143.3	144.2	126.1	102
Magadan Region	512.2	579.3	710.3	738.5	738.5	685.4	696.7	710.	711.9	705
Murmansk Region	53.9	74.2	77.1	81.9	81.9	65.6	65.2	65.5	64.8	66
Sakhalin Region	10.2	13.1	15.1	14.2	14.2	13.4	13.3	12.5	10.7	3
Tomsk Region	0.8	0.6	0.3	0.1	0.1	-	0.1	-	-	-
Tyva republic	3.1	-	9.1	11.6	11.6	10.5	11.1	11.8	13.1	10
Tyumen' Region	366.8	400.5	431.3	480.9	480.9	440.4	441.3	433.8	411.2	427
Yakutia Republic	312.9	340.6	359.3	356.3	356.3	371.9	377.8	379.2	375.9	371
Total	2054.6	2087.9	2369.3	2463.9	2463.9	2279.7	2303.0	2312.1	2249.3	2259

Introduction

Russia has always been a leading country for semi-domesticated and wild reindeer. At present (in 1999), Russia has two thirds of the world's population of semi-domesticated reindeer (1 510 000 animals) and about 1 246 000 wild reindeer. Thus, there are approximately equal numbers of wild and semi-domesticated reindeer in Russia now. The co-existence of wild and semi-domesticated reindeer has been a big problem for Russia throughout this century. Numbers of wild and semi-domesticated reindeer have changed substantially during the last 10 years. Reindeer herding has declined significantly while the number of wild reindeer has increased. The main causes of this phenomenon are social and economic. By saying so I would like to stress that population sizes of wild and semi-domesticated reindeer in Russia have for the most part never been food-limited. I have always considered as wrong the opinion widely spread in Russian scientific literature that reindeer herding in Russia has been limited by lack of pasture owing, in particular, to loss of habitat as a result of technological development. The present-day changes in reindeer numbers confirms my view. In this paper I will examine the data on changes in numbers of semi-domesticated and wild reindeer in Russia and consider the causes of changes in numbers throughout this century.

The current situation and dynamics of populations of semi-domesticated reindeer in Russia

Table 1 shows numbers of semi-domesticated reindeer in Russia from 1951 to 1998. Figs. 1 and 2 show the distribution of reindeer in 1997 and in 1984.

The number of semi-domesticated reindeer in Russia has changed significantly during the last 100 years, varying from 1.5 million to almost 2.5 million animals. The leading factors causing these changes have been socio-political in character. The changes in numbers of semi-domesticated reindeer in the 20th century can be divided into several stages:

The beginning of the century

The beginning of the century was characterised by the highest number of reindeer. The relatively low official figures in the first decades of the century (1 455 000 in 1906 and 1 674 000 in 1912) probably reflect low accuracy in counting. I do not agree with Khrushchev & Klokov (1998) that numbers increased steadily up to the 1930s although there may have been some increase in the numbers associated with the development of large-scale Nenets and Chukchi reindeer herding. The first more or less accurate registration of reindeer was carried out in

984	1991	1997	1998
3.5	12.9	10.3	9.3
4.0	190.7	182.9	171.6
-	2.1	0.9	0.7
2.4	9.2	2.0	1.3
2.6	3.9	2.0	0.5
6.6	167.1	98.3	72.3
-	-	-	-
4.6	42.7	20.0	17.2
5.3	123.6	124.0	122.8
7.0	107.4	57.8	50.3
6.0	612.5	241.1	192.3
2.4	77.3	77.0	71.4
3.6	4.0	3.1	2.9
-	-	-	-
9.6	8.1	3.1	3.4
49.6	537.6	554.0	573.6
19.9	361.5	215.9	196.4
17.1	2260.6	1592.4	1486.0

1926-1927 during the Polar census of the population and economy in Russia's Extreme North. The total figure amounted to 2 195 000 reindeer. All semi-domesticated reindeer belonged to private herders: there was no public reindeer herding of the *kolkhoz* or the *sovkhoz* type then.

The second stage

The second stage saw the development of publically owned reindeer herding in the so-called *kolkhoz* form. Transferring reindeer herds into public ownership was a painful process for Northern peoples. *Kolkhoz* reindeer herding was formed mainly through compulsory procedures. It was almost forbidden to own reindeer privately and the size of private herds was strictly limited. As a result, the total number of semi-domesticated reindeer in Russia decreased to the minimum level of 1 434 700 by 1934; 331 000 (23.1%) of these were *kolkhoz* reindeer, compared to none in 1927, while all the rest were privately owned.

The third stage

During the third stage, which began in mid-1930s, the total number of semi-domesticated teindeer increased steadily though slowly and erratically at first.

The fourth stage

The 1950s were characterised by unstable dynamics in reindeer populations owing to epizootics in Komi Autonomous Republic and West Siberia and by a crisis in taiga reindeer herding (Khrushchev & Klokov, 1998). In 1951, the total number of semi-domesticated reindeer was 2 054 500 of which in public (*kolkhoz* and *sovkhoz*) enterprises accounted for 1 664 100 animals while only 390 400 (19%) were privately owned.

The fifth stage

During the fifth stage (1960s and 1970s) the number of semi-domesticated reindeer reached a maximum of over 2 million animals. In 1968-1972 numbers exceeded 2 400 000 animals; less than 13% of these were privately owned.

The indigenous peoples of the North were still passively opposed to public reindeer herding but they gradually became accustomed to it. The Soviet government paid great attention to developing the public reindeer herding and allocated big sums of money for its development. Various zootechnic and veterinary procedures were carried out on a wide scale. In particular, a great deal of work was done in overcoming reindeer diseases like anthrax, scabies, brucellosis, necrobacillosis. Great attention was paid to scientific support of reindeer herding. In Norilsk, Yakutsk, Magadan, Naryan-Mar special institutes and a network of research stations were set up to serve agriculture in the North and reindeer herding occupied a prominent place among the agicultural projects carried out. New technologies were introduced including the use of off-road vehicles, aeroplanes, helicopters, radio communication and electric power.

This same period was characterised by a deliberate attempt to reduce the nomadic way of life of reindeer herders and other Northern peoples. The system of traditional wildlife management and of traditional way of life of the reindeer herder peoples was destroyed. Nomadism (which was the reindeer herders' normal way of life and the basis of their survival) and the aboriginal family way of life deteriorated. The introduced system of shift-work herding divided herders' families in a most unnatural manner for these people; under the new system only the men stayed in the herds while the women and children were moved to specially built settlements.

It was much easier to introduce public (*kolkhoz* or *sovkhoz*) reindeer herding in the areas for which large-scale reindeer herding was typical (the

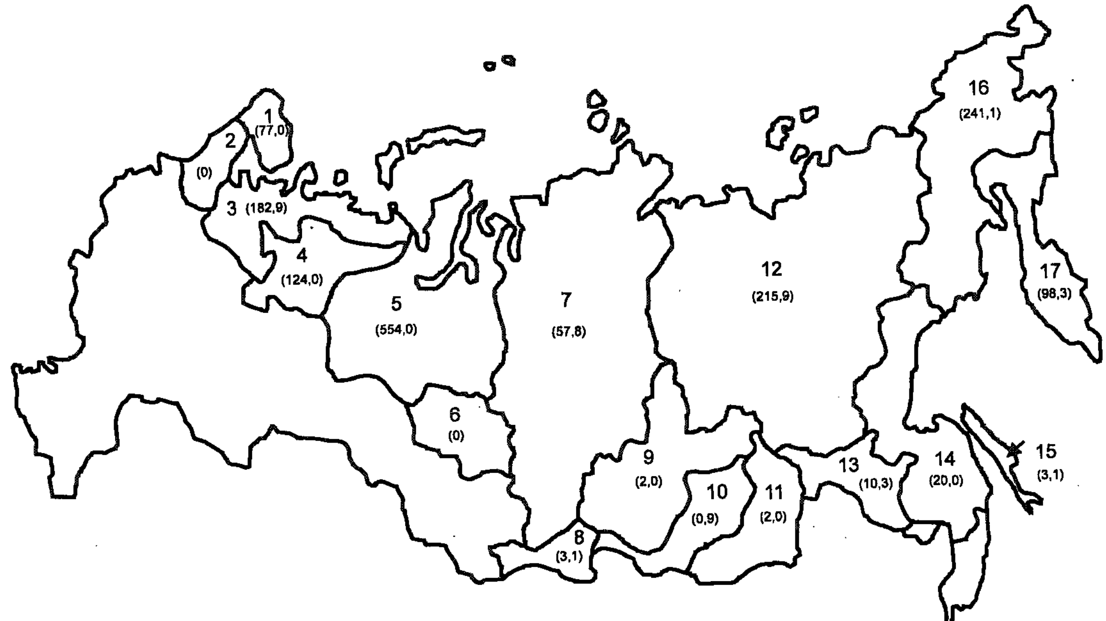

Fig. 1. Distribution of semi-domesricated reindeer and number (thousands in brackets) in Russia, 1997:

1 - Murmansk Region
2 - Karelia Republic
3 - Archangelsk Region (with Nenets Autonomous District)
4 - Komi Republic
5 - Tyumen' Region (with Yamal-Nenets & Khanty-Mansi Autonomous Districts)
6 - Tomsk Region
7 - Krasnoyarsk Territory (with Taimyr, Evenk Aut. Districrs and Khakasia Republic)
8 - Tyva Republic
9 - Irkutsk Region
10 - Buryaria Republic
11 - Chitta Region
12 - Yakutia Republic
13 - Amur Region
14 - Khabarovsk Terrirory
15 - Sakhalin Region
16 - Magadan Region (with Chukotka Autonomous District)
17 - Kamchatka Region (with Koryak Autonomous District)

Nenets, Chukchi and Komi-Izhem types). The large-scale reindeer farms in Chukchi National District were particularly successful. The Chukchi, a strong and self-dependent nationality, had begun to breed reindeer for selling meat at the market even before the Soviet period. They did it earlier than other peoples of the Russian North. It is also typical that in Tsarist times the Chukchi were the only aboriginal nationality in the Russian North

Table 2. Semi-domesticated reindeer in Russia: forms of ownership.

	1906	1912	1927	1934	1941	1946	1951	1956	1961	196
Total (thousands)	1457.7	1673.7	2194.6	1434.7	1931.2	1821.5	2054.5	1993.2	2103.7	2369
Social property	-	-	-	331.2	843.2	1274.9	1164.1	1714.2	1815.6	2109
%	-	-	-	23.1	43.7	70.0	81.0	86.0	86.3	89
Private property	1457.7	1673.7	2194.6	1103.5	1088	546.6	390.4	279	288.1	260
%	100	100	100	76.9	56.3	30.0	19.0	14.0	13.7	11

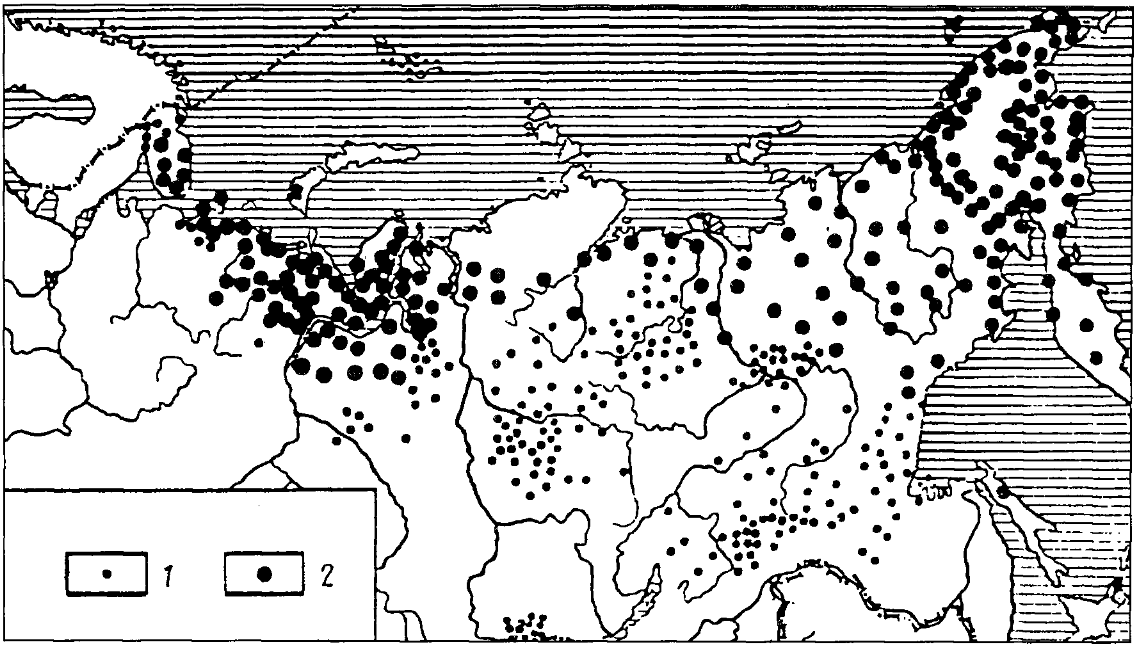

Fig. 2. Distribution of semi-domesticated reindeer in rhe USSR, 1984: 1 - 1000 reindeer; 2 - 10 000 reindeer. From Syroechkovski (1995).

who managed to maintain their independence to a great extent.

As a tesult, the extreme north-eastern part of the USSR became the world's largest region of large-scale collective reindeer herding with almost 1 million reindeer in collectives. This region comprised the Chukchi National District and a part of the Koryak National District where there were 917 400 reindeer in 1971 and 880 200 reindeer in 1981. In those years there were 738 500 reindeer in Magadan Region, including 705 300 reindeer in the Chukchi National District, while in Kamchatka Region there were 178 900 reindeer, including 174 900 reindeer in the Koryak National District.

The second largest region of semi-domesticated reindeer herding in the USSR was the Yamal-Nenets National District (in the north of West Siberia) which numbered 480 900 semi-domesticated reindeer in 1971 and 418 000 semi-domesticated reindeer in 1981. In that region, herding was done mostly by Nenets (reindeer herding on the tundra) and partially by Khanty (reindeer herding in taiga).

The third largest region of semi-domesticated reindeer herding was located in the tundra areas of the European part of Russia. Here, in the Nenets National District of Archangelsk Region, in the best years of the fifth stage there were almost 200 000 reindeer (193 200 in 1971). Reindeer herders of Komi Republic had almost 150 000 reindeer (147 100 reindeer in 1971). In total, in the European region of Russia there were about 350 000 semi-domesticated reindeer.

As this review shows, large scale reindeer herding on the tundra was done mostly by Chukchis and Nenets. The Komi-Izhem and the Khanty peoples

)71	1976	1981	1986	1991	1992	1993	1994	1995	1996	1997
3.9	2279.9	2267.6	2205.9	2260.6	2207.8	2126.6	1965.5	1833.9	1695	1592.5
9.9	1986	1978.4	1888.9	1831.7	1746.4	1579.3	1391.5	1250.5	1111.7	1006
6.9	87.1	87.2	85.6	81.0	79.1	74.3	70.8	68.2	65.6	63.2
4	293.9	289.2	317	428.9	461.4	547.3	574	583.4	583.3	586.5
3.1	12.9	12.8	14.4	19.0	20.9	25.7	29.2	31.8	34.4	36.8

practiced smaller scale reindeer herding in the taiga and forest-tundra. During calving, they drove their herds as far to the north as possible into the tundra or mountain tundra zones of the Ural Mountains. In winter they took their herds south to forest-tundra and to northern taiga.

The fifth stage was characterised by the deterioration of taiga reindeer herding of the Khanty, Mansi, Evenk, Even, Selkup peoples. In the 1970s there were 300 000 reindeer on the taiga. By 1989 reindeer herding on the taiga was reduced to 100 000-150 000 reindeer while probably at least 1-1.5 million semi-domesticated reindeer could have been successfully pastured there. Taiga reindeer herding has never been characterised by the keeping of large herds. In the traditional way of life the main trades of the people were hunting and fishing; reindeer herding was an auxiliary occupation and reindeer were kept mainly for transport. However, in the period before *kolkhoz* management was introduced, some Khanty in West Siberia and some Evenks in taiga east of the Yenisey, as well as some Even people in Yakut taiga had successfully combined hunting and reindeer herding and some owners had herds of 1000 reindeer and more.

The sixth stage

The sixth stage started in the 1990s, in the time of *Perestroika,* when the formation of the market economy and the democratisation of society began. This stage has not yet ended. On the whole, it is characterised by a significant reduction in the population size of semi-domesticated reindeer, by decline and decay of collective reindeer herding of the *kolkhoz* and *sovkhoz* type and by a gradual return to private ownership of reindeer herds.

Privately owned semi-domesticated reindeer constitute now (in 1997) almost 37% of the total number (in 1966 they made up only 11%) (Table 2). The general trend of increase in the number of privately owned reindeer has continued. Remarkable changes in reindeer numbers have taken place. The largest region of semi-domesticated reindeer herding in the north-east of Russia has undergone a threefold reduction in the number of reindeer. That region used to have almost 1 million reindeer, mostly in the Chukchi National District of Magadan Region. In 1971 the Chukchi National District had almost 740 000 semi-domesticated reindeer, while in 1998 the numbet was a little over 200 000.

The collapse of Chukchi reindeer herding can be explained as follows. The Chukchi National District had large-scale herding that more easily adapted to *sovkhoz* type reindeer herding than small scale herding. Indeed Chukchi private large-scale herding was the prototype of *sovkhoz* reindeer herding. The large herds were owned by rich reindeer herders who employed workers. That type of reindeer herding was the first to go over to market-oriented production of reindeer. When the Soviet State introduced *sovkhoz* herding, reindeer herding in the Chukchi National District became more 'industrialised' than in other places. The Chukchi were moved to large settlements and their former close ties with the herds were broken. Heavy cross-country vehicles were used for communicating with the herds resulting in the destruction of pasture. Very few privately owned reindeer remained in the Chukchi National District. It is therefore quite understandable that reindeer herding in the Chukchi National District began to decay quickly following the decline of *sovkhoz* herding throughout all northern areas of Russia.

In contrast, Nenets reindeer herding in the north of West Siberia, mainly the Yamal Peninsula, and in the Nenets National District in the European part of Russia proved to be better adapted to modern conditions. Large-scale herding was common here but the Nenets had opposed collective herding more stubbornly than the Chukchi and retained private herds to a much greater extent. Quite often Nenets owners hid their herds in remote and inaccessible parts of tundra and forest-tundra. Unlike the Chukchi, they actively resisted attempts to make them live in large settlements. Up to now, the Nenets have retained large and strong families which lead a nomadic life and roam with their herds while living in well-equipped *choom* (pyramid tents similar to the Sami 'lavvo' or North American 'tepee') outside large settlements all year round. This has helped them to preserve their culture and the characteristic elements of their traditional tundra way of life.

This traditional tundta management has been well preserved in the Nenets National District in the European part of Russia. As a result, Nenets reindeer herding suffered much less damage when the system of collective herding introduced under socialism was destroyed. So-called 'backward' Nenets reindeer herding has therefore survived much better than the so-called 'progressive' mechanised reindeer herding of the Chukchi.

As a result of these changes, radical alterations have taken place in the distribution of reindeer herding in Russia. The largest region of reindeer herding is now Nenets region in the north of the European part of Russia and in the north of West Siberia where herding is widely spread in spite of these same areas being greatly damaged by the expansion of oil and gas development.

The Yakutia Republic has remained a significant reindeer herding region. There were 380 000 semi-domesticated reindeer there in 1981. These animals were kept in large herds almost exclusively on the Yakutian tundra and forest-tundra. The Yakut people have long inhabited the central part of Yakutia with its steppes and fotest-steppes and have always engaged in the breeding of cattle and horses. Reindeer herding was mostly done by the 'Northern Yakuts', a special ethnic group formed as a result of the merging of Yakut people of Turkish origin with natives of non-Turkish origin such as the Yakagir, Dolgan, Even and Evenk peoples. In eastern part of Yakutia, large reindeer herds were owned by Evens (large-scale herding in forest-tundra and mountain taiga). During *Perestroika,* Yakut reindeer herding started declining but by 1997 there were still a little over 200 000 semi-domesticated reindeer left there.

Reindeer herding on the taiga has declined throughout Russia from Karelia in the west to the Okhotsk Sea in the east. The zone of taiga reindeer herding is no longer more or less continuous and has been broken down into separate isolated areas which are becoming smaller and smaller. Some small nationalities and separate ethnic groups in the North have given up reindeer herding altogether. This applies to the Kets (the taiga part of the Yenisey basin), the Nganassans (the central part of Taimyr), the Yukagirs (the north-eastern part of

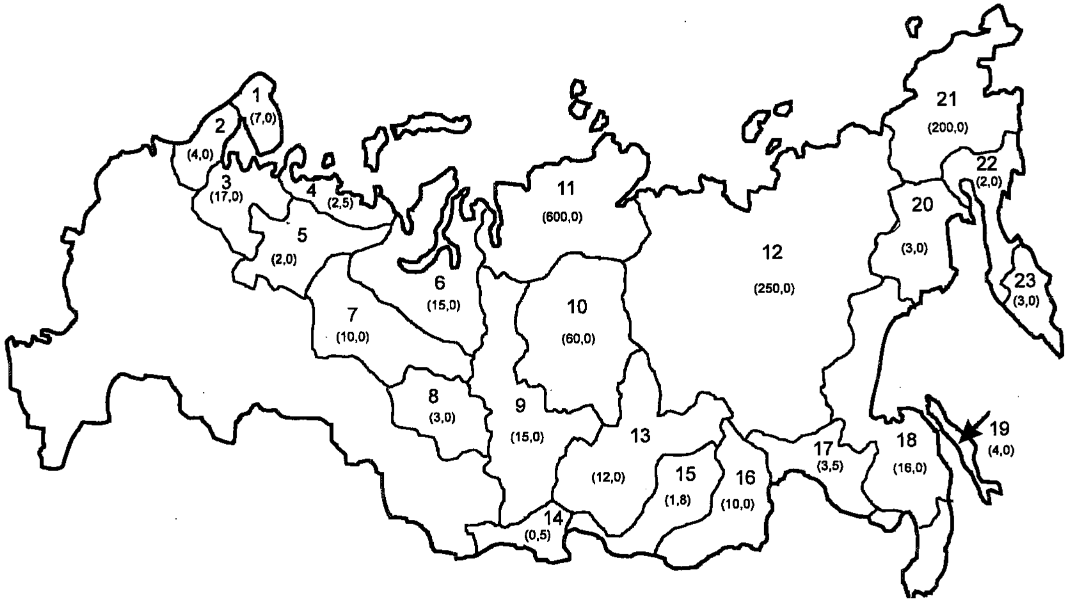

Fig. 3. Distribution and numbers (thousands in brackets) of wild reindeer in Russia, 1997-1998:

1 - Murmansk Region
2 - Karelia Republic
3 - Archangelsk Region
4 - Nenets Autonomous District
5 - Komi Republic
6 -Yamal-Nenets Autonomous District
7 - Khanty-Mansi Autonomous District
8 - Tomsk Region
9 - Krasnoyarsk Territory
10 - Evenk Autonomous Districr
11 - Taimyr Autonomous District
12 - Yakuria Republic
13 - Irkutsk Region
14 - Tyva Republic
15 - Buryatia Republic
16 - Chitta Region
17 - Amur Region
18 - Khabarovsk Territory
19 - Sakhalin Region
20 - Magadan Region
21 - Chukorka Autonomous District
22 - Koryak Autonomous District
23 - Kamchatka Region

Yakutia Republic) and the ethnic group of Selkups from the Baikha River (the Turukhan River basin).

Some small-scale but relatively stable reindeer herding remains in the western part of Russia on the Kola Peninsula. It is sustained by Kola Sami (77 000 semi-domesticated reindeer in 1997). By 1980 taiga reindeer herding disappeared in the Karelian Republic.

In the vast taiga areas of West Siberia where the Khanty and Mansi peoples engaged in reindeer herding only small isolated herding areas remain in what used to be a large well-organised herding zone. Only 34 000 semi-domesticated reindeer are now (1998) left in the vast Khanty-Mansi Autonomous District. Here the main reason for the decline in reindeer herding has been the intensive development of the gas and oil industry which has resulted in massive destruction of pastures, poaching, development of roads, pipelines and so on. The same factots have led to the deterioration of the traditional way of life among indigenous peoples on the taiga. By 1998 only 5000 reindeer were left in the vast Evenk Autonomous District in Central Siberia from what used to be a prominent region of taiga reindeer herding with 60 000 semi-domesticated reindeer in the 1930s; the remaining reindeer are scattered around the whole Autonomous District.

In mountain-taiga areas of South Siberia (Irkutsk Region, Chitta Region, Buryatia Republic, Tyva Republic) and in Sakhalin Region reindeer herding has almost disappeared. In each of these regions there are less than 3000 semi-domesticated reindeer left (Fig. 1).

The present-day situation and dynamics of wild reindeer populations in Russia

Wild and semi-domesticated reindeer both belong to the species *Rangifer tarandus* L. The biological difference between them is not great but it is nevertheless present. The semi-domesticated form of the species, in particular, is more accustomed to eating lichens which is a characteristic feature developed during in the process of domestication (Syroechkovskii, 1975; 1986). The diet of wild reindeer is much more diverse. Other differences exist in the behaviour, ecology and physiology of the two forms. Semi-domesticated reindeer in Siberia are apt to become wild and often tend to join migrating

Table 3. Population and distribution of wild reindeer in Russia (in thousands) 1961-1998.

	1961	1965	1970	1975	1976	1977	1978	1979	1980	1981	1982	1983	19
Altay Territory	-	0.1	0.1	-	-	1	-	-	1	0.4	0.4	0.4	0
Amur Region	2	2	2	-	-	8	-	-	8	4.15	3.17	3.2	2
Arkhangelsk Region	2.5	3.6	9.7	15.4	15.4	20	20	20	15	20	-	21	6
Buryat Republic	3	3	5	6.5	7	7	7	7	3.5	3.7	4	4	3
Chitta Region	-	5.6	6.7	6	6	5	5	5	5	7.5	7.2	7.2	7
Irkutsk Region	11	11	12.5	20	20	20	14.5	14.5	2	0	20	20	14
Kamchatka Region	-	5.5	8	7	6	5.5	5	5	4	7.3	4.9	5	4
Karelia Republic	1	3	1.1	7	8	3.5	6	4.8	5.3	6.6	5.8	7	5
Kemerovo Region	0.9	1	1	1	0.8	0.8	0.5	0.6	1	0.6	0.6	0.6	0
Khabarovsk Territory	5	10	10.5	11	11	13	13	5	17	11	17	17.5	17
Komi Republic	4	2	4.3	5	5.5	6	6	5.5	4	6.5	5.4	5.5	5
Krasnoyarsk Territory	103	120	340	540	543	521	500	543	480	523	565	570	575
Magadan Region	3.	3.5	3.5	3.5	4.5	14	14	15	8	16	16	11	11
Murmansk Region	7.5	10.5	22	6.4	1.5	1.5	1.5	1.3	1.2	2	1.85	2.2	2
Omsk Region	0.1	0.6	0.6	0.9	0.9	0.8	0.75	0.7	0.7	0.8	0.6	0.6	0
Perm' Region	0.4	0.4	0.6	0.22	0.5	0.6	0.55	0.55	-	0.25	0.02	-	-
Sakhalin Region	5	5	3	2.8	2.8	3	3	3	-	4.4	4.4	5	5
Sverdlovsk Region	-	1	1	-	1	-	-	1	1	1	1	1	0
Tomsk Region	7	3.5	0.7	2	2.5	2.5	2.5	1	1.8	2	1.5	5	4
Tyva Republic	0	6	2.5	3.5	3.5	3.5	4	4	4	4	4	4	4
Tyumen' Region	-	10	16	30	28	27.5	26	25	17	21.4	20	21	19
Yakutia Republic	30	100	160	170	170	170	260	170	220	170	170	240	250
Total	185.4	307.3	610.8	838.2	837.5	834.2	889.3	831.9	799.5	812.6	852.9	951.2	939

wild herds. The reverse process never occurs even though semi-domesticated reindeer originally appeared as a result of gradual domestication of wild forms. Specialists often mention Altay-Sayan, the Samoyedic (Nenets) area, as the region where reindeer herding originated. In my opinion, there were more likely to have been three such areas: the Altay-Sayan, the Baikal area and Scandinavia. This is confirmed by the location of ancient petroglyphs and other archaeological materials.

Wild and semi-domesticated reindeer are biological and ecological antagonists. The contradictions between wild and semi-domesticated reindeer are discussed in a considerable amount of scientific literature (Michel, 1938; Sdobnikov, 1933; 1939; Drury, 1949; Geller, 1969). This topic has been summarised in Syroechkovsky (1975; 1986 - for English versions see Syroechkovsky 1984; 1995). The general conclusion is that there is little possibility of the sympatric existence of wild and semi-domesticated reindeer. It is possible to reconcile the ecological contradictions only through geographically separating their home ranges, giving preference to either one or the other biological form in each specific territory. This is perfectly feasible on the vast territories of northern Russia.

The main contents of the problem of contradictions between wild and semi-domesticated reindeer have been formulated by Michel (1938):

1. the drawing away of semi-domesticated reindeer by wild reindeer;
2. the damaging the pastures by one biological form for the other;
3. the contributing to preservation of various reservoirs of infectious diseases for each other.

While the main factors affecting the changes in numbers of wild and semi-domesticated reindeer are of social and economic character, some biological factors play a role, in particular, the competition between wild and semi-domesticated reindeer on pastures. A typical example of that is the decline of the world's largest reindeer herding region in the Chukchi National District. This crisis was mainly caused by social and economic factors (above) but this resulted in the simultaneous desertion of pastures by both reindeer and people. Consequently, an ecological niche became vacant and the few wild reindeer that remained, and which had been protected by the state when almost extinct, began to increase quickly.

Nowadays (in 1998) the total population of wild reindeer in Russia is 1 246 000 (Figs. 3 and 4). This

1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
0.3	0.3	0.1	0.1	0.05	-	-	-	-	0.35	0.35	0.3	0.3	0.3
2	1.8	1.8	4	5	5	2.9	3	3	3.5	3	3.8	3.5	3.5
17	17	18	17	17	16	16	16	16	16	17	19	19	19.5
3.5	3.5	3	3	3	3.35	2.1	2.2	2.2	2.2	2.2	1.8	1.8	1.8
3	7.2	8.9	8.9	9	9.9	9.9	10	9.6	10	10	10	10	10
10.3	14	15	14	14	13.5	13	13.1	13	12	12	12	12	12
3	4.5	4.2	4	5	4.5	4.5	5.5	5.6	6	5	5	5	4.5
5	4.9	4.5	5.5	5.6	5.35	5.5	5.6	5	4.5	4	4	4	4
0.5	0.5	0.5	0.5	0.5	0.5	0.4	0.4	0.4	0.4	0.4	0.3	0.2	0.1
9.8	14.6	17.4	17	17	17	17	17	17	14	10	15	15	16
4	5.5	5.5	5.5	4.7	4,5	6.4	6	6	5.5	3	2	2	2
30	650	550	620	645	645	645	600	600	600	578	675	675	675
29	32	32	0	3	3	33	30	33	35	35	45	165	203
2.5	3.5	3	3	4	3	3.5	3.5	3.5	3.5	4	4	5	7
1	0.8	0.8	0.8	1	1	0.8	0.8	1	0.8	0.8	0.7	0.7	0.7
-	sol	sol	sol	sol	sol	sol	sol	sol	sol	sol	sol	sol	sol
4.2	4	3	2.5	2	2	2.1	2.1	2	2	2	4	4	4
0.4	0.4	0.3	0.2	0.1	0.1	0.05	0.05	0.05	-	-	-	-	
4	4.3	4	4	4	2.5	5.4	4.2	4.5	4.5	3	3	3	3
-	4	4	4	4	3	2	1	0.8	0.7	0.7	0.5	0.5	0.3
14	18.3	18	17.8	15	17	16.2	1	16	15.5	18	39.5	30	30
72	220	220	220	260	220	240	210	230	230	240	250	250	250
15.5	1011.1	914.0	951.8	1018.95	976.2	1025.75	931.45	968.65	966.45	948.45	1094.9	1206.0	1246.7

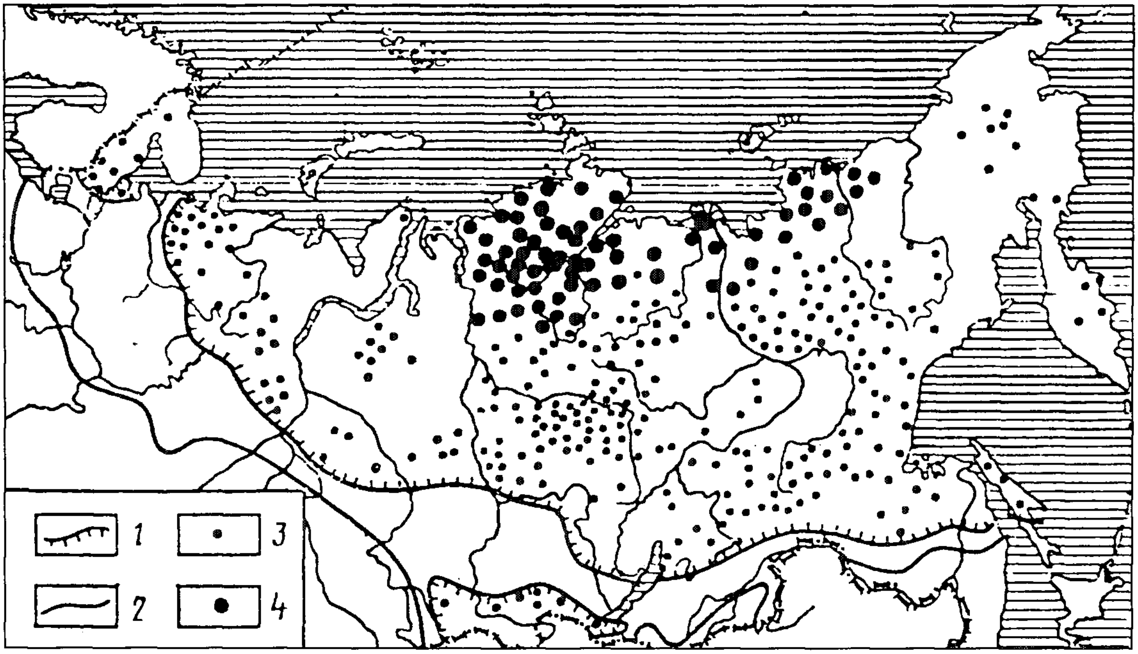

Fig. 4. Distribution of wild reindeer in the USSR, 1984: 1 - Boundary of contemporary range; 2 - Boundary of former range; 3 - 1000 reindeer; 4 - 10 000 reindeer. From Syroechkovski (1995).

is the largest total within the last 50 years, i.e. within the period when attempts were made to count the total number of wild reindeer in Russia (Table 3). It is quite possible that the present-day population has been underestimated a little because in recent yeats the number of wild reindeer has increased while census work has been much reduced.

The original population size of wild reindeer in northern Russia is unknown but according to estimates from the period when reindeer herding in Russia was still developing, i.e. in the 16th century, the total number of wild reindeer probably did not exceed 5 million. In the 20th century, the total number of both wild and semi-domesticated reindeer has never exceeded 3 400 000 (2.4 million semi-domesticated and 1 million wild reindeer) (Syroechkovskii, 1986).

According to my own estimates of the carrying capacity of reindeer pastures, it is probable that there were 5-7 million reindeer in Russia about 1000-2000 years ago before reindeer herding began. This is at least twice as many as the maximum population of both wild and semi-domesticated reindeer in the 20th century. My estimate is based (i) on the assumption that wild reindeer use pastures approximately twice as effectively as semi-domesticated reindeer and (ii) on analysis of 17th-18th century documents.

The geographic range of wild reindeer in Russia was characterised throughout most of the second half of the 20th century by the following features:

Most wild reindeet (about 85%) were concentrated in two large regions: in Taimyr and in northern Yakutia. The area of these two regions was not more than 15% of the total area occupied by wild reindeer in Russia. The distribution of the animals was continuous in these regions.

On the whole, the wild reindeer population area in Russia comprises tundta and forest-tundra zones the major part of the taiga and mountain-taiga areas in South Siberia. About 100-150 years ago the southern boundary of this area reached in the European part of Russia only 200-300 kilometres north of Moscow along the southern lower boundary of the taiga. In West Siberia, the southern boundary of this area went along the boundaries of taiga and forest-steppe. In East Siberia the zonal taiga part of this area stretched virtually down to the reindeer areas in the South Siberian mountains.

Already in the previous century, the range of wild reindeer lost its continuity within 85% of its territory (except Taimyr and northern Yakutia). Nowadays it has been broken down into numerous isolated areas which are becoming smaller and smaller. This process of insularisation is continuing. Simultaneously the general shape of the range is changing: in the European part of Russia and in West Siberia the southern boundary of the range has shifted far to the north. In Southern Siberia, a wide gap in the range has been formed around the trans-Siberian railway and adjacent territories where taiga has largely disappeared as a result of human influence.

In addition to the insularisation, areas of each separate population have become reduced in size and have even disappeared. On the whole, the number of wild reindeer has been decreasing in the major portion of the total range. A slight increase in the total number of wild reindeer in Russia can be accounted for by growth of the population in Taimyr and by the restoration of a large wild reindeer area in the Chukchi National District.

The Taimyr population of wild reindeer

At present the Taimyr wild reindeer population remains the largest in Russia and, maybe, in the world. In the last 20 years, the population has numbered about 500-600 000 reindeer. At present the aerial censusing of wild reindeer in the Taimyr population done previously by zoologists from Norilsk has virtually stopped. No accurate data are available. The population has probably increased to 700 000 animals.

Since 1971, this population has been exploited by a specially organised Taimyr State Hunting Economy which specialises in shooting wild reindeer. The population remained at a stable level despite intensive hunting of up to 60-80 000 reindeer a year. From 1971 to 1981 not less than 700 000 reindeer were shot in Taimyr and adjacent Evenkia and the western border of Yakutia whete Taimyr wild reindeer overwinter (Syroechkovskii, 1986). The reindeer were shot mainly for procuring meat for the city of Norilsk and other local populations. For a certain period reindeer were also shot for velvet antlers. These antlers were used for producing the medicament 'Rantarin' which is analogous to 'Pantocrin'. The boom for antlers was soon over mainly because of the flooding of the market and subsequent decline in ptices.

Wild reindeer from Taimyr are migratory. The distance between their calving places on the tundra and their overwintering places in the forest-tundra and northern taiga can be up to 1500 kilometres. A favourable factor for the growth of the Taimyr reindeer population was the absence of competition between wild and semi-domesticated reindeer. There were never more than 130 000 semi-domesticated reindeer husbandry on the Taimyr Peninsula even when numbers reached a peak in the 1960s. Reindeer herding on Taimyr has declined under pressure from wild reindeer, which draw semi-domesticated reindeer away, and various social influences. At present in the Taimyr Autonomous District there are only a few tens of thousands of semi-domesticated reindeer left, owned mainly by Nenets neat the western boundary of the District on the Yenisey's left bank. Reindeer herding in the central part of Taimyr has declined almost completely. The Dolgans have retained a small number of semi-domesticated reindeer. Nganasan reindeer herding has disappeared completely.

Ecological and economic control over wild reindeer on the Taimyr Peninsula has been lost in recent years. None but wolves and poachers hunt there now. These alone limit the population. Collapse is possible because of overgrazing. According to Kolpashchikov (1982) the carrying capacity of Taimyt is 820-850 000 reindeer. It cannot be excluded that epizootics, in particular anthrax, may spread there because in many places semi-domesticated reindeer which died of anthrax were buried, not burned. The infection can survive quite well in permafrost conditions and is capable of infecting animals many years later if the burial places are disturbed.

The Yakut population of wild reindeer

Many authors (e.g. Novikov, 1996) think that there are several populations in the Yakut Republic: the westernmost one is the Bulun population located in the Lena-Anabar interfluve (50-60 000 reindeer); there is the Yana-Indigirka population (116 000 teindeer); the easternmost one is the Sundrun population located west of the river Alazeya (20-25 000 reindeer). Thus, the total numbet of wild reindeer in Yakut tundra in the mid-1990s is about 200 000 animals. There are about 50 000 more wild reindeer scatteted in small isolated areas on the Yakut taiga. The above-mentioned Yakut tundra reindeer populations are actually remnants of an earlier geographically continuous tundra reindeer population that used to stretch from the River Anabar to the River Kolyma. Such was the situation in the 17th-18th centuries when there were not less than 600-

800 000 wild reindeer on the Yakut tundras (Syroechkovskii, 1986). In the 18th-19th centuries the largest North-Yakut wild reindeer herd which inhabited the lower reaches of the River Kolyma diminished gradually and by the 20th century it had virtually disappeared mainly because of the intensive development of Yakut and Even reindeer herding in this region.

The number of Yakut wild reindeer has grown a little in the last decades chiefly because of the decline of reindeer husbandry there. Yakut and Even reindeer herders think that the main reason for this decline was the leading away of semi-domesticated reindeer by wild reindeer. In my opinion, the principal causes were of social and economic character, including the break up of collective teindeer herding of the *kolkhoz* and *sovkhoz* type. However, both factors may have operated: the leading away of semi-domesticated reindeer by wild kindeer was probably enhanced by the decline of effective herding.

Today there are approximately equal numbers of wild and semi-domesticated reindeer on the Yakut tundra. Yakut reindeer herding is continuing to decline. In the 1970s-1980s there were about 360-380 000 semi-domesticated reindeer in Yakutia. Now the number is about 200 000. Yakut teindeer herding is also declining in the taiga zone but competition between wild and semi-domesticated reindeer is much more intense on the tundra. Thus, at present there are about half a million wild and semi-domesticated reindeer of the tundra and forest type in Yakutia. The pasture reserves here are big enough and cannot restrict the numerical growth of these populations.

The future is difficult to predict. It is difficult to stop the decline of reindeer herding even though reindeer herders do all they can to eliminate wild reindeer. They resort to poaching: they shoot pregnant female reindeer and shoot reindeer from helicopters. There are grounds to suppose that it will be possible to stop the decline of reindeer herding when the *kolkhoz-sovkhoz* reindeer herding has disintegrated completely and when private reindeer herding starts developing successfully. In some other parts of Russia this tendency is already quite clear - for example among the Nenets of the Yamal Peninsula and in the north of European Russia.

During the last decades, the main Russian regions inhabited by large wild reindeer herds were Taimyr and Yakutia Republic. But quite recently (in 1990-1998) a third large and quickly developing area of wild reindeer distribution has appeared in the Chukchi Autonomous District. The Chukchi Autonomous District used to be the largest area of large-scale reindeer herding and wild reindeer were almost completely ousted from this territory. In the 1970s-1980s, not more than 6-7000 wild reindeer remained there. These reindeer inhabited the central part of the Chukchi Autonomous Disttict in the area of the almost inaccessible lake Elgygytgyn. The prognoses for the preservation of that small reindeer population were negative because of poaching. There was a plan to register the population as almost extinct in the Red Data Book of Russia.

After the collapse of large-scale reindeer herding in the Chukchi Autonomous District, which started in the late 1980s, and after the abrupt decrease in the number of semi-domesticated reindeer (from over 700 000 in 1981 to about 200 000 in 1998-1999), the pasture ranges have been deserted and many people have left the tundra. As a result, very favourable conditions have developed for the increase and dispersal of wild reindeer. This has lead, in spite of a high rate of poaching, to the formation of a new, rapidly growing population of wild reindeer. In 1996 there were 40 000 reindeer there, in 1997 160 000, and in 1998 200 000. This trend is likely to continue.

Trends in semi-domesticated and wild reindeer in Russia

Reindeer herding

Up to now Russia has remained the country where about two thirds of the world's semi-domesticated reindeer exist. At present 13 aboriginal peoples in Northern Russia engage in reindeer herding. In the European part of Russia there are Sami, Nenets and Komi; in Siberia there are Nenets, Khanty, Mansi, Selkups, Evenks, Dolgans, Yakuts, Evens, Chukchi, Koryaks and Tuvinians. Five former reindeer herding peoples have given up reindeer herding: the Nganasans, Kets, Enetz, Yukagirs and Tofalars. Reindeer herding has declined among four peoples: the Selkups, Mansi, Dolgans and Tuvinians. It has declined significantly but less severely among the Komi, Sami, Khanty, Koryaks.

There is a tendency towards reduction of reindeer herding throughout the taiga zone, in particulat among the Evenks and Evens. Thus we can see a general negative trend in the development of reindeer herding in Russia. Nowhere in Russia reindeer herding has achieved the high standards of prosperity typical for Scandinavia and for Norway in particular. The strongest and most developed traditional reindeer herding can be found only with Nenets people in the Nenets Autonomous District and on the Yamal Peninsula. Quite recently Chukchi reindeer herding, which had been completely efficient, underwent a rather unexpected but explicable disintegration (see above).

It is difficult to predict the development of reindeer herding in Russia. Ten years have passed since the fall of the system of collective reindeer herding in northern Russia. That system was inefficient and unpromising for northern peoples because it undermined their traditional way of life on the tundra and the taiga resulting in the elimination of their cultures. We see signs of change for the better in the gradual restoration of private reindeer herding among peoples who have managed to retain their culture in reindeer herding. This applies first of all to the Nenets and to a certain extent to the Chukchi. There are good prospects for reindeer herding among all peoples who are numerous enough and who have conserved the basis of their traditional way of life. Such peoples include the Khants, Evenks, Evens, Yakuts, Sami and the Dolgans. Of coutse, with this purpose in mind the Russian state should create at least some minimum preconditions for restoring the reindeer herding.

Wild reindeer

The prognoses for the largest wild reindeer populations on the tundra and, in particular, for Taimyr and Yakutia are different. While the Taimyr reindeer herding tends to dwindle and the organised hunting for wild reindeer tends to diminish, the wild reindeer population will grow until it reaches its limit determined by the pastures when the laws of self-regulation will take effect. The Taimyr population should not be allowed to exceed 800 000 reindeer (maybe a little more). If that number is exceeded there may be increased danger of epizootics, in particular anthrax.

The prognosis for the Yakut tundra wild reindeer population is less clear. As long as semi-domesticated reindeer herding is preserved in the Yakutian Republic wild reindeer population will remain in the state of stagnation. If reindeer herding continues to decline in Yakutia, the wild reindeer population will expand there and have the same fate as wild reindeer on the Taimyr Peninsula. In any case, the numerical growth of large wild reindeer populations can be regulated through organised hunting which Russians are very experienced at.

Protection of wild reindeer in Russia

Wild reindeer are simultaneously hunted and protected in Russia. The large populations need rationalised exploitation. Such are reindeer populations in Taimyr and in northern Yakutia. Protection measutes for reindeer should consist in prevention of poaching and diseases and in observation of hunting rules and licensed hunting periods. A special service for the ecological control over each reindeer population should be established. The large and quickly growing Chukchi reindeer population should remain under strict control because not long ago it was nearly extinct. Today the three large populations number over 1 million reindeer.

The other vast areas occupied by this species in Russia are inhabited by only 200 000 wild reindeer. In total wild reindeer are spread over 24 regions of the Russian Federation (Table 3).

Out of these, three (Taimyr, Yakutia, the Chukchi area) have together over 1 million wild reindeer, while the other 21 regions of the Russian Federation have only a little over 200 000 wild reindeer. Of these other 21 regions, the chief ones are the Evenki area (60 000 reindeer) and the taiga zone of Yakutia (50 000 reindeer). In the latter two, the areas occupied by reindeer are not continuous but cover the major portion of the local territories. Here it is possible to hunt wild reindeer on a limited scale especially for supporting the economy of small northern indigenous peoples.

In other 20 regions there are few wild reindeer (Table 3, Fig. 4). Only seven regions have more than 10 000 animals (Archangelsk Region, Khanty-Mansi Autonomous District, Yamal-Nenets Autonomous District, Krasnoyarsk Territory, Irkutsk and Chitta Regions, Khabarovsk Territory). In the remaining 12 regions there are very few wild reindeer (from 500 reindeer in Tyva Republic to ≤ 3000 reindeer in seven regions (Nenets and Koryak Autonomous Districts, Komi and Buryatia Republics, Tomsk, Kamchatka and Magadan Regions) and to 3.5-7000 reindeer in the remaining five regions (Karelian Republic, Amur, Murmansk, Tyumen, Sakhalin Regions)).

Not included here are four regions of South Siberia (Altay-Sayan mountains) from which no data on the number of wild reindeer are available. These regions are Altay Republic, Khakassia

Republic, Altay Territory and Kemerovo Region. But we can most certainly say that in each of these regions there are not more than several hundred reindeer.

In all these 20 tegions hunting wild reindeer should be prohibited and measures should be taken for protecting and restoring the populations. In particular, special reserves or refuges should be organised. On the Russian Federal level a number of measures have been taken for protecting small wild reindeer populations. All small populations of mountain and taiga reindeer in Altay-Sayan mountains have been registered in the Red Data Book of Russia since 1998. On the islands of Novaya Zemlya there is a special wild reindeer population (*Rangifer tarandus pearsoni*) which might be a subspecies of wild reindeer. It numbers about 5-7000 and is listed in the Red Data Book of Russia.

One should mention specially arctic island populations of wild reindeer the largest of which is on the Novosibirsk islands (up to 6000 reindeer). It is not sufficient at all to include only two wild reindeer populations in the Red Data Book of Russia. This does not solve the problem of protecting rare populations of a species. The Red Data Book of Russia should include a considerable number of rare and disappearing populations both on the periphery of the species' distribution and inside it. This will contribute not only to preserving and restoring the species as such but also to conserving its genetic diversity.

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Aspects of the ecology of mat-forming lichens

P. D. Crittenden

School of Biological Sciences, University of Nottingham, Nottingham NG7 2RD, UK
(Peter.Crittenden@nottingham.ac.uk).

Abstract: Lichen species in the genera *Cladonia* (subgenus *Cladina*), *Cetraria, Stereocaulon* and *Alectoria* are important vegetation components on well-drained terrain and on elevated micro-sites in peatlands in boreal-Arctic regions. These lichens often form closed mats, the component thalli in which grow vertically upwards at the apices and die off in the older basal regions; they are therefore only loosely attached to the underlying soil. This growth habit is relatively unusual in lichens being found in <0.5% of known species. It might facilitate internal nutrient recycling and higher growth rates and, together with the production of allelochemicals, it might underlie the considerable ecological success of mat-forming lichens; experiments to critically assess the importance of these processes are required. Mat-forming lichens can constitute in excess of 60% of the winter food intake of caribou and reindeer. Accordingly there is a pressing need for data on lichen growth rates, measured as mass increment, in order to help determine the carrying capacity of winter ranges for these herbivores and to better predict recovery rates following grazing. Trampling during the snow-free season fragments lichen thalli; mat-forming lichens regenerate very successfully from thallus fragments provided trampling does not re-occur. Frequent recurrence of trampling creates disturbed habitats from which lichens will rapidly become eliminated consistent with J.P. Grime's CSR strategy theory. Such damage to lichen ground cover has occurred where reindeer or caribou are unable to migrate away from their winter range such as on small islands or where political boundaries have been fenced; it can also occur on summer range that contains a significant lichen component and on winter range where numbers of migratory animals become excessive. Species of *Stereocaulon,* and other genera that contain cyanobacteria (most notably *Peltigera* and *Nephroma*), are among the principal agents of nitrogen fixation in boreal-arctic regions. *Stereocaulon*-dominated subarctic woodlands provide excellent model systems in which to investigate the role of lichens in nitrogen cycling. Mat-forming lichens are sensitive indicators of atmospheric deposition partly because they occur in open situations in which they intercept precipitation and particulates directly with minimal modification by vascular plant overstoreys. Data from both the UK and northern Russia are presented to illustrate geographical relationships between lichen chemistry and atmospheric deposition of nitrogen and acidity. The ecology of mat-forming lichens remains under-researched and good opportunities exist for making significant contributions to this field including areas that relate directly to the management of arctic ungulates.

Key words: acid rain, allelopathy, grazing, growth, lichens, nitrogen fixation, recycling, trampling.

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Introduction

That lichens are eaten by reindeer and caribou is one of the better known facts about lichens amongst lay people of mid latitudes. It is also quite widely understood that lichens are symbiotic organisms and not plants in the strict sense. Although they are primary producers, and frequently have dimensions of small vascular plants, they are in fact composed of fungi deriving nutrition (carbon and sometimes nitrogen) from unicellular or filamentous algae and/or cyanobacteria in mutualistic symbiotic associations. Accordingly, it is strictly inappropriate to refer to lichens as organisms but for the sake of brevity it is often convenient to do so. Lichen-forming fungi constitute about one fifth of the fungal kingdom (Hawksworth *et al.,* 1995) and there is evidence that lichens represent an ancient association that was present amongst terrestrial crust communities during the early to mid Paleozoic Era (Shear, 1991; Taylor *et al.,* 1995). Yet because of

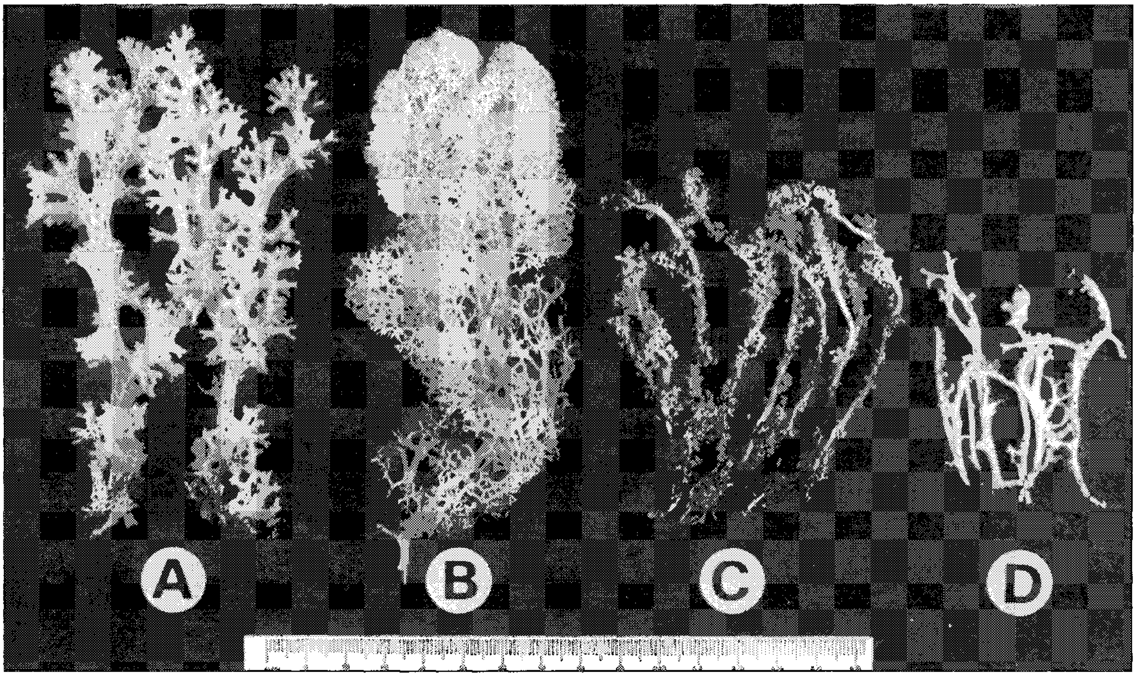

Fig. 1. Examples of mat-forming lichens. a) *Cladia retipora* (Australasia), b) *Cladonia stellaris,* c) *Stereocaulon paschale* and d) *Cetraria cucullata* (boreal-arctic zone). *Cladia retipora* occurs in coastal and alpine heathlands in Australasia. *Cladonia stellaris* is the supreme example of a mat-forming lichen and possibly one of the world's most abundant fungi; species that are morphologically similar to *C. stellaris* occur in the Southern Hemisphere e.g. *C. pycnoclada, C. leptoclada* and *C. confusa,* which locally form extensive ground cover.

their minor economic importance the biology of lichens remains poorly understood in comparison to the other principal types of terrestrial mutualistic "plant" symbioses (i.e. mycorrhizas and legumes/actinorrhizas).

Lichens grow on substrata that are deficient in nitrogen and phosphorus, and that are subject to frequent episodes of acute drought. Such substrata are relatively abundant in boreal-arctic regions. In particular, the pootly developed to skeletal soils typical of high latitudes frequently support lichen-rich ground cover. According to Larson (1987) lichen-dominated vegetation covers approximately 8% of the world's terrestrial surface and much of this is in the Subarctic and Arctic. However, factors that control the development of lichen-dominated terrain remain incompletely understood. Such vegetation appears to be largely restricted to well-drained surfaces, including elevated microsites in peat bogs (Kershaw, 1977; Foster & Glaser, 1986; Ahti & Oksanen, 1990); these are sites in which vascular plant vigour is reduced due to low soil fertility and/or that are at an early successional stage following fire. Precipitation does not appear to determine the frequency of lichen-dominated terrain; for example, lichen woodland is abundant in both north-central Canada (*c.* 300 mm annual precipitation) and Labrador (*c.* 800 mm) although the relative importance of particular lichen species may differ (Kershaw, 1977). The most ecologically successful terricolous lichens are mat-forming species of the genera *Cladonia* (subgenus *Cladina*), *Cetraria, Stereocaulon,* and *Alectoria* (Fig. 1). Certain key species in these genera can form extensive ground cover in subarctic lichen woodland, forest tundra and tundra heathlands. They form the principal component of lichen intake by reindeer and caribou on their winter ranges (e.g. Miller, 1976; Holleman & Luick, 1977; Boertje, 1990), although epiphytic species are also important in the diet of some populations (e.g. Rominger *et al.*, 1994). This review focuses on aspects of the ecology of mat-forming lichens.

The mat-forming habit

Mat-forming lichens grow acropetally (i.e. at their apices) and vertically upwards while in mature mats the thallus bases die off. Thus the upper living parts of the mats are often supported physically by a deep layer of dead, structurally intact, thallus or necromass. This growth habit is relatively unusual in lichens being found in <0.5% of the 13 500 known species; the vast majority of lichens are firmly attached to their substrata. Precipitation and dry deposition of dust particles and gases are believed to be the primary sources of N and P for lichen growth. Thus in deep mats, zones of depletion develop in the lower strata due to interception of light and nutrients by the surface layers. Several authors have discussed the horizontal stratification of microclimate and thallus morphology that occurs within lichen mats (Carstaits & Oechel, 1978; Lechowicz, 1983; Pakarinen, 1985; Sveinbjörnsson, 1987; Coxson & Lancaster, 1989; Crittenden, 1991). Thallus below the light compensation depth (i.e. the depth at which photosynthetic CO_2 assimilation equals respiratory loss of CO_2) represents a respiratory burden and is therefore expendable. In the northern hemisphere, *Cladonia stellaris* is the supreme example of a mat-forming lichen.

Lichens, being essentially fungal mycelia, are poikilohydric, i.e. their water status is coupled to that of the atmosphere. Under the influence of evaporative forces lichens lose water becoming dry and largely metabolically inactive. A widely held view is that lichens are C-limited because photosynthetic activity is restricted to intermittent periods of adequate water availability. However, there is evidence that the more productive mat-forming lichens are N and/or P limited (Crittenden *et al.*, 1994). Several of the above authors have suggested that N and P in senescing basal parts of lichen thalli might be remobilized and translocated to the growing apices. Such internal recycling would be ecologically advantageous because it would permit a higher growth rate at the apices than could be sustained by new atmospheric supplies alone. This, in turn, would result in a higher rate of necromass production and deeper mats with the capacity to cast deep shade. In vascular plant ecology the development of a tall closed canopy is a mechanism by which some plant species exclude potential competitors and exert dominance (Grime, 1979). The capacity to recycle nutrients, which would be dependent on the loss of attachment between living thallus and the substratum, might underlie the ecological success of mat-forming lichens.

There is conflicting information on the occurrence of viable seed banks beneath lichen ground cover. Johnson (1975) failed to find germinable seeds in spruce-lichen woodland soils in the Northwest Territories in Canada whereas I have found abundant viable seeds beneath mats of *Cladonia stellaris* and *Stereocaulon paschale* in Finnmarksvidda in Norway. It is probable that seeds that descend to the bottom of mats will suffer light-deprivation sufficient to inhibit either germination or seedling growth (Kershaw, 1977) while Allen (1929) described seedlings in lichen mats being uprooted or damaged by the expansion of dry mats upon rehydration. Thus vascular plant species reproducing by small seeds may be excluded from well-developed lichen mats. However, studies in Sweden (Steijlen *et al.,* 1995; Zackrisson *et al.*, 1995) have shown that *Cladonia*-dominated ground cover in coniferous forests is a more favourable environment for the establishment and survival of spruce and pine seedlings than vegetation dominated by either *Empetrum hermaphroditum* or *Pleurozium schreberi.* Germination of pine and spruce seeds is not completely suppressed by light deprivation (Sarvas, 1950) and it is possible that a larger seed size might sustain the growth of pine and spruce seedlings through the lichen canopy into the 'photic' zone. However, Cowles (1982) found the centres of deep lichen cushions to be formidable barriers to the establishment of spruce in lichen woodland in northern Quebec whereas, in contrast, polygonal cracks that form in desiccated mats were favourable sites for establishment.

Allelopathic activity

Lichens produce a diverse range of secondary chemical products, many of them phenolic derivatives, and most being unique to lichens (Fahselt, 1994). Such products probably have several functions in the lichen thallus. Since many have antimicrobial properties, and/or are effective in deterring potential herbivores, it seems reasonable to suggest that one of their functions is chemical defence of the thallus (Lawrey, 1986, 1989). The yellow compound usnic acid is one of the more potent lichen products in terms of antimicrobial activity and is produced commercially as a pharmaceutical (Vartia, 1973); it occurs in a large number of lichen genera and is a typical compound for the subgenus *Cladina*; for example, it contributes about 2% of the dry mass of *C. stellaris* (Huovinen & Ahti, 1986). Although most lichen secondary products are only sparingly soluble in water, it has been suggested that trace quantities released into the soil from healthy thalli during rainfall, and from decomposing thalli, might inhibit the growth of neighboring vascular plants. Species of *Cladonia* (subgenus *Cladina*) have been reported to retard growth and mycorrhizal development in boreal forest trees (Brown & Mikola, 1974; Fisher, 1979). This is an attractive idea because such allelopathic effects provide yet another mechanism by which a plant can reduce the growth rate of its neighbours and exert dominance. However, despite a sizeable literature on this topic (reviewed by Lawrey, 1984; 1986) the importance of allelopathy in the ecological success of mat-forming lichens still remains to be critically assessed.

There are several potential pitfalls in experiments designed to test for allelopathic interactions between plants (Harper, 1975; Qasem & Hill, 1989). One of these is that quantities of metabolites to which test plants are exposed can greatly exceed those occurring in nature so that reported toxic effects can be exaggerated, if not entirely a product of the experimental conditions. Thus lichen extracts prepared using organic solvents (e.g. Goldner *et al.*, 1986) or by homogenizing thalli in water (e.g. Brown & Mikola, 1974; Kaitera *et al.*, 1996) may contain ecologically improbable concentrations of metabolites. Cowles (1982) conducted a field experiment in northern Quebec, that has been frequently cited in the literature, to investigate the effects of lichens on the growth of spruce. He removed lichen ground cover from plots in lichen woodland and found that this had a negative effect on the growth of black spruce as indicated by a reduction in the rate of branch elongation. This negative effect might have resulted from enhanced evapotranspiration since it could be counteracted by covering lichen-free plots with polyethylene sheet. Cowles also investigated the potential role of lichen allelopathy by soaking lichen mats in barrels of water for 24 h and then applying the filtrate to lichen-free plots covered with polyethylene sheet to compensate for the lost insulating effect of the lichens. This procedure was repeated daily during the snow-free seasons for 4 y and resulted in a negative growth response of broadly similar magnitude to the positive effect of lichen cover. However, the author does not indicate the frequency with which lichen in the barrels was renewed during the experiment; water that has passed through a dense mass of dead, and possibly fermenting, lichen is likely to differ markedly in chemical composition from rainfall that has percolated through a living lichen stand. It should also be remembered that lichens are not the only producers of allelochemicals in these ecosystems: evidence suggests that ericaceous shrubs (Pellissier, 1993; Nilsson *et al.*, 1993; Inderjit & Mallik, 1997; Yamasaki *et al.*, 1998) and feather mosses (Steijlen *et al.*, 1995) also produce phytotoxins that inhibit the establishment and/or growth of trees (see discussion of seed banks above).

P. D. Crittenden and R. P. Beckett (unpubl.) investigated the effects of lichen-modified rainwater on mycorrhizal development and growth in the cultivated cranberry (*Vaccinium macrocarpon*) grown in sand-solution culture. Mats of *Cladonia stellaris* and *Stereocaulon paschale* were reconstructed on stainless steel grilles superimposed over rain gauges in lichen-rich birch woodland at Kevo, northern Finland, following the method of Crittenden (1983). Water that percolated through the mats during natural rainfall events was collected quantitatively, filtered to pass 0.22 µm and applied in 5 ml aliquots to the surface of the sand surrounding each *Vaccinium* plant; these additions were repeated at intervals of several hours until all water that had been collected during a rainfall event was exhausted. Control plants received either unmodified rainfall or deionized water, and the *Vaccinium* was grown either in the mycorrhizal (inoculated with the fungus *Hymenoscyphus ericaea* [Smith & Read, 1997]) or non-mycorrhizal states and under either low or high nitrogen regimes (2.7 or 27 parts N/10^6, respectively, in applied nutrient solutions). The only statistically significant effect of lichen-modified rainwater during a three month gtowth period was an *increase* in the extent of mycorrhizal infection in the low nitrogen treatment (Fig. 2). In this experiment the quantities of lichen products added to the experimental plants were probably ecologically relevant. The two lichen species supported over the replicate rain guages appeared to remain in a healthy state: they increased in dry mass during the experiment and did not release K^+ into the percolating rain water, indicating cell membrane integrity (see Buck & Brown, 1979; Tarhanen *et al.*, 1996). The promotion of ericoid mycorrhizal development may have been due to utilization by the mycorrhizal fungus of exogenous organic carbon present in the lichen-modified rainfall thus promoting more effective colonization of the thizosphere prior to establishing infection points. It is debatable whether this effect would be evident in podzolic soils containing abundant soluble organic compounds. Nonetheless,

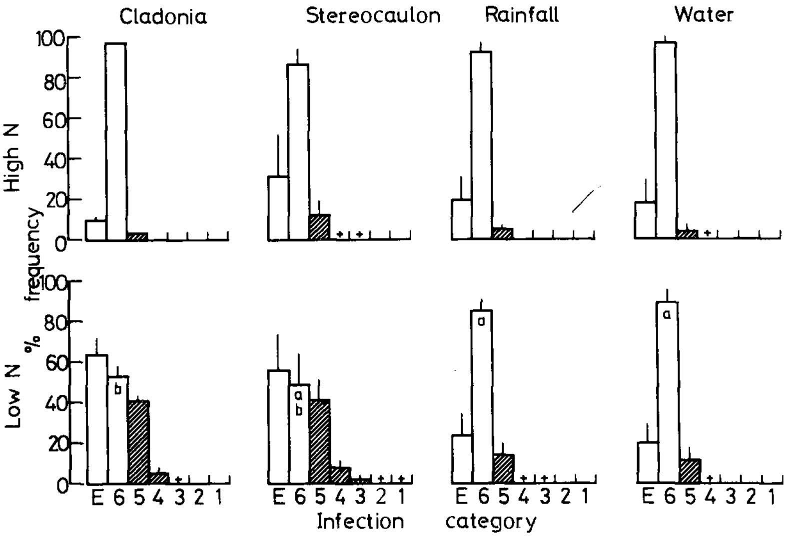

Fig. 2. The effect of lichens on mycorrhizal infection in the cultivated cranberry (*Vaccinium macrocarpon*). Plants were watered with lichen-modified rainwater (*Cladonia*, or *Stereocaulon*), unmodified rainwater or deionized water, and harvested at 107 days from planting. Plants in the low N treatment received 2.7 parts/ 10^6 NH_4^+-N in nutrient solution, high N plants received 27 parts/ 10^6 NH_4^+-N. Root subsamples were stained in cotton and lactophenol and scanned with a light microscope at a magnification of x 200, each field of view being assessed for mycorrhizal infection according to the scale of Read and Stribley (1975): category 1, 98-100% of cortical cells infected; category 2, 75-98% infected; category 3, 50-75% infected; category 4, 25-50% infected; category 5, 0-25% infected; category 6, no infection. The frequency of fields of view in which extramatricullar hyphae were visible (E) was also noted. (Number of fields of view per sample ranged between 228-985; mean values [n = 3] are plotted with 1 standard error; + = ≤ 2%). Frequencies of category 6 infection level with the same letter are not significantly different ($P>0.05$, ANOVAR and Duncan's multiple range test). The combined frequency of category 6 infection level for low N plants receiving lichen leachates was significantly lower ($P<0.05$) than for low N plants receiving rainfall or water.

the results do not support the popular belief that lichens inhibit mycorrhizal development. My own observations in lichen woodland are that shrubs and trees rooting beneath lichen mats have well-developed mycorrhizal associations.

Co-existence with vascular plants

Terricolous lichens grow on oligotrophic sandy or podzolic soils on at least moderately well-drained terrain. Vascular plants adapted to these conditions have low growth rates (Grime, 1979) and have the capacity to absorb simple and complex organic forms of nitrogen either directly (Kielland, 1994; Schimel & Chapin, 1996) or via mycorrhizal associations (Smith & Read, 1997; Näsholm *et al.*, 1998), thus largely by-passing the need for microbiologically-driven mineralization processes. Vascular plants show plasticity in their root/shoot ratio and typically develop larger root systems in nutrient deficient soils (e.g. Chapin, 1980; Tilman & Wedin,1991) increasing the carbon cost of mineral nutrient recovery. Clearly, with increasing nutrient scarcity there is a limit to how "rooty" a plant can become given the increased respiratory cost of expanding below-ground biomass. As this limit is approached and plant vigour declines, a point will be reached at which productive terricolous mat-forming lichens can co-exist with vascular plants (cf. Manseau *et al.*, 1996).

Lichens do not have root systems and are probably almost entirely dependent on atmospheric deposition for supplies of N and P (Crittenden *et al.*, 1994). The seasonal intake of these elements by lichens may be substantially less than their vascular plant neighbours but the carbon cost of this acquisition is probably small in comparison. Thus the growth rates of above-ground phytomass in lichens and vascular plants could be similar or, in extremely nutrient poor soils, greater in lichens. Being rootless, lichens are largely uncoupled from soil water and thus must tolerate periods of desiccation during which metabolic activity is minimal. Lichen ecophysiologists tend to view desiccation negatively since it is believed that this limits lichen growth rates. In addition, there is evidence that rewetting of lichen thalli (e.g. during the onset of rainfall) is itself associated with a carbon cost (e.g. Lechowicz, 1981; Dudley & Lechowicz, 1987). However, because precipitation is one of the major processes that delivers nutrients to lichens, periods of desiccation between infrequent precipitation events might decrease the carbon cost of nutrient capture. However, fertilization of these oligotrophic communities can increase plant growth rates and result in the competitive exclusion of lichens (e.g. Persson, 1981; Jonasson, 1992). It is quite common in the Subarctic for well-drained terrain to experience acute summer droughts that could be lethal to fine roots of trees and dwarf shrubs which develop close to the soil surface. Thus, in addition to paucity of soil mineral nutrients, periodic drought may also be a significant factor suppressing vascular plant vigour and promoting the development of lichen ground cover.

Lichen growth and the impact of trampling and grazing

Terricolous lichens typically constitute in excess of 60% of the winter food intake by reindeer and caribou (Miller, 1976; Boertje, 1990). Lichen consumption declines markedly during the summer months when graminoids and dwarf shrubs comprise the major food items. Crête *et al.* (1990) estimated that the average lichen biomass on the winter range of the Rivière George caribou herd (*c.* 680 000 individuals in 1988) in northern Quebec averaged 1223 kg ha^{-1} and that in 1987 0.5-0.9% of this was consumed annually. The significance of this consumption is dependent on lichen productivity; unfortunately, as the authors point out, appropriate data on lichen growth are largely lacking. Sveinbjörnsson (1990) has discussed some of the approaches available for measuring lichen growth rate: these range from morphological analyses (that to my knowledge have nevet been critically evaluated) to simulation modelling based on net CO_2-exchange measurements. Probably the best method, and possibly the only method that should be considered for long-term productivity determination, is the measurement of mass increment (Jónsdóttir *et al.*, 1998). Few investigators have measured mass-increment in lichens and only Kärenlampi (1971), Hooker (1980), Crittenden (1983, 1989; summarized in Crittenden *et al.*, 1994) and Hyvärinen & Crittenden (1998a) have done so for mat-forming lichens. The method suffers from the criticism that lichen thalli must be detached from the ground (or underlying necromass) in order to make the initial (time zero) weighing. The effect of such detachment has not been fully investigated.

In northern Finland, thalli of *Cladonia stellaris* and *Stereocaulon paschale* that were pre-weighed and inserted into reconstructed lichen mats increased in dry mass by at least 26% pet year (Crittenden *et al.*, 1994). This equates with a mean relative growrh rate (RGR) of *c.* 0.004 mg mg^{-1} d^{-1}, a value that compares favourably with those recorded by Kärenlampi (1971) for the same species using a similar method. However, Kärenlampi showed that in wet years RGR for *C. stellaris* could rise to 0.005-0.01 d^{-1}. It is instructive to compare these lichen RGR values with those for vascular plants. Grime & Hunt (1975) measured the RGR of plant species in the local flora of the Sheffield region in the UK under optimum conditions of temperature and supplies of light, water and nutrients. Of the 132 species screened *Urtica dioica* was found to have the highest mean RGR of 0.3 d^{-1} and *Vaccinium vitis-idaea*, a species that frequently co-occurs with mat-forming lichens in the boreal-Arctic, had the lowest value of 0.03 d^{-1}. When *V. vitis-idaea* was grown in organic top-soil collected from beneath *C. stellaris* mats in Finnmarksvidda, Norway, but otherwise under favourable conditions of light, temperature and water supply, mean RGR values of 0.016 d^{-1} were observed (Crittenden, 1989). Thus, under harsher field conditions (e.g. exposute to periodic summer drought, lower temperatures) it is not improbable that RGR of *V. vitis-idaea* would approach that of *C. stellaris* consistent with the co-existence of the two species. The measured growth rates for *C. stellaris* and *S. paschale* are in broad general agreement with the observation that recovery of *C. stellaris* ground cover that is harvested by man for ornamental purposes in northern Finland takes 5-6 years (Søchting, 1984). Virtala (1992) estimated that lichen biomass in overgrazed lichen woodland in Fennoscandia could recover from 300 kg ha^{-1} to 1000 kg ha^{-1} in about 9 years, and to 2000 kg ha^{-1} in 16 years.

Mat-forming lichens are relatively loosely attached to the ground. I have argued above that this loss of firm attachment to the substratum may have permitted an increased productivity in those species adopting this growth habit. Lichen species that form deep mats (e.g. *C. stellaris, C. mitis, S. paschale*) are generally restricted to sheltered sites experiencing comparatively low wind speeds: these are woodlands and low arctic tundra sites with at least moderate winter snow cover (Larson & Kershaw, 1975; Larsen, 1980). The extent to which the distribution of these species is linked to snow depth, and whether this link is causal, is not known. In contrast, other species such as *Cetraria nivalis* and *Alectoria ochroleuca* frequently occur on exposed sites experiencing minimal winter snow cover (Larson & Kershaw, 1975; Petzold & Mulhern, 1987; Ahti & Oksanen, 1990). Lichens beneath deep snow are afforded protection against trampling by reindeer and caribou herds on their winter ranges (Miller, 1976). In order to graze terricolous lichens the animals excavate craters in the snow. This causes mechanical damage to mats ovet and above the loss due to consumption; estimates of this wastage range between to 2 - 10 times the lichen mass ingested (Virtala, 1992). Kauppi (1990) has shown that in middle Finland *C. stellaris*-dominated lichen mats that become covered with debris, such as conifer needles and bark fragments, can fully recover in 3-8 years; comparable disturbance effects might occur due to deposition of faeces and mat-fragments in areas where caribou and reindeer have cratered intensively (Miller, 1976).

In summer, dry lichen mats are destroyed rapidly by trampling (cf. Bayfield, Urquhart & Cooper, 1981). In the case of migratory herds such damage may be largely confined to migration routes (Boertje, 1990) or to summer ranges where these have a significant lichen component. For example, Manseau *et al.* (1996) have reported marked depletion of lichens in tundra used by migratory caribou as summer range in northern Quebec. My own observations in shrub tundra between Votkuta and the Polar Ural Mountains in Russia suggest that reindeer herding has largely eliminated mat-forming lichens from the ground cover in this region. Here, *Cladonia arbuscular* can be found in most 1 m^2 quadrats randomly located on well-drained terrain but usually only in trace quantities, possibly indicating that efficient foraging is as least as important as trampling; Moser, Nash & Thompson (1979) made a similar observation in Alaskan tundta. According to Ahti & Oksanen (1990) and Vilchek (1997), depletion of lichen cover in tundra due to reindeer herding is widespread in Russia.

Severe degradation of winter range owing to summer trampling can also occur where migratory movements are prevented by artificial barriers at political boundaries or by the stocking of small islands (Anon, 1974; Oksanen, 1978; Swanson & Barker, 1992; Väre *et al.,* 1996). Deterioration of winter range in northern Finland, a result primarily of summer-time trampling, is particularly marked and on a scale that is evident in satellite images (Käyhkö & Pellikka, 1994; Väre *et al.,* 1996). Where numbers of migratory animals exceed the range carrying capacity then excessive winter-time foraging can also lead to depletion of the lichen resource. Such a situation has been described for caribou in northern Quebec (Arseneault *et al.,* 1997) and Alaska (Moser, Nash & Thompson; 1979), and for reindeeer in Finnmarksvidda (E. Gaare, pers. comm.; Kashulina *et al.,* 1997) and Russia (Vilchek, 1997).

Mat-forming lichens appeat to regenerate well following fragmentation. This is exemplified by lichen monocultures established at the Kevo Subarctic Research Station in northern Finland by P. Kallio in 1971. Kallio cleared vegetation from 1 m x 1 m plots on the floor of an open stand of Scots pine and then spread 200 g crushed thalli of a single lichen species into each. Monocultures of *Cl. stellaris, Cl. rangiferina, Ce. nivalis* and *S. paschale* had developed by 1978 and in 1998 most species were present as luxurious mats. Many lichen-forming fungi in the genera *Cladonia* and *Stereocaulon* can be readily isolated into pure culture by plating small (60-200 μm long) alga-free fragments of macerated thallus onto agar (Crittenden *et al.,* 1995) and this may also be indicative of the importance of fragmentation as a means of dispersal and regeneration in these important lichen genera.

Kallio's lichen plots demonstrate that mat-forming lichens can regenerate following a massive disturbance if subsequently left undisturbed but where disturbance recurs frequently lichens will not recover. The reason for this is succinctly explained by Grime's (1979) CSR strategy theory which states that no plant strategy has evolved that can facilitate survival in habitats that are subject to high levels of both stress and disturbance. Since mat-forming lichens are supremely good tolerators of environmental stress then, in accordance with Grime, they must also be intolerant of frequent disturbance. Thus lichens are rapidly eliminated from summer range by repeated trampling and will only recover if ungulate numbers are reduced (cf. Virtala, 1992).

Nitrogen fixation

Lichens that contain a cyanobacterium fix nitrogen. An important finding of the International Biological Programme's Tundra Biome investigations was that cyanobacterial lichens (principally of the genera *Peltigera, Stereocaulon* and *Nephroma*) are among the major agents of nitrogen fixation in the

Subarctic and Arctic (Stewart, 1976). There has been a sufficiently large number of studies of nitrogenase activity in lichens to provide a relatively good understanding of which genera and species are the most active fixers (e.g. *Peltigera* spp.) and how rates of nitrogenase activity are controlled by environmental factors such as thallus water content, temperature and incident light (Kershaw, 1985).

But what is the ecological significance of nitrogen fixation by lichens? There have been several attempts to produce annual rates of N input by lichens in both northern boreal forests (Billington & Alexander, 1983) and tundra habitats (Gunther, 1989; Getsen *et al.,* 1997). However, almost invariably these estimates have been derived from the results of the acetylene reduction assay, an analogue enzymatic reaction which, at best, only gives an approximate measute of absolute nitrogen fixation rates. Where feasible, annual rates of nitrogen fixation can probably be more appropriately obtained from the product of growth (as mass increment - see above) and thallus nitrogen concentration but as yet such calculations have not been made [with the exception of Crittenden (1989)]. Further, estimates of N input by lichens have not been placed in context with other N fluxes in the ecosystems under study. Larsen (1980) constructed a schematic N cycle for the boreal forest which incorporated an estimate of nitrogen fixation for *S. paschale* derived from acetylene reduction data of Crittenden & Kershaw (1979). This suggested that nitrogen fixation by this species ≤20 kg ha^{-1} y^{-1}) could potentially provide much of the annual N requirement ofi vascular plants (10-40 kg ha^{-1} y^{-1}) in upland spruce forest. *Stereocaulon paschale* is an active nitrogen fixer that has the potential to form extensive, almost monospecific, groundcover in lichen-woodlands. Such ecosystems are abundant in notth-centtal Canada (Kershaw, 1977) and parts of Russia (Lavrenko & Sochava, 1956; Karev, 1961) and will make excellent model systems in which to investigate some key questions that to date remain unexplored. For example, by which pathways and in what quantities does N_2 fixed by lichens reach vascular plants? Does the presence of N_2-fixing lichens influence rooting patterns, and promote the growth, of shrubs and trees? These questions have a direct bearing on the primary productivity of lichen-rich ecosystems. Moreover, N_2-fixing lichens are particularly sensitive to air pollution (e.g. Hallingbäck & Kellner, 1992) giving added significance to these questions. Species of *Peltigera* and *Nephroma* ate likely to be among the first lichens to be eliminated from subarctic areas affected by acid rain and there is a pressing need to better understand their ecological role.

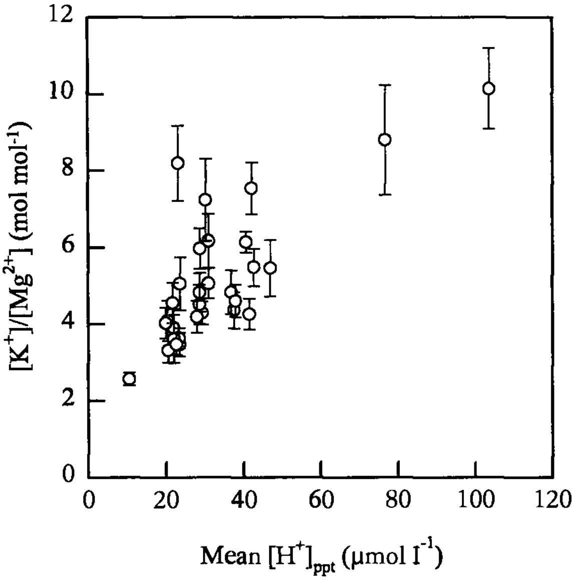

Fig. 3. The relationship between mean values (with ±1 standard error) of the ratio $[K^+]$:$[Mg^{2+}]$ (n=5-10) in the apices of *Cladonia portentosa* and hydrogen ion concentration in precipiration ($[H^+]_{ppt}$) at 31 sites in the British Isles.

Response to pollution

Lichens are renowned for their ability to accumulate pollutants and for their usefulness as indicators of pollution loads. Perhaps of most significance for reindeer and caribou production is the capacity for lichens to intercept and accumulate radionuclides in atmospheric deposits (Nevstrueva *et al.,* 1967; Taylor *et al.*, 1988; Feige *et al.*, 1990; Baskaran *et al.*, 1991; Strandberg, 1997). The food chain concentrating effect has been implicated as the cause of an increased incidence of cancer among some native peoples in the Arctic (Crittenden, 1995).

There is now growing interest in the impact of acid rain in northern latitudes. Acid rain contains elevated concentrations of both acidity and N, principally as nitrate. The concentration of NO_3^- in precipitation has steadily increased in northern latitudes during the past century (Brimblecombe & Stedman, 1982; Rodhe & Rood, 1986; Fischer *et al.*, 1998). Recent studies have shown mat-forming lichens to be sensitive indicators of N and acid deposition. Using *Cladonia portentosa* in British

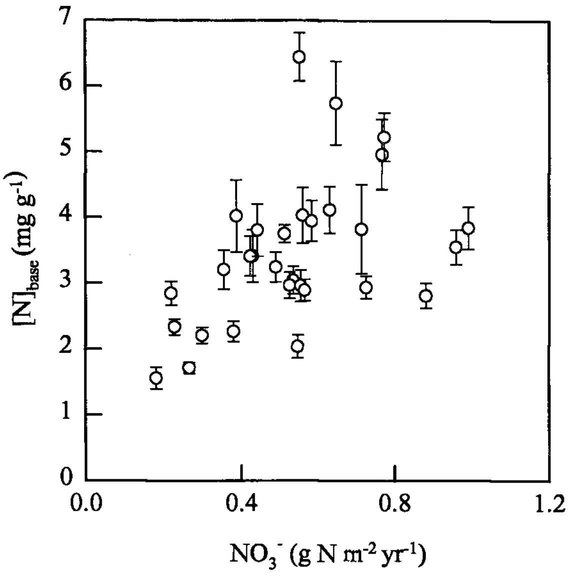

Fig. 4. The relationship between mean values (with ±1 standard error) of total nitrogen concentration (n=5-10) in a horizontal stratum of *Cladonia portentosa* between 40-50 mm from the thallus apices ($[N]_{base}$) and wet deposition of NO_3^- as a function of total N deposition.

heathlands as a model system, Hyvärinen & Crittenden (1996; 1998b) showed that the ratio $K^+ : Mg^{2+}$ in the thallus apices was highly correlated with H^+ concentration in precipitation (Fig. 3), and that thallus N concentration was related to total N deposition (Fig. 4). While a preliminary study could not find any evidence that the growth of *C. portentosa* was impaired by acid rain (Hyvärinen & Crittenden, 1998a) it was often absent from eutrophicated heathlands. This is probably owing to competitive exclusion by mosses and vascular plants, the growth of which is believed to be stimulated by elevated N deposition driving a change from slower to faster growing species. Mat-forming lichens may provide particularly sensitive indicators of atmospheric chemistry because (i) they occur in open situations where they intercept atmospheric deposits directly and largely unmodified by plant canopies, (ii) they are partially isolated from the chemical status of underlying soil by a layer of necromass, and (iii) they are very efficient scavengers of inorganic N (and probably P) in precipitation (Crittenden, 1983; 1989; Hyvärinen & Crittenden, 1998c). For example, nitrogen concentration in the apical 5 mm of *C. stellaris* was measured at sites distributed along a 240 km long transect across the taiga-tundra ecotone in northern Russia and found to gradually decrease from south to north (Fig. 5). This change probably reflects a south to north decrease in N deposition due to either a decline in total precipitation (ranging from *c.* 1200 mm at the southern end of the transect to *c.* 620 mm at the northern end) or a pollution gradient, or both. However, a comparable gradient in nitrate concentration in winter snow pack was not observed (Walker, Crittenden & Young, unpubl.).

Ecosystems at high latitudes are classically N-limited and potentially responsive to N pollution. This is likely to increase in the future due to such activities as exploitation of oil and gas reserves located deep within the Subarctic. Nitrogen pollution has been implicated as a factor contributing to increased growth rates of northern boreal forest trees (D'Arrigo *et al.*, 1987; Myneni *et al.*, 1997; Nadelhoffer *et al.*, 1999). The effect on lichens will depend on the N load. Species containing cyanobacteria, such as *Stereocaulon, Peltigera* and *Nephroma* may be particularly susceptible to increased N and acid deposition although the latter species are not favoured by reindeer or caribou. However, increased vascular plant vigour could result in the competitive exclusion of terricolous lichens in the most

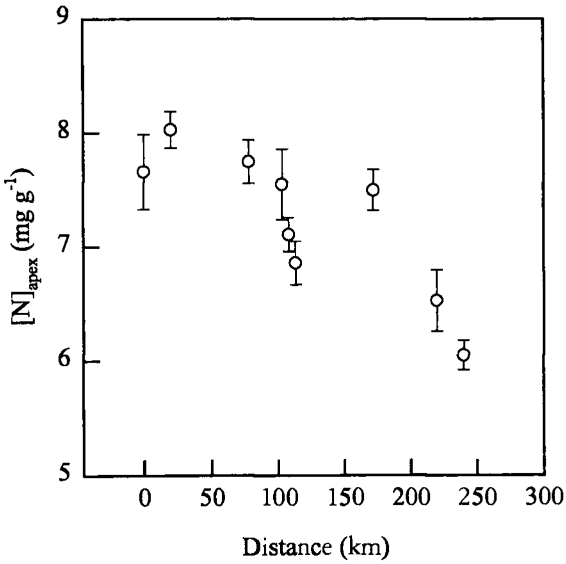

Fig. 5. Variation in mean values (with ±1 standard error) of total nitrogen concentration (n=18) in the apical 5 mm of *Cladonia stellaris* along a 240 km transect in the Usa River catchment, northern Russia. The transect extends from Vangyr (lat 64°14'N, long 59°12'E) in the boreal forest northwards to the Khosedayu River in the tundra (lat 67°15'N, long 59°37'E).

affected areas. Søchting (1990; 1995) considers this to be a contributory factor in the decline of *Cladonia* (subgenus *Cladina*) spp. in Danish heathlands. In some of the most eutrophicated heathlands in the Netherlands and the UK there has been an incursion of graminoids resulting in competitive exclusion of not only lichens but also ericaceous shrubs: in these areas heathlands are changing into grasslands (Aerts & Heil, 1993; Marrs, 1993).

Concluding remarks

The majority of lichen research is curiosity-driven and takes place in countries without reindeer industries. It attracts minimal financial support and lichenologists are not generally accustomed to having end-users who consider lichens of practical importance. Perhaps it is not surprising, therefore, that lichenology is poorly equipped to address some of the range management issues facing reindeer herding. One way forward is for those working in reindeer range management to identify key questions that they think lichenologists should address. These can be publicised in international fora and will hopefully provide incentive for research on topics that are currently neglected and perhaps viewed as unfashionable. The rate of mass increase in mat-forming lichens is clearly one such topic.

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Equilibrium and non-equilibrium models of livestock population dynamics in pastoral Africa: their relevance to Arctic grazing systems

R. H. Behnke

Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, Great Britain
(r.behnke@mluri.sari.ac.uk).

Abstract: Equilibrium grazing systems are characterised by climatic stability that resulrs in predictable primary production. Non-equilibrium grazing sysrems receive low and erratic rainfall that produces unpredictable fluctuations in forage supplies. In semi-arid Africa, these two types of environment present livestock owners with very different management problems. Identifying and maintaining optimal stocking rates is useful in equilibrium systems because livestock reproduce and produce at a rate determined by the availability of feed, which is an inverse function of stock density. The only problem is ro determine what stocking rate is optimal. The correct stocking rate for a grazing system will vary depending on rhe production strategy and the social and economic circumstances of the rangeland user - there is no single, biologically predetermined optimum density. Variable rainfall complicares the picture in non-equilibrium systems. Set stocking rates of any kind have little value if fluctuation in rainfall has a stronger effect than animal numbers on the abundance of forage. More useful in such an environment is the ability to adjust stocking rates rapidly to track sudden changes in feed availability. In semi-arid Africa, the distinction between equilibrium and non-equilibrium sysrems hinges on the reliability of rainfall. In northern latitudes, at least three primary variables important for plant growth and the survival of herbivores must be considered: rainfall, snow cover and temperature. It is probably nor useful to consider arctic grazing sysrems as equilibrium systems; on the other hand, the non-equilibrium models developed in hot semi-arid environments do not capture the range of complexity which may be an inherent feature of plant-herbivore dynamics on the mountain and tundra pastures where reindeer are herded or hunted.

Key words: caribou, carrying capacity, drought, overgrazing, *Rangifer,* reindeer, semi-arid rangelands.

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Introduction

Like many of the applied agricultural sciences, range management was developed to meet the needs of commercial producers in temperate climates. In the 1960s international aid agencies began to spend large amounts of money to transfer the new technologies to the open ranges of semi-arid Africa. The transplant did not work and - by the early 1980s when enthusiasm for the endeavour had worn off - sub-Saharan range management projects earned a justified reputation as failures (Simpson & Sullivan, 1984; Swift, 1991; Baxter, 1994). In retrospect, it is clear that range management in Africa had been deprived of several of the prerequisites for its success in industrial countries: large-scale commercial producers, private land ownership and a temperate climate. Classical range management had packed its standard conceptual tool bag, migrated south to equatorial latitudes but failed to take note of the particular socio-economic and ecological circumstances that confronted it there.

Like the tropics, the Arctic is a potential consumer of temperate notions of rational livestock production and resource management. A decade ago Beach (1990) identified a standard package of policies promoted by Scandinavian governments to rationalize traditional forms of reindeer herding. The package included the introduction of novel culling practices, selective breeding, grazing rotation and destocking - proven ingredients in the success of commercial livestock husbandry in most of Europe and North America. These techniques were either heavily modified or abandoned when they were applied to small holders in pastoral Africa;

whether they will work in the Arctic is far from certain.

There has been little sustained communication by researchers across the latitudinal gradient that separates the tropics and the Arctic and sub-Arctic. This paper contributes to such a dialogue. It recounts a tale of lessons learned the hard way over the course of several decades in equatorial Africa and speculates briefly about the convergence of arctic and tropical range and livestock policy. My treatment of the arctic material is, at best, impressionistic. Real dialogue takes partners, but pastoral studies are still regionally compartmentalized and we have yet systematically to exploit the comparison between temperate, tropical and arctic forms of extensive livestock production.

The standard interpretation and alternative hypotheses

Many African rangelands are heavily stocked with domestic animals and have been for some time (Sandford, 1983). In a dry year, or after a run of dry years, the animals often yield very little output in terms of secondary production and occasionally die in large numbers (McCabe, 1987; Moris, 1988; Bernus, 1988; Fratkin, 1991; Scoones, 1992). The causes and consequences of such fluctuations have been poorly understood. The most common interpretation has been that the rangelands were overstocked, that they were used unproductively and that their long-term productivity declined with each crisis (reviewed in Sandford, 1983; Shackleton, 1993; Turner, 1993; Dahlberg, 1996). Inefficient land use practices were seen to be the problem and destocking was commonly recommended as the remedy (Brown, 1971; Lamprey, 1983; Jarvis, 1991).

In the last ten years this standard interpretation has been challenged by a number of alternative hypotheses about how grazing systems function in semi-arid environments. Central to these arguments is a distinction between equilibrium grazing systems, in which annual rainfall is relatively high and reliable from year to year, and non-equilibrium systems in which it is low and erratic. These two kinds of environments present herd owners with different kinds of management problems and environmental risks.

Equilibrium grazing systems are characterized by relatively high climatic stability resulting in predictable primary production. In this setting, 'fine tuning' for optimal output is possible because livestock renew themselves - reproduce, grow and produce meat and milk - at a rate determined by the availability of feed, which is an inverse function of stock density. Provided with a reliable feed supply, livestock populations can grow to the point where they have considerable impact on the species composition and density of the vegetation on which they depend.

Rangelands that receive low and erratic rainfall present a different picture. In these areas, annual fluctuations in rainfall may have a much stronger effect on the abundance of forage than animal numbers. Productivity levels will therefore be determined by abiotic perturbations - droughts in particular - which the manager cannot predict and which he is unable to control. If droughts and livestock die-offs are severe and frequent, these grazing systems cannot sustain livestock populations at or near long-term ecological carrying capacity. In non-equilibrium systems like this, the potential impact of the livestock on their forage resources is reduced. Rather than providing evidence of mismanagement, periodic livestock population crashes represent one of the mechanisms that promote the persistence of such systems despite the instability and harshness of the environments in which they operate (see references in Ellis & Swift, 1988 and Little & Leslie, 1997 for an analysis of this process among the Turkana of northern Kenya, probably the best studied pastoral system in sub-Saharan Africa).

A coefficient of inter-annual rainfall variability (CV) of 33% probably marks the boundary between African livestock systems dominated by stability

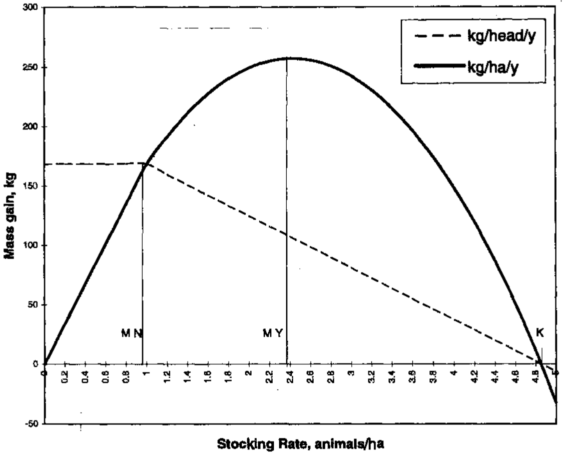

Fig. 1. Stocking rate and beef production (Jones & Sandland, 1974).

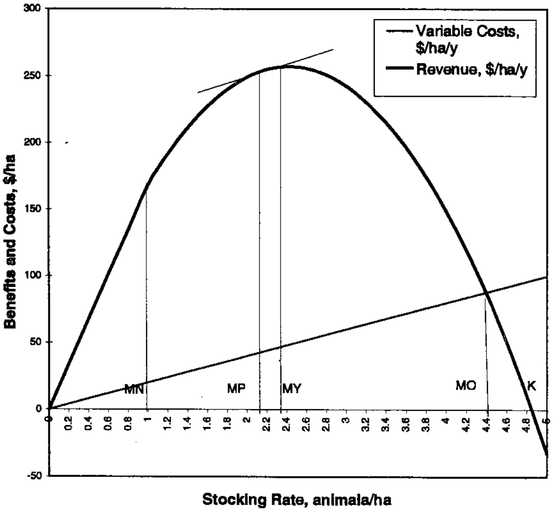

Fig. 2. Economically and biologically optimal stocking rates.

Notes to Fig. 2.

- Beyond *MN*, increases in density entail a progressive decline in livestock nutritional levels, individual animal productivity and overall herd condition (Malechek, 1984).
- *MP* is the most advantageous stocking density for commercial ranchers trying to maximize their profits. The precise location of the commercial optimum is sensitive to changing cost levels and output prices (Workman, 1986; Wilson & Macleod, 1991; Jarvis, 1991).
- *MY*, maximum yield, marks the density at which a herd owner can obtain maximum aggregate output per unit area a consideration important to subsistence-oriented pastoralists who directly consume their own produce and seek to provide food for large human populations (Behnke, 1994).
- Stocking densities in the vicinity of *MO* are possible when herders are free to enter and use a pasture at their own discretion. New operators and their animals will be attracted to the area until aggregate stocking densities approach *MO* and declining revenues equal rising operational expenses, removing any further incentive for new entrants. This 'open access equilibrium' can occur at high densities which depress yields and is not a desirable stocking target for any group of producers except the very poor.
- *K* is what wildlife and population biologists refer to as 'ecological carrying capacity' - the level at which a herbivore population would naturally stabilize assuming a relatively constant forage supply. Since herds at *K* generate no offtake but simply maintain themselves, this stocking density is not of interest to owners of domestic stock.
- The expansion of animal numbers beyond *K* can occur in cyclic irruptions or when new herbivore species are introduced into favorable habitats, temporarily releasing normal controls on population growth. The botanical asset stripping which underpins the herbivore irruption has commercial parallels. Assuming that a rangeland cannot maintain pastoral incomes at levels comparable to opportunities elsewhere in the economy, the rapid depletion of vegetation at *K*+ densities is a feasible commercial proposition. An area is 'mined', abandoned and profits are re-deployed elsewhere.

and instability. CVs of 33% or higher are possible anywhere in Africa with 600 mm or less of rainfall per year and, in southern and eastern Africa, even where rainfall exceeds 1000 mm per year. This means that about half the continent's land area is potentially exposed to the effects of severe climate variability, drought, and non-equilibrium dynamics (Ellis, 1994).

The opening sections of this paper summarize some of the evidence for, and policy implications of, the equilibrium/non-equilibrium dichotomy as it has been applied to semi-arid grazing systems. The last part of the paper discusses the relevance of this dichotomy for management regimes for ungulates in the Arctic and sub-Arctic.

Carrying capacity in equilibrium systems

Figs. 1-3 illustrate the effect of alternative stocking densities on livestock output in equilibrium grazing regimes. Fig. 1 depicts physical product output from a beef ranching system and Fig. 2 examines the economic profitability of such a system. Figs. 1 and 2 summarize the results of numerous experiments carried out under the reasonably stable conditions typical of equilibrium systems (Jones & Sandland, 1974; Butterworth, 1985; Wilson & MacLeod, 1991; Ash & Stafford Smith, 1996). Fig. 3 compares the outputs from commercial ranching versus those from mixed subsistence/market-oriented African husbandry systems.

In Fig. 1 weight gain per animal is constant at very low stocking densities when forage is abundant and does not constrain animal performance (*0-MN*) but decreases as an inverse linear function of stocking density when density exceeds *MN*. Gain per hectare initially increases with increasing stocking rate to a point of maximum yield (*MY*) and then declines quadratically to zero at *K*, the feed-imposed ceiling on further herd growth, often called 'ecological carrying capacity'.

Fig. 2 converts physical outputs in Fig. 1 into cash equivalents and compares the returns with operating costs at different stocking densities. For

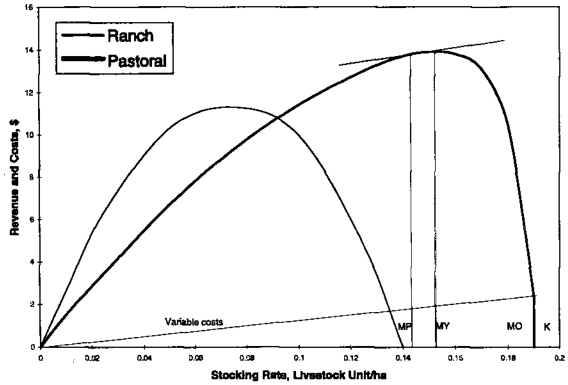

Fig. 3. Ranch and pastoral revenues and costs at various stocking rates.

Notes to Fig. 3.

- At low stocking densities pastoral output is probably lower than ranch output. Under favorable nutritional conditions, indigenous African cattle can match neither the absolute level of output per animal nor the efficiency of the rate of feed conversion into livestock product achieved by commercial breeds (Richardson, 1994).
- In pastoral systems both maximum yield (*MY*) and maximum herd size (*K*) occur at higher stocking densities compared to ranching systems, reflecting the capacity of pastoral stock to withstand nutritional stress. African cattle breeds can survive, produce and reproduce under nutritional conditions that are inadequate by the standards of commercial breeds in temperate climates.
- In pastoral systems, herd output falls precipitately from the point of *MY* to zero yield at ecological carrying capacity, reflecting a non-linear relationship between stocking density and live animal outputs such as fibre, milk or manure. If production and reproduction can continue during periods of weight loss, stocking rates that maximize live animal outputs will be higher than those that maximize meat output (Donnelly *et al.*, 1983; Donnelly *et al.*, 1985; Behnke & Abel, 1996)
- Pastoralists can obtain over 2.5 times more energy from combined meat and milk production than from meat production alone, because of the greater efficiency of conversion of both feed energy and nutrients - principally nitrogen - from pasture into milk (Western, 1982; Western & Finch, 1986; Blaxter, 1962; King, 1983; Spedding, 1971).
- Operating costs for inputs other than labour are very low for many subsistence-oriented herders, giving a gently sloping variable cost curve. When variable costs are minimal, *MP*, the stocking rate that maximizes net revenue, shifts to the right, effectively eliminating for subsistence-oriented systems the distinction between those stocking rates that optimize economic profits (*MP*) versus gross output (*MY*) (Tapson, 1990).

commercial ranchers, the economically optimal stocking density – *MP* or maximum profit - is the stocking rate which maximizes the differential between total revenue and variable costs. This economic optimum can be identified by inspection; it occurs at the point of greatest vertical distance between the revenue and variable cost curves. Finally, *MO* – the density beyond which rising costs exceed revenue - represents the outer margin of viable economic operation on the rangeland in question. Beyond *MO* net revenue is nil, rendering insolvent any unsubsidized herd owner who persistently operates at these densities.

In Figs. 1 and 2, livestock and plant populations are closely coupled by density-dependent negative feedback - more livestock result in more pasture eaten, therefore less pasture available and consequently fewer livestock (Caughley, 1987: 168). Stable densities of plants and herbivores and predictable levels of herd output are made possible by this feedback and because these systems are not unduly buffeted by the vagaries of climate. It only remains for the manager to decide what level and what kind of output is required from the system and what densities of plants and animals will deliver this output.

Fig. 2 addresses this issue. It identifies at least six distinct management objectives and associated stocking densities at which different observers - or producers - might conclude that the system contained the correct number of animals: optimal individual animal performance (*MN*), profit maximization (*MP*), yield maximization (*MY*), maximization of the number of herding operations supported by the resource (*MO*) and, finally, the maximum total number of livestock which could be supported on a permanent (*K*) or temporary basis (*K*+, not shown in Fig. 2). With the exception of *K*+ all these stocking densities are potential equilibria at which the rate of growth of plants equals the rate at which plants are consumed by herbivores. With the exception of *K*, all these potential optima are managed equilibria sustained by alternative culling rates. Although all are technically feasible, each of these different 'equilibrium' densities is appropriate to a particular management and production system or is advocated by different sets of professional observers.

In contrast to large-scale market-oriented ranching, however, open-range African herding is characterized by different livestock breeds, species and product combinations, variable levels of market involvement and different systems of land tenure.

Fig. 3 presents hypothetical revenue or physical product curves for fenced beef ranching systems and subsistence-oriented African husbandry systems using communal rangelands. These curves illustrate some of the principal differences between commercial and pastoral productivity and the likely impact of these differences on stocking policy. The altered shape of the pastoral output curve combined with a 'flat' variable cost curve for subsistence producers minimizes the difference between *MP, MY, MO* and *K;* it also positions these thresholds at very high stocking densities compared to commercial ranching. Maximum yield at *MY.* is higher in the pastoral system than in the ranch system as a result of the combined effects of a broader product mix, exploitation of live rather than terminal animal products, and the greater physiological resilience of indigenous breeds. These factors help explain why African pastoral producers can achieve their production goals at stocking rates near ecological carrying capacity.

Figs. 1-3 also illustrate why carrying capacity has proved such a slippery concept. Within the limits of what is biologically feasible, the correct stocking rate for a grazing system must be determined in relation to the production strategy and the social and economic circumstances of the rangeland user. There is no single, biologically predetermined optimum equilibrium density and, hence, little point in simply characterizing an area as 'overstocked'.

This analysis explains why outside observers commonly perceive African rangelands as chronically overstocked. Due to the historical association of range management with commercial beef ranching, many of the standard botanical indicators used to assess 'carrying capacity' have actually been implicitly derived to identify economically profitable stocking rates for commercial ranchers which is shown as the density *MP.* in Fig. 2. Subsistence producers are likely to target an alternative density, *MY,* situated along an entirely separate production function depicted in Fig. 3. Here we have an explanation of how livestock numbers in some parts of Africa have continued to grow, in some instances for decades, beyond the purported limits of carrying capacity. What was being estimated were not ecological but economic carrying capacity levels and, moreover, economic carrying capacity levels for kinds of production systems that did not exist in the areas being assessed (Behnke & Scoones, 1993)

Fig. 3 also demonstrates why the controversy over pastoral overstocking has been so intractable in semi-arid regions of Africa. Mixed-product output per hectare from subsistence-oriented pastoralism is routinely several orders of magnitude higher than beef output from commercial ranching in comparable environments (Prins, 1989; Behnke & Abel, 1996). In climatically stable environments these economic benefits are achieved at the cost of lowered plant density and destocking would immediately make many people poorer (Abel, 1993).

That subsistence-oriented producers can meet their production targets at much higher stocking rates than commercial producers does not mean that the land they occupy is more resilient (Stafford Smith, 1996). On the contrary, it implies that there are strong incentives for African herd owners to stock heavily for their immediate benefit but with potentially disastrous long-term environmental consequences. This is not, unfortunately, a problem that most stocking experiments are equipped to examine because they rarely continue long enough to pick up the lagged effect of high stocking densities on output levels (Ash & Stafford Smith, 1996). For African husbandry systems, reliable data on the long term sustainability of highly productive and highly stocked systems are virtually non-existent.

The population dynamics of non-equilibrium systems

Semi-arid grazing systems are arrayed along a continuum ranging from non-equilibrium to equilibrium, with most African grazing systems probably lying somewhere between the extremes (Wiens, 1984; Ellis & Swift, 1988; Coppock, 1993; Scoones, 1993). For purposes of comparison, the following account ignotes the intermediate forms and presents a simplified picture of several important features of strongly non-equilibrium grazing systems.

At low rainfall levels, semi-arid grazing systems are driven by one dominant input - water - which arrives in discontinuous pulses some of which are large enough to send waves of biological activity cascading through the system (Noy-Meir, 1973). Biotic activity is regulated by a sporadic aboitic variable. In these environments, predictable seasonal fluctuations in rainfall are compounded by stochastic annual variations. Since annual variability in rainfall is inversely correlated with mean annual rainfall levels, the supply of water becomes more erratic as the total amount declines (Nicholson *et al.,* 1986; Nicholls & Wong, 1990). This combination of a harsh and unstable climate has several consequences for the relationship between livestock and vegetation:

- *Seasonality.* In semi-arid areas livestock populations are commonly limited by the abundance and quality of forage in the dry season. It may be difficult to maintain livestock in sufficiently high numbers through the dry season to challenge the vegetation in the wet season when it is growing, vulnerable to damage but abundant relative to feed requirements. Conversely, when grazing pressure is high - i.e. in dry seasons or during droughts when demand for feed often outstrips supply - the plants are relatively impervious to abuse, the living bits having retreated behind thorns, inside woody structures, below ground or been stored in seeds.
- *Stochastic disturbance.* Seasonal fluctuations in food supply are compounded by stochastic annual variations. Plants and herbivores respond to and recover from droughts at different rates (Caughley, 1987; Ellis & Swift, 1988). If droughts are frequent and severe enough, differential die-back and recovery rates will ensure that livestock populations will be almost continuously out of synchronization with their food supply in a particular year. In extreme instances, the herbivores are 'ambushed when at high density by a drought that cuts the food from under them, and ... trapped inappropriately at low density when a burst of pasture growth provides enough food to maintain a hundred times their number' (Caughley, 1987: 179, referring to kangaroos). In these systems, any equilibrium between the supply and demand of feed is largely coincidental - a fortuitous match between forage production and rainfall in one year and livestock population levels generated by rainfall and forage production in past years (Ellis & Swift, 1988).
- *Weak habitat saturation.* If herds die off in droughts more quickly than they recover in good years, mean stocking rates in environments subject to stochastic rainfall variation will be lower than they would be under comparable but constant conditions (Caughley, 1987; Scoones, 1993). If livestock densities that are in theory sustainable under stable conditions are equated with 'carrying capacity', then these systems will maintain mean stocking densities below carrying capacity (Ellis & Swift, 1988; McLeod, 1997; Hary *et al.*, 1997).
- *Density independence.* Shortfalls in feed supply are a consequence of periods of plant senescence that result in declines in the quality and quantity of forage. If forage quality routinely declines below maintenance levels as the vegetation cures, most animals begin to starve at the start of the dry season (Coppock *et al.*, 1986 a; b). The rate at which animals die will depend more on the length of the dry period than on the number of animals subjected to it. To an extent that is remarkably independent of their density, livestock in semi-arid Africa lose weight in normal dry seasons, recruitment and reproduction suffer in poor years and adult animals die in severe multi-year droughts (Coughenour *et al.*, 1985; McCabe, 1987; Homewood & Rodgers, 1991).
- *Spatial heterogeneity.* Despite the loose overall coupling between livestock populations and their feed resources, thete may be intense, density-dependent competition for the limited amount of high quality forage that is available to livestock in key resource areas in the dry season (Scoones, 1993; 1995).

In general, we might expect the impact of livestock on vegetation to diminish with increased distance from water and key resource areas, during the wet season, and in the early years of post-drought herd recovery when livestock populations are low. There is ample evidence that the reverse also holds true: that livestock impacts on vegetation can be intense in 'sacrifice' areas around watering points and in riparian areas that are key dry-season grazing resources (references in Illius & O'Connor, in press).

It is also possible that droughts may 'focus the impact of animals on the vegetation into intense episodes' thereby precipitating sudden, discontinuous changes in plant species composition over wider areas (Illius & O'Connor, in press). The extent to which this happens or is likely to happen is unknown. Numerous experiments show that the species composition of vegetation in semi-arid areas changes in response to constant high grazing pressure. But these results are not pertinent to non-equilibrium dynamics, which are characterized by alternating periods of high and low stocking densities and recurrent imbalances in the supply and demand for forage. Field studies that document the negative consequences of pastoral land use are more compelling but are conttadicted by case material that suggests little widespread rangeland degradation even in the Sahel, long presumed to be the locus classicus of desertification (Tucker *et al.*, 1991; Hiernaux, 1996).

The relevance of the equilibrium/non-equilibrium dichotomy for arctic ungulates

In their comparison of kangaroos and caribou, Caughley & Gunn (1993) noted parallels between semi-arid and arctic grazing systems in terms of structural simplicity, exposure to uncertain weather extremes and the instability of herbivore populations. Their analysis suggests that non-equilibrium grazing systems comparable to those in the semi-arid tropics may exist in the Arctic. In both settings the 'components of climate that determine plant growth...vary prodigiously from year to year' (Caughley & Gunn, 1993: 52), forage availability rather than herbivore density drives changes in herbivore populations and does so quickly: 'Populations of both red kangaroos and caribou appear to be buffeted, and occasionally hammered, by changes in the availability of food mediated entirely by capricious weather' (Caughley & Gunn, 1993: 53, 54). As Caughley (1987) showed for kangaroos, major changes in herbivore population size can be generated simply by compounding frequent but less extreme perturbations. Long term fluctuations in caribou/reindeer populations could therefore be 'essentially a mathematical artifact of year-to-year fluctuations in weather...even when the weather has no time trend' (Caughley & Gunn 1993: 54).

Subsequent to the publication of Caughley & Gunn (1993) there has accumulated additional evidence that sustains their interpretation, as follows:

- More complete data have been assembled on population trends for the major barren-ground caribou herds in Northwest Territories, Canada, and this material makes an even stronger case for population instability than the data initially summarized by Caughley & Gunn (Gunn, 1998: Fig. 13.2, and Fig. 13.3 for Peary caribou on Bathurst Island, Northwest Territories, Canada).
- Additional evidence has emerged that insular caribou populations are 'loosely regulated by food at low populations density' due to 'the impact of frequent density independent factors', a conclusion that could be sustained despite the possibility that the index of winter severity used in the study was 'too simplistic' and that one of the study islands had no weather station (Ouellet *et al.*, 1996; see also Nagy *et al.*, 1996 for Peary caribou on Banks Island; Tyler *et al.*, 1999 for Svalbard reindeer).
- Whitten's (1996) analysis of the demography of the Porcupine caribou herd in Alaska has moved on from a presentation of census results (Fancy *et al.*, 1994) to an analysis of the mechanisms of population regulation, summarized as follows:

  > The Porcupine Herd undergoes population fluctuations of variable amplitude and period because weather setbacks come at irregular intervals. Recovery rates under normally prevailing conditions ate slow enough and weather setbacks occur frequently enough that the population tends to stay within a fairly narrow range of densities and seldom, if ever, reaches levels where there would be population regulation through food competition if access to forage were never restricted. There is no true equilibrium in this system.

- Similar conclusions apply to the population dynamics of a mountainous caribou herd in the Alaskan interior: 'The size of a caribou herd in a given year is likely to be largely a function of its size during the previous population low and the number of years of favorable weather in the interim' (Valkenburg *et al.*, 1996).

There are, however, also likely to be consistent differences in the way semi-arid tropical and arctic climates stress animals, differences that complicate simple comparison between unstable, weather-driven population dynamics in these two types of systems. In semi-arid Africa and Australia weather affects livestock viability in a remarkably simple way: either it rains or it does not. Plant growth and senescence, livestock malnutrition and recovery all hinge on the presence or absence of a single physical input. No other climatic factor comes close to having the importance of rainfall, which can be exceedingly unstable in areas where it is scarce. This means that the character of an entire year is established by rainfall in the preceding wet seasons.

The situation is more complex at higher latitudes where fluctuations in both temperature and precipitation influence both the growth and the availability of forage in summer or winter, respectively. At northern latitudes, one set of weather variables - such as rainfall or the timing of the onset of warmer weather in spring - may cause fluctuations in the quality and quantity of feed production, while a second set of weather factors - such the prevalence of ground ice or the depth of snow cover - determine how much of total primary production is accessible to herbivores in winter (Mech *et al.*, 1987; Tyler 1987; McRoberts *et al.*, 1995; Langvatn *et al.*, 1996; Post *et al.*, 1997; Forchhammer *et al.*, 1998). With multiple factors determining the outcome, weather-induced stress is a function of the impact of individual factors, their correlation, and their additive or offsetting consequences. Multiple confounding factors could dampen or exacerbate climatic instability. Caughley & Gunn (1993) documented high coefficients of variation for important individual climate factors. How this variability is 'packaged' in individual years will present analytical problems and is likely to have impacts on herbivore dynamics that are not apparent in semi-arid grazing systems.

The picture is further complicated by the way different kinds of arctic vegetation respond to weather and to grazing. Herbaceous vegetation in semi-arid Africa and Australia responds quickly to rainfall. In the arctic green biomass production may also react rapidly to fluctuating weather stimuli, but at least one kind of forage - lichens - does not. Lichen recovery from fire or heavy grazing is measured in decades (Thomas *et al.*, 1995; Arseneault *et al.*, 1997). Depending on the relative availability of winter and summer ranges in an area, reindeer/caribou populations may be constrained by vegetation resources that fluctuate either annually or across decades. Because they are grazed in different seasons, these feed sources may also influence different vital rates (Sæther, 1997) with different levels of variance and elasticity (Walsh *et al.*, 1995; Gaillard *et al.*, 1997). Just this sort of complexity is suggested by the dynamics of the George River caribou herd which may be regulated by winter or summer feed availability, or both (Messier *et al.*, 1988; Crête & Huot, 1993; Manseau *et al.*, 1996; Arseneault *et al.*, 1997). What initially looked like a simple system now looks rather complicated.

Constrained by forage resources that respond to grazing pressure on different time scales and influence different vital rates, reindeer/caribou grazing systems appear to exhibit locally specific patterns of population regulation depending on the relative abundance of winter and summer forage in an area. For example, marked yearly fluctuations in herd size are not apparent in the data on Norwegian wild reindeer summarized by Skogland (1990) who emphasized density-dependent population regulation and attributed large crashes to over-hunting:

> The primary factor in population regulation of wild reindeer herds is density-dependent food limitation in winter, and...density-independent effects are most likely to be a contributory factor only at high population density (Skogland, 1985).

On the other hand, Adamczewski *et al.* (1986) and Tyler (1987) describe island grazing systems in which seasonal and inter-annual fluctuations in feed availability create intriguing parallels with semi-arid Africa grazing systems. Reindeer/caribou are not limited by summer nutrition and populations can be severely reduced by icing; winter nutrition is limited and stocking rates may be maintained below summer carrying capacity. Substitute 'dry season' for 'winter', 'wet season' for 'summer' and 'drought' for 'ice' and we could be talking about African livestock-vegetation interactions rather than island reindeer/caribou. Non-equilibrium dynamics caused by stochastic disturbance may represent an appropriate model.

Policy implications for reindeer management

Two decades ago Ingold (1980: 27, 47, 211) argued that reindeer pastoralism destabilised arctic grazing systems by encouraging violent oscillations in ungulate numbers and pasture availability in a 'vicious circle' in which 'impoverishment results from a cultural failure to impose effective limits to [herd] growth, just as the impetus for growth derives from the prospect of impoverishment'. For Ingold, reindeer pastoralism destroyed natural balances or exacerbated natural imbalances. In the semi-arid tropics, remarkably similar arguments were part of what Sandford (1983) has called the 'Mainstream view' - the assertion that contemporary pastoralism upset natural homeostasis, degraded the environment and impoverished those who practiced it. The work summarized in the first two sections of this paper was an attempt to dismantle parts of the ecological rationale that underpinned Mainstream perceptions of semi-arid Africa. A similar debate is underway in the Arctic, with some scholars arguing that the flexibility and opportunism characteristic of indigenous production systems are appropriate responses to an erratic and harsh environment (Beach, 1990; Krupnik, 1993; Fox, 1998; Tyler, 1999) while others take the opposite point of view (Riseth & Vatn, 1998; Skonhoft, 1998; Karlstad, 1998).

In Africa and I suspect in the Arctic as well, these debates have practical implications for the design of public policy. Our perception of the resource management capacities of local communities, the relationship between rural communities and regulatory authorities and pastoral development priorities all turn on the extent to which grazing systems are naturally homeostatic and subsequently perturbed, or intrinsically non-equilibrial. There are several reasons for suspecting that these questions can be usefully investigated for arctic and sub-arctic pastoral systems. To an extent rare in sub-Saharan Africa, circumpolar real-estate is controlled by powerful industrial states that possess the means to enforce their will. It is unlikely that the official policies promulgated by these states will be so inadequately funded or erratically implemented as to be irrelevant to the daily lives of reindeer herders. Even in their hinterlands, central government policies make a difference, as will any contributions that science makes to the formulation of better policies.

Recent advances in the understanding of semi-arid tropical grazing systems resulted from a re-examination of agricultural problems from an ecological perspective. Ecological analyses provided an alternative to the prescriptive formulae of the applied agricultural sciences, formulae that were better suited for temperate rather than tropical environments and for commercial rather than subsistence producers. The ecological sciences are well qualified to fulfill a similar role with respect to debates on reindeer pastoralism. Because they reside in the industrialized north, reindeer/caribou have been extensively studied. We probably already know more about *Rangifer* than we will ever, unfortunately, be able to discover about the agro-ecology of African cattle breeds managed under subsistence conditions on Africa's open ranges. Domesticated reindeer share both their geographical range and their genetic constitution with caribou which facilitates comparison between the ecology of wild and domesticated populations. Despite the inevitable shortcomings, the empirical record on *Rangifer* ecology is robust enough to enable ecologists usefully to scrutinize the development of grazing management policy. Routine ecological studies, clear synthesis of results and vigorous engagement may contribute a great deal.

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Rangifer and human interests

David G. Anderson

Department of Sociology, University of Aberdeen, Edward Wright Building., Dunbar Street, Aberdeen, Scotland AB24 3QY (david.anderson@abdn.ac.uk).

Abstract: This article reviews biological and anthropological literature on wild and tame *Rangifer* to demonstrate the powerful effect that this species has had on the imaginations of biologists, social scientists and local hunters. Through identifying a general 'human interest' in *Rangifer*, the author argues that there is great potential for these three communities to work together. To demonstrate this idea, the paper reviews several examples of successful and unsuccessful 'alliances' between local peoples and both natural and social scientists which have had a fundamental impact upon the history of these sciences. The paper examines recent theoretical models which suggest that human action is a major factor in the behaviour and ecology of the animals. The paper also analyses the ideas of many indigenous people for whom there is no categorical difference between semi-domesticated, semi-sedentary and migratory *Rangifer* through comparison with many 'anomalous' texts in English and Russian language wildlife biology. By reviewing the history of scholarly interest in *Rangifer*, the author argues that contemporary models of *Rangifer* behaviour and identity could be 'revitalised' and 'recalibrated' through the establishment of that dialogue between scientists and local peoples which so characterised the 19th century. Such a dialogue, it is argued, would help mediate many of the political conflicts now appearing in those districts where *Rangifer* migrate.

Key words: Arctic, caribou, indigenous peoples, migration, nomenclature, reindeer, systematics, traditional ecological knowledge.

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Introduction

Reindeer or caribou occupy a special place in the minds of scholars and hunters alike. There may be disagreement as to the degree to which *Rangifer* shape northern landscapes but it is impossible to imagine a boreal or tundra ecoscape not punctuated by this species. Migrating *Rangifer* leave a trail deeper than a simple trophic equation. They represent a powerful image which engages many communities in conversation. When rural peoples from all over the circumpolar North encounter one another, photographs of *Rangifer* provide an immediate focus for discussion. Images of *Rangifer* also link far more distant human communities. They often fan the imaginations of urban-based ecological activists intent on 'saving the caribou' and, of course, frame the dreams of small children in urban centres at Christmas time. One should expand this list to include, of course, the distant community of university scholars. In this paper I would like to reflect on the way that *Rangifer* represents a common human interest. By this I mean to show that anthropologists, biologists, local hunters and ecological activists alike to a great degree build their own nations, disciplines and identities through thinking about *Rangifer*. Moreover, I suggest that all this talk and action surrounding *Rangifer* by different human communities is a significant part of *Rangifer* ecology.

The content and style of this paper, is something of an experiment. It has been drafted by a 'social' scientist especially for the delegates of 10th Arctic Ungulate Conference, the vast majority of whom are trained as 'natural' scientists. In addition, it has been drafted by a peculiar anthropologist who not only believes that knowledge systems cannot be easily divided into 'natural' and 'social' types but who also believes that there exist forms of useful or important knowledge which cannot be tested or replicated empirically. These two beliefs have led me to adopt a point of view which may seem unexpected to many readers. First, I take it as self-evident that scholarly communities, like any other human community, have their own histories, ideologies and biases and therefore are open to anthropological and histotical analysis. The first two sections of the paper, therefore, consist of a broad review of the scholarly literature generated on *Rangifer* in both biology and anthropology from the middle of the 19th century to the end of the last century. The review acknowledges the insights given to both biologists and anthropologists by aboriginal peoples but also indicates that four concepts in each discipline ('gradual social evolution', 'specific and sub-specific identity', 'caribou management' and 'calving-ground fidelity') represent contingent doctrines that have had positive and negative implications for the communities involved with *Rangifer* populations. The conclusion that I draw from this analysis is a happy one: biologists, anthropologists and local 'aboriginal' hunters have historically demonstrated the ability to identify common intetests in the study of *Rangifer*. At certain times, however, this alliance of interest has been silenced or even worked against the interests of science and of local peoples. Second, I present the idea that people play a great role in shaping landscapes and thus indirectly effect the size and nature of *Rangifer* populations. This idea is developed in the last section and in the conclusions of the paper. In these sections, as throughout the paper, I take as accepted many ideas taken from discussions with *Rangifer* hunters and herders throughout the circumpolar north. These ideas include the notion that there is no clear difference between semi-domesticated, semi-sedentary and migratory *Rangifer* and that the behaviour of scholars, wildlife managers and local peoples has a strong influence on the migrarory behaviour and the population sttucture of *Rangifer*, and that *Rangifer* movements and behaviour are best described with adjectives that ascribe intentionality and a certain subjectivity rather those which imply that they are solely physical entities. I take these ideas as starting points for a discussion; I do not baldly assert them. In the last two sections I make references to controversies and anomalies in the biological literature to indicate that the analysis of existing data is not so tidy and there is room for discussion of fundamental concepts. Finally, this paper takes a truly circumpolar perspective. A major part of my argument defending behavioural and various models of understanding *Rangifer* ecology rests upon the content of little known texts on *Rangifer* ethology and management published in the former Soviet Union between 1930 and 1970. This literature can be best described as 'anthropo-biological' since it is pitched midway between the 'natural' and 'social' sciences as understood in Europe and North America and also, interestingly enough, also midway between 'local knowledge' and 'professional scholarship'.

While composing this article it occurred to me that many of the arguments would strike the reader as 'anecdotal' (which is not necessarily bad, according to Blehr, 1997). This suspicion has come from some unsuccessful attempts at defending these ideas in the past and also from the fact that time did not permit me to elaborate ideas with graphs, charts, and long textual examples. However, unethical experiments upon two anonymous referees of an earlier version of this text established that many of the arguments came across not only as anecdotal but as unsubstantiated opinions which in one case were felt to be attacks on wildlife biology itself. This is not my intention and indeed is the opposite of my intention. The main argument of the paper is that it is possible to identify a general human interest in *Rangifer* which is scientifically rigorous, empirically based and ethically sound. I argue this through comparing the ideas on *Rangifer* of many human communities. I do not privilege either western biology or anthropology; indeed I argue that in different periods both have been culpable of gross exaggerations as well as capable of making fine and refined distinctions. Although I use several indigenous idioms I do not argue that 'local knowledge' is mysteriously more truthful than 'scientific knowledge' but instead suggest that the two are always in a partnership whether they like it or not. However, I will concede that if one strongly believes that a statistically based analysis of certain attributes of *Rangifer* is the only reliable way of knowing *Rangifer*, then this article might seem more controversial than most. Although I suspect that it is beyond my power to offer sufficient data to engage a strict statistical empiricist, I would offer only one observation: there are many important issues in the relationship between *Rangifer* upon which decisions must be taken without empirical data. These range from setting a proper course of action befote an irrupting caribou population to trying to guess the impact of various human activities upon *Rangifer* behaviour. Empirically, the only way objectively to understand the implications of one course of action or another is take a sample of a dozen populations and to deliberately let the populations crash, be disrupted, or to grow wild for want of human interaction. The results of these experiments would take decades if not centuries to analyse and would, in the meantime, generate not only considerable hardship on local communities but would make most northern landscapes unrecognisable. It is difficult to prove if the error margins of the insights of an experienced caribou hunter are valid nine times out of ten. The purpose of this papet is to establish that these insights are valid at the very least as hypotheses and at the most as examples of successful strategies of action which, to a great degree, are responsible for cultivating the populations of *Rangifer* which we are all analysing.

Although the paper may already seem impossibly broad, I have concentrated on the literature describing three specific contexts: the situations of the Taimyr and the northern Yukon (Porcupine River) populations of wild reindeer/caribou - of which I have direct experience - and the northern Québec/ Labrador population, of which I have learned exclusively through library research. For my purposes these three examples are interesting for they are all 'classic' cases of the theoretical and practical problems created for people by large populations of migratory *Rangifer*. All three cases are complex. In two of the three, semi-domesticatedated *Rangifer* form part of the story of these populations. Furthermore, in each setting there is an understudied interaction with sedentary 'woodland' caribou which always fit rather uncomfortably in models of migration and hetd identity. Finally, in all three settings these populations have been directed, managed and even harnessed by a multitude of human hosts. All three populations travel through multiple political jurisdictions - in one case over an international border. In each case more than one indigenous population takes responsibility for setting ethical relationships to the animals. Furthermore, each of the three situations have become laboratories for the efficiency of three different state management regimes: rational nature-use in Taimyr, co-management in the northern Yukon and classical wildlife management in northern Québec/Labrador. However this choice is somewhat arbitrary and I have been forced to leave out interesting literature on Scandinavian and Kola peninsula populations and the large literature on other Alaskan and Canadian barren-ground populations.

A short history of *Rangifer* and circumpolar interests

To paraphrase the title of a classic paper on caribou management, *Rangifer* are universally a 'vital resource' (Allison, 1978). Whether one is drinking tea in a reindeer-skin Evenki tepee (*d'iu*) in the heart of the Putoran plateau, or watching the movements of groups of bull caribou while sitting in a half-ton truck on the Dempstet highway, people all across the Arctic rim are vitally concerned with observing, consuming and knowing this living resource. Caribou provide an important element of the diet of aboriginal families world-wide. In Siberia, Alaska, and Scandinavia, semi-domesticatedated *Rangifer* provide an important source of income and pride for local families. *Rangifer* world-wide help people in arguments about their identity. With the rise in power of circumpolar state administrations after the Second World War, and more recently with the rise of First Nation, Siberian, and Sami nationalism, control over the range of *Rangifer* has become important in discussions about managing landscapes, people and the future of nations. At the end of this century a common emblem of authority for administrators, northern politicians, or entire First Nations themselves is the silhouette of a (male) reindeer or caribou on the cover of a report, the corner of letterhead, or in the centre of a flag or a shirt.

Since the turn of the century there have been three peaks of interest among Eurasian, North American and European students of *Rangifer*. Each peak genetated a great deal of literatute and in some cases has created entirely new ecological relationships. Ironically, the very earliest circumpolar discussions were the most comptehensive in terms of the exchange of ideas between local hunters, biologists and anthropologists. In the post-War period, although there has perhaps been an increase in citations concerning *Rangifer*, there has been a considerable reticence by scholars and local peoples to engage with each other's terminology. With the relaxing of Cold War tensions and the rise of co-management regimes throughout the North, the present millennium now promises a return to an intensive exchange of ideas on the significance of *Rangifer* between all circumpolar communities.

The last century began with extreme curiosity about the concrete cultural, biological, and zoological links which united the continents. This period is perhaps one of the better examples of a dialogue between local observers and scholars, as represented in the ethnogtaphic works of the Committee on the Northwest Tribes of Canada (Tylor, 1884) or the Jesup North Pacific expedition (Bogoras, 1902; 1929; Krupnik, 1996). Both of these collaborative endeavours strove to understand the social evolutionary status of peoples living along both sides the Pacific Rim. Within wildlife biology, circumpolar interest was represented in the ambitious cultural experiment of translocating of semi-domesticated *Rangifer* from Siberia to Alaska and Canada at the behest of northern administrations with the help of Sami herdsmen (Olson, 1969). The early circumpolar interest can best be categorised as an interest in cataloguing and cultivating northern landscapes. Both the ethnological and biological literature stress the need to identify the languages and habits of local peoples precisely as well as the need to focus upon suitable species for 'taming the frontier'. Specific policy actions connected to these scholarly studies had far reaching ecological effects. In the case of ethnology, early investigation of the language and identity of aboriginal peoples would eventually alter the human geography of whole nations as hunters were settled into villages or special enclaves which were not always designed to respect the specific relationships that those communities maintained with the lands and animals around them. In the case of biology, the penetration of Sami and Siberian knowledge of semi-domesticated *Rangifer* into a setting dominated by migratory *Rangifer*, introduced a different type of ecological concern over the carrying capacity of the land and the significance of migrations and also created a new setting in which to discuss *Rangifer*. As will be argued below, the influential ideas of 'calving ground fidelity' can be traced to this particular penetration of ideas on how to manage migratory and semi-domesticated *Rangifer* Interestingly, it is also in this period of closest collaboration between scholars and indigenous people that there is the most experimentation with trying to typify and distinguish different sub-species of *Rangifer*. Dialogues with local communities considerably enrich the vocabulary of scholars with respect to sub-species and ecotype.

Directly following the Russian Revolution and Civil War, there was an intense, competitive interest in various ways of harnessing wild and tame reindeer for social development. This literature is perhaps best illustrated in the pages of the journal *Sovetskoe olenevodstvo* [the Soviet Reindeer Industry] or in the typescript volumes of the Canadian Royal Commission to Investigate the Possibilities of the Reindeer and Musk-Ox Industries (Canada, 1922). This literature, while continuing certain economic interests from the turn of the century, treats indigenous ideas concerning *Rangifer* and muskoxen as obstacles to the intensification of northern production. Indigenous people figure as rather passive recipients of knowledge and aid rather than active partners in the 'taming of the frontier'. Within this period the works of scholars from both sides of the growing circumpolar political divide are cited to establish legitimate parameters of study and state action. It is to this period that one can identify the origins of state wildlife management in both Russia and North America.

One can identify the most attentive reading of information on communities vitally linked to *Rangifer* at the height of the Cold War. In the 1960s, North American biologists such as Pruitt (1960) or Lent (1966) integrated into their own work Formozov's (1946) research on the effects of snow-cover on migrations or Michurin's (1963; 1965) work on systematics. Although ethnogtaphers in the same period rarely wrote comparative works, there was an implicit applied interest in identifying advantageous development policies for local communities. In Russia, state policy was held to be a positive example of how technology and science could integrate *Rangifer* hunting and herding into a national economy (Gurvich, 1961; 1977). In Canada and Alaska, research was conducted into how best to separate *Rangifer* hunting (and to a lesser degree, herding) into 'subsistence' sectors which operated independently from general market principles (Baliksi, 1963; Nelson, 1973; Caulfield, 1983). In terms of action, in the late 1960s and 1970s the circumpolar states invested in several experiments in the translocation of muskoxen ostensibly to make the high Arctic landscape more 'economically useful' (Yakushkin, 1978; Klein, 1988). It was also in this period a classic text of Syroechekovskii (1975; 1984) concerning the 'rational use' of wild *Rangifer* was made available in English translation. This period, corresponding to the apex of the period of state wildlife management, is peculiar for its aggressive neglecting of local traditions. While the indigenous hunter was seen to have a romantic aura at the beginning of the century, or a simple nature before the Second World War, in the 1960s and 1970s aboriginal peoples were held to be culpable for the potential or past extinction of circumpolar species such as the bison and the musk-ox (Hone, 1934; Owen-Smith, 1987; Morgan, 1997; Isenberg, 1997; Lent, 1998). Thus this period is characterised not so much as by an economic interest in *Rangifer* but by a highly centralised and protective interest in the animal aligned to the imperatives of state building. Interestingly, in terms of a social history of the study of systematics, this period of centralisation coincides with consensus on there being a single generic and specific type of *Rangifer* which could be measured and understood without much attention to local categories and observations. This conviction, characteristic of North American wildlife biology, has caused some debate concerning the proper way to divide up populations.

Although these 'peaks' of interest have generated significant work and discussion, the reticence with which scholars based in the circumpolar region have used this material in model building is remarkable. These diplomatic (or perhaps 'cold') rules of engagement between circumpolar sites are most obvious in works published in Russian or English, where authors from both intellectual traditions conservatively acknowledge the presence or absence of parallel research initiatives but rarely experiment with each other's concepts or terms. This lack of engagement is most noticeable, sadly, in my own field where the number of fundamental comparative works in circumpolar ethnography since the Jesup expedition can be counted on two hands (Schweitzer, 1993; 2000). Recent North American concepts of 'herd' as defined by a 'calving ground' are not compared with the behaviourally based Russian aggregate of *stado.* Fundamental articles on *Rangifer* are more concerned with raw population statistics (Klein & Kuzyakin, 1982, Williams & Heard, 1986) or 'impacts' and 'management' (Klein, 1991; 1996) rather than the subtler issues of migratory behaviour or collaborative arrangements with indigenous communities. What is also noticeable in this cold 'lack of engagement' between circumpolar scholars is the marked contrast with the passion local peoples display for details of the lives of their animal neighbours. Thanks to the Inuit Circumpolar Conference, the International Working Group on Indigenous Affairs and the growing interest of many local aboriginal land-claim administrations, aboriginal 'wildlife users' are becoming more aware of common problems with heavy metal contaminants, the dislocating effects of resettlement policies and the bitter-sweet experiments with wildlife management and the construction of parks and wildlife reserves. I expect that it is this locally generated agenda of a circumpolar interest which will generate renewed interest in the skills of anthropologists and biologists alike.

To summarise, in studying the history of scholarly interests in *Rangifer* it is possible to identify three tendencies. First, though *Rangifer* are a universal interest for all circumpolar communities, there has been a growing reticence to acknowledge and incorporate the models of indigenous thinkers in scholarly discussions on *Rangifer.* As will be argued below, even recent attempts to recognise 'traditional ecological knowledge' (TEK) or 'local knowledge' pale before the quality of collabotation that one can identify at the start of the last century. Second, the set of published analyses among scholars tends to reflect the interests of state administrations in a region that has increasingly become an arena of political tension rather than the interests of local populations. Finally, the future of scholarly interests in this region and this species will depend upon 'revitalising' academic models such that they reflect the lived interest in *Rangifer* of local communities. I have not identified these three tendencies in order to criticise the validity of current models or to predict the course of future developments. However this short overview suggests that scientific interests can be calibrated to reflecr general circumpolar interests be they those of nation-states, local communities, or various definitions of economic development. This raises the question of what is the best calibration?

Calibrating scientific interest in *Rangifer*

There has been much debate on how scientific interests in *Rangifer* differ epistemologically from the 'knowledge' of local rural hunters (Freeman & Carbyn, 1988; Osherenko, 1988; Thomas & Schaefer, 1991; Stevenson, 1996, Johnson, 1992). Typically, scientifically valid statements about the world are felt to be empirical and quantitative. They are said to be honed to provide predictive models which can be proven or disproved and, in the field of wildlife biology at least, they focus upon the parameters of the population in question in terms of discreteness, size and recruitment. By contrast, models which are extrapolated from 'tradition' or 'local knowledge' are primarily qualitative. They are oriented towards providing a guide for ethical action and, with respect to *Rangifer*, tend to be more interested in describing the behaviour of groups or bands without much reference to the macropopulation. While in many specific cases it is clear that there is a difference in approach, there is growing literature which disputes the extent to which differing methodologies amount to a different way of knowing (Agrawal, 1995; Cruikshank, 1998;

Dorais *et al*, 1998). Although I agree with the general lines of this critique, it is not my intention to weigh the various philosophical and political arguments within this literature. Instead I wish to take a shortcut to two simple points. First, some of the most 'scientific' concepts have their roots in the most 'traditional' settings. I suggest that groups of people who today distinguish themselves as *Rangifer* 'scientists' and 'users' have been knowingly or unknowingly engaged in a sort of partnership of inquiry for at least a century. Second, in sketching out this history I point out that the scientific interest can be calibrated or focused in multiple ways which may either emphasise or ignore the pragmatic interests of local groups. It is possible that both 'users' and 'scientists' may recently have developed radically different paradigms of perception and action.

This analysis in the history of *Rangifer* scholarship focuses on four examples, two of which have had positive implications for this alliance and two of which have had negative implications. In terms of a positive alliance I will cite the examples of the earliest work which went into distinguishing *Rangifer* genus itself, and the most recent investigation into the relationship of *Rangifer* to the so-called 'calving grounds'. In both instances I argue that the mingling of 'local knowledge' and 'science' is so complete that the two merge into one. In terms of a negative alliance I will cite the powerful idea of 'gradualist social evolution' and the no less influential idea that wildlife can and should be managed by state administrations. In both cases I make the argument that although indigenous perspectives may seem to be silenced or even rejected by these models, images of indigenous hunters nevertheless play a crucial role in each theory. In short, Europe could never crown the scale of social evolution without first becoming obsessed with the idea that early man chased a *migratory* animal. Neither could state managers establish their authority without first creating the image of the careless or childish caribou hunter. Thus in all four examples, indigenous images are harnessed at all levels in the creation of *Rangifer* science in what ate described as principled and unprincipled ways.

Rangifer *and social evolution*

Rangifer tarandus is a classic 'species' in both the history of zoology as in the history of anthropology. One finds thoughts on the significance of reindeer and caribou structuting the very foundations of each profession. In the first and successive editions of his *Systema Naturae* (1758-1767), Linnaeus identified a circumpolar type (*Cervus tarandus*) on the basis of his own observations of Scandinavian wild and domesticated reindeer and on written reports of barren-ground caribou (Banfield, 1961: 48, 53). The origins of social anthropology can be traced to same period. The awareness of the mutability of human society and the human form itself owes its origin to 18th and 19th century meditations on the significance of *Rangifer* remains found in early archaeological sites. Early theorists wove broad theories linking the material remains left by early *Rangifer* hunters within caves in France and explorers' accounts of actual *Rangifer* hunters in the expanding European colonies (Trigger, 1989). This alliance of interest is often acknowledged in the foreword of major works on wildlife biology. The enigma of cave drawings, or the account of a caribou corral, are often used to draw readers into an analysis of the systematics ot population dynamics of a species representing a common and ancient human interest (Murie, 1935; Banfield, 1961). The early appearance of *Rangifer* in the scientific imagination is more than an historical curiosity; it has influenced many concepts which still shape scientific action.

The most important but capricious 'alliance' between anthropologists, taxonomists, and indigenous peoples revolves around one of the roots of positivistic science today - evolution. The first collections of chipped stones and split legbones found in France were equally useful as proof of a Biblical flood as they were of the presence of an ancient culture of reindeer hunters. It required a considerable marshalling of geological, palaeontological and archaeological evidence to establish that the landscape had as deep a history in terms of time as it had extended engagement with the human form (Eiseley, 1961; Stocking, 1987). To pull examples from only one prominent populariser of gradualist evolution, Sir John Lubbock (1890: 300-304; 1978: 26), lithographic reproductions of cave drawings of reindeer hunts were superimposed upon descriptions of primitive abattoirs in an effort to prod the Victorian public to accept the idea that human activity is not only recognisable in subtettanean digs but also the simpler point that human activity had progressed. This was on the whole successful. As is well known in overviews of the history of 'civilisation', the movement from hunting *Rangifer* to herding them captures the dawn of the first organised productive activity (Childe, 1951: Ch.6).

Rangifer hunter/herders are said to straddle humanity's first adventure into rational productive activity (Ingold, 1980: Ch.2). There were two inescapable conclusions to be drawn from the successfully negotiated image of 'man' as the Palaeolithic hunter: first, that time brought with it progressive change and second, that people maintaining a relationship with wild *Rangifer* were already living in the past.

There are numerous printed examples of how early travellers, ethnologists, biologists and publishers used descriptions of *Rangifer* and their human hosts to contradictory ends. On the one hand, those people who hunted of wild migratory *Rangifer* provided prosaic material illustrating the independence and hardiness of the human spirit and yet were almost invariably classified as the most 'savage' and 'primitive' in the newly discovered spectrum of human forms. On the other, those who herded semi-domesticated *Rangifer* were respected as founders of humankind's productive tradition. Of the nations considered in this paper, Gwich'ins (*Dene dinje*, *Loucheux*), despite their refined and respectful way of attending to migratory *Rangifer*, play the thankless role in early ethnography of representing a society which contrasts so much with civilisation as to define it. Two early anthropological theorists neatly capture the consensus by citing Gwich'ins as 'the most northern, the most bastardised but also the most primitive of Indians' (Durkheim & Mauss, 1975: 63). In another widely read account of diffusionist evolution, these 'undoubtedly really primitive' people serve as bookends to the epic story of mankind, appearing only twice; at the beginning and the end (Perry, 1923: 5, 469). For Frank Speck (1935: 3), who wrote in other respects a very sensitive ethnography of Naskapi religion and ritual, the 'savage hunters of the Labrador peninsula' represented 'the bordetline of the life of the past merging with that of the present'. Reindeer herders, although often employing similar concepts and rituals to Gwich'in and Naskapi hunters (and often hunting similar populations of caribou) were described with much more sympathy. Although the teindeer herders of Taimyr were described in Middendorf's (1859: 489-90) volume on fauna, they were praised for the 'economic' use of their deer right until 'the last drop of blood'. Moreover, their talents of domestication were placed at a higher 'level of development' than the 'primitive' people of North America. Kastren (1860: 343) went as far to identify Yenisei Evenkis as 'aristocrats of the tundra'.

The adjectives used by these turn-of-the century authors seem so naive and exaggerated that they are now politely ignored when reading these fundamental works. However, it is important to recognise that these examples were not chosen randomly or in error by these theorists. Our scholarly forerunners in geology, biology and ethnology were under great pressure to exaggerate the mutability of human relationships to drive home the point that evolution, both biological and social, existed. Further, these examples were not simple cases of overzealousness. There was an important subtlety in this struggle. Any admission by an author of too much kinship between urban Europeans and the savage hunters ran the risk of discrediting the arguments of liberal evolutionists (Stocking, 1971). Strategically, the hunt of the wild caribou needed to be represented as a 'survival' of past forms of adaptation linked to the 'impulsive' and 'childlike' behaviour of savages in order to underscore the rational nature of agricultural or industrial society (see Lubbock, 1978 [1870]). Thus, from an early date, scientific workers entered into a marriage of convenience with *Rangifer* hunters. Hunters and their prey might be studied with interest and with sympathy but the authority of scientific classification was vested in the irrationality of the modern savage. Although the relationship between proponents of TEK and those of applied zoology might be a warmer one today, it is not new.

The genus Rangifer

The strategic exaggerations in early evolutionist thought belies the implicit evidence of strong collaboration between travellers field explorers and the so-called savages. As Banfield (1961) illustrates throughout his 'revision' of the genus, the earliest systematics of *Rangifer* owe much to the insight of local rural hunters in various encounters with explorers going back to 1487. The first sample of *R. t. pearyi* made its way to a museum as a gift from Samuel Hearne's Chipewyan guide (Glover, 1960). The earliest prototype of Gmelin's *R. t. caribou* was chased down by a group of Métis hunters on the St. Lawrence river (Banfield, 1961: 78). Although Linnaeus reputedly made his own observations of Sami reindeer, one wonders how his attention might have been directed if there were not Sami present. At a more conceptual level, thoughts on the identity and discreteness of the species have been guided by debates with aboriginal informants. The concept of the 'woodland caribou' comes from a Micmac behavioural category of 'the shoveller' (Wright, 1929). According to Banfield (1961: 3), the generic name for the species, *Rangifer*, is derived from a Sami term for a young reindeer. A quick glance at history of the regional distribution of specific and sub-specific categorisation of the genus shows that the first classic encounters between the biologist and *Rangifer* occurred at the main cross-roads of Wesrern and Eastern trade colonialism: the St. Lawrence river valley, the Mackenzie Delta, the Ob' river system, the Seward peninsula. The idea of *Rangifer* itself, in contrast to the idea of social evolution, is a product of a successful calibration of scientific with local interests.

'The Buffalo of the North'

There is a remarkable reconfiguration of scientific interests in wildlife following the world wars. Paralleling the growth of new, nationalistic political orders there also appears a new idea that states must play a major role in the regulation of relationships between people, animals and national territories. Anthropology itself was created as a profession during this period through the successful argument that professional ethnological observation was useful to governments interested in regulating culturally diverse rural populations (Stocking, 1971; Kuklick, 1991). Although biology and zoology have rather older professional genealogies, the idea that a government should support professional and applied wildlife biology dates from this post-colonial period (Feit, 1998). The interests of scholars in making their research areas into professions would lead to perhaps the sttictest and least principled alliance with local populations.

The paternal issue at the heart of this new intellectual development was the responsibility of states in the protection of rural peoples and rural species. The seminal idea of this movement, like with the campaign to propagate an idea of social evolution, was the need to wrest control of environments from local residents and to vest it in the hands of properly trained professionals. The management of *Rangifer* became the test case for demonstrating the viability of this idea.

In order to justify this idea, there was a need to develop a negative example. The sad fate of another migratory species was useful in this exercise: the near extinction of the North American bison. Through a revival of earlier 18th century stereotypes of savage life, it became a common (but untested) assumption that with the provision of new technologies, such as rifles, the undisciplined nature of rural peoples would lead to the extinction of another rather romantically portrayed migratory animal (Trudel, 1985; Kelsall, 1968). Without dwelling on the history of this issue, it is a remarkable exercise to trace the genealogy of this example in the very first works of wildlife biology on two continents. In both Canada and Russia, *Rangifer* came to be thought of as 'the buffalo of the North' (e.g. Bergerud *et al.,* 1984).

The foundation of *Rangifer* management in Canada came from a series of widely read works in Canada by A.W.F Banfield (1954; 1956) which made the strong argument that there was a 'caribou crisis' stemming from the overkill of 'barren ground' caribou by native hunters in Labrador and the Northwest Territories. It was surmised that without immediate state action, the nomadic caribou would soon disappear as had the North American bison. The actions of the growing Canadian state apparatus were swift. In the late 1950s the Canadian Technical Committee for the Preservation of the Caribou was formed to discuss various courses of action ranging from the organisation of the first tagging of migrating caribou (Thomas, 1969; Parker, 1972; Kofinas, 1998: 87-88) to proposed restrictions on the sale and export of caribou skin clothing (Banfield, 1950). As with an earlier epoch, the relation between people and *Rangifer* and the perceived lack of restraint and foresight on the part of a population which came to be called 'users' would only bolster the authority and power of a closed group of managers. The strategy of identifying caribou crises has framed the success of wildlife biology from the original 1954 barren ground crisis (Banfield, 1954), the 1983 Kaminuriak and Beverly caribou crisis (Miller, 1983) through to the most recent 1993 Porcupine caribou crisis (Kofinas, 1998).

In the former Soviet Union, the distinct management school proposing the 'rational use of natural resources' (Kriuchkov, 1973; Syroechekovskii, 1984; 1990) was justified by similar anxieties of mass extinctions at the hands of improvident citizens. In one of the founding works of this school, Kriuchkov (1973: 40) prominently cites the example of the extermination of the North American bison to support his vision of the planned use of the landscape (for an even more exaggerated post-Soviet example see Zimov & Chuprynin, 1991: 94). As is well known, the proposals and the actions of managers in the former Soviet Union differed in emphasis but not in theme. Instead of protecting populations of migratory *Rangifer*, the solution most often proposed was the zoning of human use such that significant portions of the landscape are reserved for the exclusive use of semi-domesticated *Rangifer* while other portions become the settings for massive industrial hunts of the migratory population (Sdobnikov, 1958; Andreev, 1968, Syroechkovskii, 1986; Pavlov, 1983; Klein, 1980).

The rhetoric of the rational use of nature, as practised in Taimyr, is different from the rhetoric of 'caribou preservation'. Indeed, it is an interesting example for my purposes that the recommended methods of slaughter at river crossings are in fact industrialised versions of traditional Dolgan and Nganasan techniques of harvesting migrating *Rangifer* (Gracheva & Kholbystin, 1984). Despite a somewhat different engagement with *Rangifer*, and with local hunters, the political structure of this school of management is nonetheless quite similat to that of their North American colleagues. Decisions as to the timing and scale of slaughters and the location of zones reserved for semi-domesticated and wild *Rangifer*, are made in centralised locations by professional rural economists and not in local communities. The justification for rigid control over land use came from the example of chaotic use illustrated by the myth of the bison.

While the notion of a crisis can be lauded for directing state resources to the study of *Rangifer*, it should be treated carefully as a scientific strategy. I characterise it as an unprincipled alliance of scholarly and local interests for four reasons. First, although the notion of a crisis speaks to in imputed 'global' interest in the preservation of a species it can only do so through the allied but and silent presence of local 'users'. As Feit (1998) identifies clearly, wildlife managers pitch their arguments on behalf of the wildlife or the 'ecosystem' (and not the people) but can only justify practical action in the name of future generations of people (and not in the name of the landscape). As much as local interests are ignored, or in fact seen as contradictory to the preservation of the species, they are necessary to make an effective argument for management. This is a rhetorical strategy which contrasts remarkably with botany and medicine, both of which also tequite the participation of local populations and both of which have managed to negotiate a more equal alliance (Feit, 1998). Second, as has been often noted in histories of past crises, the predictions of the imminent collapse of a population is often followed by unexpected jumps in the population - often to quite unsustainable levels. This criticism points out not deception but a lack of humility in developing and applying technical tools in complex environments. It would seem that in each setting where a crisis has been declared there has been a corresponding jump in population size several years later as a result either of curtailed hunting or better measurement techniques. This was the case in Québec/Labrador (compare Banfield, 1954, Juniper, 1975, and Courtier *et al.,* 1990), the barren grounds (compare Banfield, 1956, Gates, 1985 and Osherenko, 1988) and the Taimyr peninsula (compare Syroechekovskii, 1966; Andreev, 1983; and Pavlov, 1996). Thirdly, the idiom of a crisis, as efficient as it is in attracting the attention of distant administrators, weakens the basis for future collaboration. The time frame of a crisis implies quick, coarse and estimated action but not discussion and consensus between actors. Finally, restrictions on hunting which may come out of an imputed crisis in fact change the ecology of *Rangifer* itself. In addition to restricted predation, restrictions on hunting through licenses, committees and outright bans change the telationship between people and deer. In most cases, strict regulations interfere with the transfer of skills from elders to youth. Encounters with *Rangifer* might be re-centred in new localities, or become 'grey' activities. Although it is difficult to identify a direct correlation, it is interesting to note that as local communities become increasingly regulated by wildlife regimes, whose goal is to rationalise the hunting of *Rangifer*, the population structure and migratory behaviour of *Rangifer* becomes more chaotic, unpredictable and unmanageable.

Rangifer *'herds'*

Although from the very first identification of the species in the 18th century it has been clear to both local hunters and European travellers that *Rangifer* often move in large and impressive aggregations, the nature of those aggregations has been a source of debate. In North America it has become an unquestioned doctrine that 'sub-populations' of migratory *Rangifer* can be identified on the basis of their 'fidelity' to a 'traditional calving ground' (Skoog, 1968; Davis *et al.,* 1986). This idea, which seems to have appeared in print in the mid-1950s with reference to the border region between Alaska and the Yukon Territory, is a second positive example of a successful collaboration between applied scholars and local hunters.

It has proven difficult to research the genesis of the widely-accepted idea of 'calving ground fidelity'. The classic citations for the idea of distinguishing populations by the repeated or regular use of specific calving grounds are Skoog (1968: 213-14) and Thomas, 1969: 7). It is significant that although each of these authors name populations by the name of a prominent lake or river located at the calving 'area' each of them keep the idea of a subpopulation separate from the idea of a herd. LeResche (1975: 127), Lent (1966: 484), and Kofinas (1998: 170-171) indicate that this idea was general knowledge among Alaskans throughout the 1950s. Earlier glimpses of the idea are said to be found in the works of Munro (1953), Skoog (1957; 1962) and (Buckley, 1957) but I have not been able to verify these citations.

Local informants have played an active role in identifying exactly which deer are 'different'. The clearest cases of aboriginal involvement in the doctrine of herd identity is in the case of the 'George River', 'Leaf River' and 'Torngat Mountain' populations of *R. t. caribou.* In northern Québec/Labrador Low (1897) and Elton (1942: 363) first popularised the idea that there are three 'herds' which overwinter in discrete ranges in Northern Québec. Both were drawn to these observations by a nameless Naskapi informant (Low 1897: 319). Although local peoples were most likely aware of regions where caribou preferred to drop calves, the search for 'the calving grounds' was only undertaken in 1973 (Goudreault, 1985: 246). The idea of Québec/Labrador caribou herds as a distinct units identified with a discrete space was published for the first time at the end of the 1970s (Juniper, 1979; Le Henaff, 1980). As late as 1988 'incidental reports from residents of the Ungava' led to the formal identification of another population, the Torngat Mountain herd (Schaefer & Luttich, 1998: 486).

The penetration of local knowledge and the process of identifying calving grounds seems tighter in the northern Yukon, although the process is poorly described. Murie (1935: 68-9) in his discussion of the 'migratory habit' of 'northern herds' quotes an 'Indian at Old Crow Village' who identified that the caribou of the Northern Yukon effected North-South migrations to the coast where they 'mingled' with other groups. The recent work of Kofinas (1998: 171) implies Gwich'in hunters spoke consistently of a preference of *R. t. granti* for certain calving 'localities' as early as the 1940s but that this idea was acted upon by biologists only at the end of the 1950s. His interpretation comes from a rather nicely phrased manuscript observation by the local hunter Knut Lang (1952):

> *I believe, as many old natives do too, that the cows prefer to return to localities where they raised their fawns the previous year, and the young animals like to return to the parts in which they were born, if no serious hazards prevent it.*

This statement refers to discussions with Inuvialiut and Gwich'in people from 1922-52. Although this observation is quoted in at least in one significant Canadian government report (Kevan, 1970), there is no surviving evidence that it or the three decades of previous personal communications had any direct effect on biological field work or concept formation. The only hint of past debates is the rather modest and defensive way that the old man insists on this idea, as if he already realised that he was contradicting closely held ideas. The final signpost to the possible existence of a dialogue with local hunters as to the migratory behaviour of populations comes from the classic work of Ronald Skoog (1968) himself. In the two places in his epic dissertation on Alaskan caribou where he discusses the propensity of caribou to return to regular calving grounds (pp. 103, 213-14) he exclusively cites literature referring to the calving habits of semi-domesticated reindeer either in Alaska or in Scandinavia. His key authority is Palmer (1926). This general model of comparing the behaviour of semi-domesticated reindeer with migratory caribou is hallmark of the thought of aboriginal reindeer herders.

What is remarkable about this example of the blending of local and scholarly thought is not the seamless and anonymous manner in which it occurred but the speed with which it took root. From an epicentre in Alaska and the northern Yukon, the idea diffused quickly across North America such that by the mid 1970's the entire map of North America had been divided up into a series of bounded and generally mutually exclusive territories representing the 'range' of a particular 'herds' (see, for example, Hemming, 1971; Williams & Heard, 1986; Crête *et al.*, 1990). This development, again to the eyes of an outsider, represents a remarkably quick adoption of a common paradigm and a corresponding rapid amnesia concerning older models of caribou and reindeer dispersion. For example, pre-1960 works tend to characterise caribou movements as 'nomadic' and somewhat unpredictable. The images range from subtle descriptions of relative density (see the illustration in Murie, 1935: 51) to nuclear-age comparisons with effect of magnetic fields upon metal filings (Banfield, 1954: 17). There seems to have been much ambivalence concerning the sudden appearance of the hypothesis of calving ground fidelity as a description of caribou social structure. The fine ethological work by Pruitt (1960) uses the words 'herd' and 'calving ground' in quotations. Banfield's (1954: 23) flatly rejects the idea that there can be a concrete 'calving ground' and instead describes populations of cows dropping calves in a wide arc along a general trajectory. Skoog (1968: 213) identifies herds as sub-populations displaying 'an attachment of sorts, for certain portions of their range (especially the calving grounds)' [parenthesis in the original] and in his strongest formulation uses an optical metaphor to categorise them as merely 'a focal point for population dispersion' (1968: 202) and 'which encompasses the best habitat' (1968: 356). Skoog's seminal idea of a 'focal' point is perhaps the most honest rendition of a process whereby a complex set of ideas was very quickly 'refocused' in order to emphasise management priorities. In the next section, I question whether the notion of there being calving 'grounds' which attract 'discrete and fidel herds' is a useful concept from the point of view of local interests.

I do not think that in identifying four discrete instances of overt or implicit conversations between scholars and local peoples that I am establishing anything new. In this boreal community of scholars and locals, as in any other community, it is only common sense that these intetested groups should be talking, comparing models, and learning from each other. However in discussions about the comparative virtues of 'science' and 'TEK' it seems that this element of common sense sometimes gets overlooked. Rather than inventing a story of a recent *détente* between these groups, which are now often colleagues on co-management boards, it is useful to reflect on the fact that there has been conversation for at least a century.

Scientific interest is not a stable configuration but one that can be calibrated, focused or refocused. It is, therefore, possible to identify a set of unprincipled calibrations orchestrated to ratify certain 'globalising' conceptions - such as gradualist evolution or the idea of a 'caribou [population] crisis'. Ingold (1993) argues that concepts which seek to attain such an overarching perspective risk negating the meaning and indeed the purpose of scholarly inquiry. At the same time, it is possible to identify cases where local and academic voices merge and become indistinguishable as in the two examples of the identification of discrete forms and identity structure of *Rangifer* populations. By establishing that scientific interests have a rather wide 'focal length' for calibration, it becomes possible to atgue for more negotiation on what exactly are the common human interests in deer, rather than assuming that 'TEK' and 'science' are mutually exclusive bodies of thought. Like wild and semi-domesticated *Rangifer*, 'TEK' and 'science' are in fact part of the same species.

Finally, this history of collaboration between scholars and local peoples can be used to illusttate one important point in the controversy between 'scientists' and proponents of 'TEK'. If there is any widely recognised role for 'TEK' in the study of *Rangifer* it is merely as one technique of many which is useful for gathering data on the nature of reindeer and caribou. In contemporary studies of co-managed populations, the words of knowledgeable elders occupy equal space but do not carry equal weight among graphic representations of recent aerial surveys or satellite tracked deer (Kofinas, 1998; GRRB, 1997; Legat *et al.,* 1997). If there is any single lesson to be learned from studying the history of collaboration between scholars and local people it is that the insights generated from these conversations are far more profound that just a set of statements which can later be proved or disproved by experimental techniques. Instead, these conversations tend to lead to the heart of the matter through the formation of several fundamental categories and by direct attention of field workers to significant observations. Thus if 'TEK' is to be merely one of many techniques in the tepertoite of scientific study, this will represent a considerable demotion in the significance of this dialogue. Instead of condensing 'traditional ecological knowledge' into a neat acronym which merely supports more articulate expositions of population dynamics or systematics, it would seem more appropriate that this alliance of interest be spelled out in detail.

Human interests in the cultivation of *Rangifer*

Up until this point I have considered the histoty of common interest between anthropologists, biologists and local hunters and herders which has manifested itself in historically stable categories of 'herd fidelity', systematics and somewhat less fortunate ideas of management and social evolution. I have also suggested that the history of this common intetest can be categorised as a series of principled and unprincipled alliances. In considering the shape of possible future alliances I will instead concentrate upon recent instances where scientific interests are becoming calibrated with those of local communities. I have deliberately chosen the word 'cultivation' for this process both to underscore the idea that hunting, too, is a productive activity but also the idea that 'savage' local thoughts are also 'cultivated'. Many examples of this cultivation have been exercised by local populations for centuries and have now been undertaken anew by tegional and First Nations administrations engaged in co-management of local populations of *Rangifer*.

Cultivating difference in Rangifer

As has been implicit from the start, I have not made a strict division between migratory, semi-sedentary, and semi-domesticated *Rangifer* but have followed Evenki and Dolgan consultants by considering them all a single species with differing behavioural and ecological qualities. The lumping of vatious sub-types of *Rangifer* as members of a single taxonomic species has been accepted since the works of Flerov (1922), Sokolov (1937) and Banfield (1961). Moreover, as every reindeer herder knows and fears, there is very little practical difference between the physiology of so-called wild and semi-domesticated populations such that the unexpected arrival of migratory *Rangifer* in the Spring or during the rut can easily break the domestic hold that people hold over 'tame' *Rangifer*.

There are of course some important morphological differences between semi-domesticated reindeer and migratory caribou which may stem from the domestication project itself. World-wide, biologists and herders distinguish the reproductive cycles of the two sub-species such that the rut and calving period is separated by several weeks. Without this crucial difference it might prove impossible to hold semi-domesticated *Rangifer* at all. As Banfield (1961) notes, in Siberia, pelage is an important second qualifier. Finally, as Druri (1949: 60-61) notes, the differing travels of the two types imply that migtatory *Rangifer* are a better fed and better culled which holds implications for their behaviour and health.

Despite the current unanimity on the circumpolar specificity of *Rangifer*, there has been a remarkable elaboration of the debate as to which groups nevertheless represent different discrete sub-species. Again, this debate is not surprising from either a scholarly or practical viewpoint. To argue that all *Rangifer* are similar is not to argue that they are the same. However what is surprising is the fact that authoritatively ratified differences at this level tend to hinge upon identifying elusive morphological qualities, which are closed to modification, rather than considering behavioural qualification, which are open to cultivation. It is this aspect which turns out to be most at odds with both local assumptions but local interests. This sub-section will argue that a range of historically stable behavioural traits in *Rangifer* constitute a distinction which can be useful in organising scholarly activity. It will do so through a set of questions on morphology and with examples of successful biological studies of behaviour.

The manner in which various taxonomic clines are segregated, or gradually blend, is a mystifying area for an anthropologist reading the zoological literature. In tracing the history of these ideas it would seem that the search for objective typological considerations are not entirely unrelated to the search for manageable sub-populations of *Rangifer*. The best example of this overlap is in the work of Banfield (1954) who often intertwined the concept of 'race', 'herd' and 'population'. However, what makes this search seem forced is a large set of anomalies in the circumpolar literature on morphological classification. Working from the ideas of the Number One Reindeer Brigade in Taimyr and some recent conversations with Gwich'in hunters, it would seem that a number of these typological paradoxes could be better resolved with reference to behavioural parameters.

One of the most anomalous populations in the literature seems to be that of the northern Yukon ('Porcupine') population of migratory caribou. Although from a relatively early date several wintering grounds and somewhat capricious migration routes have been documented, there has constantly been trouble in identifying the boundaries of the population. Banfield (1961: 58-59) commented that the morphological identification of Alaska-Yukon caribou was the 'most difficult problem' in his revision of the genus. The difficulty for Banfield and other scholars came from the exchange between semi-domesticated reindeer of the Mackenzie Delta

(*R. t. sibiricus*), barren-ground caribou (*R. t. groenlandicus*) of the 'Bluenose' population, semi-sedentary woodland caribou (*R. t. caribou*) of the upper Peel river (Farnell & Russell, 1984; Watson *et al.*, 1973) and Alaskan 'herds' of *R. t. granti* (LeResche, 1975; Skoog, 1968: 259). This was challenging for those, such as Banfield (1961), who tried to identify 'pure races' and for various generations of managers who have tried to estimate population size. It also poses a particular challenge for the North American orthodoxy of the 'herd' with calving ground fidelity because a large proportion of the *Rangifer* there do not have a distinct calving area. The 'traditional calving ground' may be a successful idea in so far that it identifies a rough region where aerial surveys can be conducted but it does not capture all the complexity of the relationship between *Rangifer* and the landscape.

The paradoxes of the 'Porcupine' population have led some scholars to suggest a revisiting of Banfield's (1954:23) idea that *Rangifer* develop a trajectory upon which caribou drop calves - but not a 'calving ground' (Surrendi & Debock, 1976). Farnell & Russell (1984) suggest the necessity of experimenting with ideas of distinct or 'traditional' rutting areas in this region (Fatnell & Russell, 1984). Although the idea of a traditional calving ground is also a behavioural distinction, it is one that somewhat mechanically depends upon a concept of instinct or a propensity to 'home in' to a particular spot in the landscape. The ideas of a calving trajectory, or a rutting area, represent a different set of behavioural attributes better suited to ecological relationships. At the very least, these ideas are echoed well in local ideas about these populations. For local hunters, the disappointing tendencies for *Rangifer* to be 'unfaithful', 'indiscreet', or 'unpredictable' only adds to the beauty of a landscape which can be counted upon to offer wholesome meat in any season at a number of different sites. The task in this instance becomes understanding what factors led various forms of *Rangifer* to choose differing routes or trails, rather than assuming that *Rangifer* is bound to a single route. It is this interest which dominates conversations in the Gwich'in community of Fott McPherson. Many factors influence the complex migratory pattern of *Rangifer* according to Gwich'in hunters. They may refer to the quality of snow cover or the effect of fires. Or, they may refer to the impact of the scent of recently translocated musk-oxen or the garbage littering the side of the highway. While a focus upon different migratory propensities (rather than specific calving sites) may not directly imply that people have a cultivating influence like the way that a herder 'breaks' a young bull reindeer, it does open the possibility that the landscape can be made attractive to *Rangifer*.

The ecological and behavioural moments distinguishing various grades of *Rangifer* has been echoed in recent biological research. Bergerud (1996) makes a strong argument that the zoological distinctions between barren-ground and woodland caribou be abandoned in favour of an *eco-typical* distinction between *Rangifer* which choose a semi-sedentary strategy and those which choose a migratory strategy to avoid predation. This corresponds to the reports of other researchers who have identified a difference in type, for instance, between Taimyr or Québec/Labrador caribou on the basis of their behavioural propensities (Michurin & Murenko, 1966; Harrington, 1991).

To an anthropological eye, it is striking how much the discussion of 'race' in *Rangifer* studies overlaps with politics, just as politics distorts the discussion of race in studies of *Homo sapiens*. One difficulty with identifying the typological discreteness of 'Porcupine' caribou is that they are not the property of a single nation-state. This is not the case with Québec and Taimyr caribou. In both cases, intensive study has led local zoologists to suggest unique names for these populations. Thus there was a very energetic but evidently unsuccessful movement to have the populations of *R. t. tarandus* in Taimyr renamed as *R. t. taimyrensis* (Michurin, 1965; Pavlov *et al.*, 1989). Recently a morphological study of the 'George River' herd in northern Québec suggests that they have physical qualities distinct from other populations (Couturier *et al.*, 1989). I do not want to suggest that these physical differences are 'imagined' in either population but as with the discussion of human race it seems more likely that these populations are large enough to be in turn distinguished into even more discrete categories, as local hunters in Taimyr do, on the basis of behaviour.

This logic of being attentive to the strategic and behavioural qualities of *Rangifer* is the subject of my own research into the local understandings of 'wild' (*baiur*) and 'tame' (*oror*) reindeer amongst Evenki hunters and herders in Siberia (Anderson, 1998; 2000). Although Evenki 'tundramen' make a linguistic difference between migratory and sedentary *Rangifer* they see the actions of people as one significant factor which determines the predictability of the movements of the deer. Through careless actions, a semi-domesticated 'herd' can 'go wild'. Indeed their major critique of state management policies since the 1960s is that their Evenki reindeer have changed in behaviour to such a degree that they are becoming similar in type to 'wild' migratory reindeer. This process usually begins because of political pressure to increase herd size, which in turn leads to reindeer losing their gregarious consciousness of 'herdness'. These bureaucratically managed 'wild' herds may bolt back to older abandoned pastures or to be swept away by an irrupting wild population (Syroechkovskii, 1984; Klokov, 1997). Instead of using a different set of concepts or terms to study semi-domesticated, semi-sedentary, or migratory *Rangifer*, local herdsman use the same set of conceptual tools. This includes a seamless identification of fotage and pastures to identify good spots to cultivate wild and tame deer, a knowledge of places which are preferred migration routes and ritualised notions of respect which are important for attracting or holding both types of *Rangifer*. Many of these ideas of the unity of wild and tame populations have been built into classic Russian works on wildlife biology (Naumov, 1933; Slobodnikov, 1935). Although the local ecology of Taimyr has been severely disrupted both by industry and by the 'rational' hunts of meat-hungry state planners, older herders still speak fondly of 'their' own reindeer which they may have raised by hand as well as 'their' own wild reindeer which they greeted at special places in the mountains twice a year as they effected their regular and predictable migrations.

An emphasis upon behavioural gradations or contingencies in *Rangifer* may not be a classic zoological strategy but it is an interesting area which serves to underscore human interests in *Rangifer*. One clear example of how ecological and behavioural research can supplement taxnomic categorisation is in Daniel Clément's work (1995: 427-8) on Montaignais ethnozoology (translated from French):

> *In describing phentotypes, the habitat of an animal is perceived by the Montaignais as one of the criteria for describing phenotypes and taxa. ... Therefore, for the Montaignais, or at least for those who participated in our survey, there exists at least three terms for distinguishing caribou as a function of their habitat:* minâshkuâu-atiku *'the caribou of the forest',* mûshuâu-atîku *'the caribou from the place where there are no trees' and* uîmipeku-atîku *'the caribou from the ocean shore'. ... A mammologist would recognise only one sub-species for the caribou present in the territory {traditionally} occupied by the Montagnais:* Rangifer tarandus caribou.

The measurement of morphological differences may seem objective and replicable (and may indeed be so) but it is a scientific endeavour closed to considerations of the effect of people on landscapes. However a discussion of behavioural distinctness opens the consideration of anthropogenetic influences on *Rangifer* populations. The radical thought of knowledgeable Gwich'ins, Evenkis and other circumpolar peoples is that their own actions towards *Rangifer* and towards the landscape in which *Rangifer* travel directly effect the behaviour and, thus, the discreteness of those populations. These actions may range from strictures on personal appearance and demeanour, such as the way that one speaks about caribou or keeps one clothing clean during a hunt (GRRB, 1997: 25, 37), and ranges to way that one should keep the landscape clean of distracting litter (Zoe *et al.*, 1997) to altering the landscape with corrals or fences (GRRB, 1997). All of these are examples of ways that migratory *Rangifer* can be cultivated.

I do not want to argue that personal models of behaviour should replace the study of morphology, or the study of *Rangifer* aggregations which facilitate aerial surveying. However, I do want to suggest that attention to contingent behavioural factors is not only an interesting topic but a topic which is allied closely to local concerns. Moreover, ir opens the discussion of techniques of landscape management which can be used directly or indirectly to attract *Rangifer* populations.

Managing movements

The link of human action to a study of the discreteness *Rangifer* populations opens up an area of 'management tools' which may not be as disruptive to local communities as are the tools used to measure and control population dynamics. The well known ethological biases of local, circumpolar peoples in understanding *Rangifer* have different management implications. Almost all circumpolar communities that I have encountered, or have read about, identify their local populations of *Rangifer* with the places where those deer can regularly and predictably be encountered. I have yet to hear of or encounter a local community which has developed a passion for surveying, tagging, and enumetating its local population of deer. Rather than assuming that this lack of interest in concrete numbers represents a lack of discipline, as suggested by 'savage survival' models of the past, it might be constructive to focus on that area of human action in these local communities which is strictly regulated in day-to-day life. I suggest that the more principled management interest in the circumpolar north is not the use of aerial surveys or satellite tagging but the strict and subtle management of the movements of people and deer. This can be illustrated with reference to two literatures - the older 'pre-calving ground' North American literature and also the Soviet literature on *Rangifer* behaviour.

In the older scholarly literature on *Rangifer* there is much to suggest a strong alliance of interest in *Rangifer* habitual movements. Older models of *Rangifer* aggregations show not so much an interest in identifying those places where *Rangifer* gather so that they can be easily counted from an aeroplane but instead where *Rangifer* are practically encountered by both biologists and hunters. Murie (1935), Banfield (1965), Bergerud (1973) all place the emphasis in their models of *Rangifer* discreteness not upon where deer drop their calves but upon where herds *over-winter.* Although the wintering grounds may not be distinct not repeated they are significant if one wishes to know *Rangifer* in order to interact with them.

The subtle study of *Rangifer* movements is a hallmark of Soviet ethology science. The fundamental work of I.V. Druri (1949: 39-43), for example, uses a relational and behaviour definition of 'aggregation' (*stado*) which changes by season and activity. Borrowing language from local herders, winter activities of deer are described as somewhat unstructured and chaotic. Spring and summer actions, on the other hand, are described using the language of reindeer husbandry (*pastitsia*, *vstrechat'sia*, *vypas*). Empirically, the 'herdness' of *Rangifer* is shown to vary during the microecological conditions of each season. An emphasis upon the behaviour foundations of migrations and social structure also characterises the work of Baskin (1969; 1970). Syroechekovskii (1990; 1995: 47) is well known for his colourful metaphors of kaleidoscopic and pendulous movements of *Rangifer*. While these descriptors again make *Rangifer* seem like rather logical mechanisms, they do suggest a rather more complex set of relations between populations and landscapes than a fixed or centred 'calving ground'.

The relational character of Russian work on populations is also evident in the broad way that populations are characterised on a regional basis. The Taimyr population of caribou is usually described on the basis of its migratory behaviour and in direct contrast to the North American school, not by its calving areas. Typically, the population is distinguished by Western and Eastern 'flows' (*potoka*) (Geller & Vostryakov, 1984; Kolpashchikov *et al.*, 1989) and not by the fact that it has three discrete calving regions (see Pavlov, 1996). It is ironic to imagine that if the pioneering work of Skoog (1968) and Bergerud (1973) had been conducted on Taimyr we would be today writing of the Vorontsovo and Agapa 'herds' rather than a single Taimyr 'population'.

The interesting aspect of the story of the study of population behaviour in Russia is that the *lack* of a model of calving ground fidelity does not harm the management interest. The Russian interest in discrete migratory routes, rather than in discrete calving grounds, is rooted in the state's industrial interest in knowing where to establish their butchering points along the Piasina river. Although the scale of this hunt is rather shocking when compared to the much more respectful way that local hunting is effected, this interest in migratory routes can clearly be seen to stem from careful consultation with local observers and a clearly formulated alliance of scholarship with respect to harvesting.

These relational models of migrations are supported by a rather less well known side of Soviet biology and ethology which stresses the voluntaristic and direct effects of people on natural phenomena. This is a rather controversial issue because of the scientific legacy (or heresy) of Trofim Lysenko, who championed a very old Lamarkian argument about the capacity of an organism to control its own adaptation to its own surroundings (which he unfortunstely connected to genetics). However, Russian biology has built upon multiple variants of this argument, just as the work of Charles Darwin also relied upon this old idea (Eiseley, 1964). For example, an entire school of more conservative thinkers have been investigating the zoogenetic effects of large herbivores on the construction of entire climates (Tiskhov, 1985; Zimov *et al.*, 1995). I.V. Druri (1949: 54) in his classic work on wild reindeer directly speculates that the efforts of people might be able to direct the course of migration of wild reindeer. S.M. Druri (1956) reported experiments on the translocation of forest domesticated reindeer into tundra zones of the Kola peninsula. Experiments like this with semi-domesticated reindeer became a hallmark of Soviet reindeer ranching in the 1960s (Anderson, 2000) and reached a fever's pitch with various experiments with the translocation of muskoxen and a recent proposal for the translocation of Canadian wood bison into high Arctic settings (Stone, 1998).

While these portrayals of *Rangifer* as a rather plastic and responsive species might seem unorthodox in contrast to models of movement which stress the importance of forage, 'instinct' and hunger, they do bear a provocative overlap with indigenous conceptions. Evenki and Dolgan pastoralists in Taimyr insist that it is the actions of people which attract migratory *Rangifer* and not the vagaries of climate. Ethnographic accounts from across the circumpolar north stress a similar philosophy. Innu elders in Labrador suggest that the relocations of people from certain regions have dramatically impacted the migratory behaviour of caribou (LIA, 1977: 112, 165; Elton, 1941: 370). While models of forage-controlled migrations are becoming increasingly popular among Gwich'in managers, statements of older hunters also stress the importance of 'luck', proper use of meat and proper care of the land when considering the migration of 'Porcupine' caribou (GRRB, 1997). The hypotheses of local hunters based on their very intimate and petsonal relationships with *Rangifer* have not been given as much direct support in the North American biological literature as in the Soviet literature. However there are models which are compatible. Instead of using models which focus upon the behaviour of *Rangifer* as appropriate to effecting population counts, a signpost to a more subtle alliance with local interests might be an interest in other types of regular behaviour such as repeated migratory water crossing points, habitual wintering grounds, regular migratory 'corridors', and other management tools which lend themselves to *Rangifer* cultivation (Surrendi, 1997; Banfield, 1954; Crête *et al.,* 1991).

To summarise, having established that scientific interests can be calibrated in multiple ways to reflect local interests, this section argued that the scientific study of how to make landscapes attractive for *Rangifer*, and the scientific study of migratory behaviour, represents a possible avenue for collaborative research. I did not argue that studies of morphological discreteness or 'calving-ground' fidelity need to be abandoned. But I did atgue that attention towards how landscape ecology affects herd discreteness, and how human action affects migratory behaviour might be an equally fruitful area of research. In a positive manner, it was shown how Soviet models of *Rangifer* discreteness have successfully incorporated behavioural and ecological information. It was also suggested that a concern for understanding how *Rangifer* choose strategies of aggregation, as well as strategies of migration, reflects not only the views of circumpolar indigenous communities but is also echoed in certain works of North American wildlife biology.

Conclusion: towards an environmental history of *Rangifer*

The intention of this article has been to survey a wide literature on *Rangifer* with the aim of demonstrating an alliance of interests between all circumpolar communities, local and scholarly. This alliance can be demonstrated historically by studying the history of academic disciplines. It can also be demonstrated practically by demonstrating the compatibility of insights on the variability of *Rangifer* or *Rangifer* movement. Moreover, I have tried to establish the need to be conscious of the human interests to which scholarly activity is calibrated. Scholarly concerns which are allied to the nationalist project of states perform a useful role in gathering fundamental data on the size of populations and have developed, in alliance with local people, useful notions of herd identity and fidelity. However these same interests could be better applied to developing an equally rich store of concepts which describe *Rangifer* motions and establish the foundation for a discussion of what kinds of landscapes *Rangifer* finds attractive.

One way to recalibrate biological interests might be to link the history of scholarly categories to the history of communities in the circumpolar North. In his prominent critique of population studies, Bergerud (1996) goes some distance towards constructing an environmental history of *Rangifer*. He calls for the development of complex models of predation, and predation avoidance, which take into account the effect of anthropogenetic effects scaled broadly. For example, he argues the significance of calculating into population models the effects of centralised wolf control programmes, the effect of snowmobiles on wolf harvests and the changing fortunes of fur markets. I would suggest that his graph (1996: 104) might be made even more responsive to human interests by adding in the local use of snowmobiles for hunting and herding. For example, the classic study of reindeer herding in Scandinavia by Pelto (1973) demonstrates that the introduction of snowmobiles into reindeer herding alters the behaviour and attitude of reindeer. Similarly, the shift to snowmobiles by local hunters in the Canadian Arctic simultaneously reduced the need to feed dogs caribou meat in the barren-lands but also changed the pattern and quality of *Rangifer* movements around northern communities. Other human factors might be added such as predation on moose populations (which also will in turn affect wolf populations), or examples of direct local control over wolf populations. An ambitious modelling system might also enter into the equation the effects on *Rangifer* ecology of the massive resettling of experienced caribou hunters throughout the North in the 1950s and 1960s.

The behavioural and ecological hypothesis that I am defending here for the understanding of the nature of *Rangifer* also has far-reaching implications for studying the history of *Rangifer* population cycles. Present accounts of population dynamics rather assume that *Rangifer* macropopulations are discrete entities which have not only been stable since the beginning of aerial surveys in the 1950s but that also reach far back in time. One radical extension of this thought extends the Beverly and Kaminuriak caribou 'herds' back into prehistoric times as geographic markers by which to interpret archaeological remains (Gordon, 1996). A serious consideration of the anthropogenetic capacity to cultivate herds suggests that aggregations are relational entities which respond to current actions. Thus, while it is unquestionable that *Rangifer* have existed for as long as we find remains of human culture, when we know that the history of human communities has changed is it not reasonable to assume that the identity and quality of *Rangifer* populations has also changed? A careful study of environmental history would be necessary to answer this question.

This survey of the literature on the human interest in *Rangifer* suggests that *Rangifer* is a prominent circumpolar species with a special alliance to boreal populations. Both indigenous consultants and biological researchers argue that *Rangifer* do not merely supply food to eat and food for thought but that they also respond to the quality of the ecological setting. While it might be difficult for applied zoology to accept that *Rangifer* are best regulated through keeping one's clothing clean and being attentive to one's dreams, this survey of the literature in the northern Yukon, Taimyr, and Québec/Labrador suggests that the cultivation of boreal landscapes has an important impact on the kind of deer that one would expect to find. This leads to an interesting thought with which to close this review. If *Rangifer* behaviour and population discreteness is a responsive trait, as indigenous hunters assert, then it is entirely possible that the last few decades of state controlled predation in the northern Yukon and northern Québec, as well as 'rational use' in Taimyr, have cultivated a historically unique ecotype of *Rangifer*. This is a hypothesis raised recently by many indigenous observers throughout the circumpolar North. In Taimyr and the northern Yukon, elderly hunters report that contemporary migratory *Rangifer* no longer behave predictably, have become too many, or have 'gone wild'. To extend the ecotypes of Bergerud (1996) one step farther, it might be possible at the beginning of this century to note the existence of two *anthropogenetic* ecotypes of *Rangifer* in the circumpolar North based on a reading of environmental history: *Rangifer tarandus habitus* characterised by a close and intimate interrelationship with local communities who depend on them and *Rangifer tarandus étatocraticus*, whose identity, behaviour and discreteness has been shaped by the strict zoning and licensing regulations of state-sponsored management organisations.

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On nature and reindeer luck

Nils Oskal

Nordic Sami Institute, PO Box 220, N-9520 Kautokeino, Norway (nils.oskal@nsi.no).

Abstract: This paper describes the teindeer Sami understanding of a worthy life expressed in qualitative distinctions centred around the term 'reindeer luck'. Reindeer luck does not in itself mean a good life but is an ingredient of a good life. Reindeer luck lasts from cradle to grave but it can change along the way. To a certain degree it is possible to influence your own reindeer luck, bur you can also spoil it through actions, behaviour, words and thoughts. These ate more important than means-to-end rational actions with the aim of intentionally improving reindeer luck. The paths to reindeer luck are discussed with the aim of articulating the moral ideals implied in this type of understanding. This theme is discussed in regard to what we may learn from relations to natute.

Key words: herding, moral luck, nomadism, pastoralism, *Rangifer,* Sami.

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Do aboriginal societies really possess a kind of 'primitive ecological wisdom' and what is the content of this wisdom? I will try to answer this question by examining the place of reindeer in Sami reindeer herders' conception of human agency and nature.

Both natural scientists and reindeer herding peoples are engaged in interaction with reindeer. The main source of data on how herders and scientists perceive and interact with this animal is the language that is used to describe it and the explanations of the ensuing descriptions. A common view has been that herders' perceptions of reindeer differ from the 'real *Rangifer*' owing to their ordering their observations according to their imposed cultural scheme. The perception of teindeer is perhaps in every case cultutally defined and made meaningful through practical engagement and cognition. I think this is relevant for scientific perception and interpretation of reindeer, too. Hence, the difference between a scientific and native perception of reindeer is not a question about the cultural characteristics of knowledge but about the validity of knowledge.

It is a well established and accepted view that traditional knowledge has no cross-cultural validity. Its validity is widely held as internal to a particular language and culture. Scientific knowledge is clearly widely perceived as having cross-cultural validity. This is not necessarily untrue but it should not be treated as a dogma with no need of proof or refutation. The privileged status of scientific knowledge cannot be assumed a *priori* and it is rather a question of accurate and concrete argumentation from case to case.

Human societies differ greatly in their culture and values. They present different ways of being humans. The problem of the cross-cultural validity and commensurability of knowledge involves aspects of morality, our ethical approach to facts and the validity of empirical knowledge. There may be different kinds of human realisation which really are incommensurable but commensurability is a question of how far articulation can be extended. It might be that our contact with certain cultures will force us to accept the incommensurability of different kinds of knowledge but we cannot assume this *a priori.* Until we meet this limit there is no reason to take for granted that the conception of good in other cultures has nothing to say to us or perhaps ours to theirs.

However, my main concerns are ethical and moral questions and the place of reindeer in Sami reindeer herders' evaluation of their lives as meaningful, fulfilling, good, etc. Questions as 'Who are we?', 'How is it best to live our lives?', 'What is the best way to understand ourselves and others?' have to be answered with reference to conceptions of the good life and hence to reindeer.

After these preliminary comments, I will attempt to articulate reindeer Samis' understanding of what is human and what is a worthy life, as expressed in qualitative distinctions centred around the concept of 'reindeer luck'. My aim is to articulate the style of reasoning concerning these types of questions. The following might be an example of reindeer Sami conceptions of the telations between humans and nature as these were expressed for 30 or more years ago. I do not pretend to give a social scientific investigation of the empirical distribution of this style of reasoning or to analyse how moral reasoning is changed. Of course, moral concepts change as society changes but not because society changes. I do not suggest that society and morality are two different things and that there is merely an external, contingent causal relationship between them. Moral concepts are embodied in and are in a particular way constitutive of forms of society. One way in which we may identify one form of society from another, as identifying social change supposes, is by identifying differences in moral concepts.

The Sami writer Johan Turi (1854-1936) wrote that knowledge is not enough to ensure success in reindeer husbandry and trapping (Turi, 1910). One must also have luck. We each have ten adult female reindeer. In the spring yours have eight calves, seven females and one male. Mine have five calves, three females and two males. By autumn seven of yout calves are alive, while only three of mine have survived. The following years are similar. Why? At this point we can say that you have good reindeer luck, while mine is not so good.

There is a difference between reindeer luck and plain luck. Reindeer survival can be ascribed to eithet, or more correctly, plain luck can come from reindeer luck. Reindeer luck is not co-incidental. You are lucky if the summer grazing land is good or if no avalanche takes any of your reindeer in winter. This could be plain luck or reindeer luck depending on whether it was an accident or not. For example, your reindeer luck can even improve if the summer grazing land is bad or the avalanche is just taking its due. If such is the case, being lucky or unlucky is not an issue. It is easier to describe plain luck than reindeer luck. You have reindeer luck if your reindeer survive and the herd prospers. The cows calve. The herd is healthy, well provided for and beautiful.

The herd is beautiful if it is composed of many reindeer of different shapes and colours giving it a picturesque unity with contrasting black and white in different patterns. In addition, it should contain many adult bulls and animals of all ages. But a colourful reindeer (*girjjat*) in itself is not necessarily beautiful. Reindeer with large contrasting spots (*lamsku*) are not necessarily considered beautiful and do not bring reindeer luck with them. But, while colourful reindeer are not necessarily attractive, they can be useful in many situations. Everyone in the *siida* (herding group) remembers particular colourful animals and will immediately notice if any one is missing - and in that way will also notice if other reindeer are missing, something which might otherwise not have been noticed until much later. It can be difficult to locate a herd in summer and colourful reindeer are therefore useful because they are conspicuous. With good reindeer luck rhere can be a beautiful and large herd. The herd should not just be large, it should also be beautiful. It should not be just beautiful but also large. But it is preferable to have a small and beautiful herd rather than just a large herd. To be rich in reindeer is not a goal in itself but it is a value. You can say that there are enough reindeer to meet your needs even though it wouldn't hurt to have more. It is rare to meet anyone who complains about having too few reindeer because this would insult the herd.

Reindeer luck lasts from cradle to grave but it can change along the way. You can influence your own reindeer luck through actions, behaviour, words or thoughts. These are more important than working to improve reindeer luck. To a certain degree you can improve your own reindeer luck but you can also spoil it, sometimes for a long time. Reindeer luck has certain unique characteristics that neither fishing luck nor dog luck have.

Some people have good fishing luck. When, for example, two people who know the water and weather equally well, fish at the same time and same place and get dramatically different results, we say that the succesful person has fishing luck. Fishing luck also lasts a lifetime and it can get better or worse. Where it comes from is unclear but it certainly has something to do with how the lake and the fish are treated. Acting in an unrestrained manner, swearing, or making fun of the lake or the fish is not good. It is better to focus on catching fish and to show interest in the fish. Catching only as many fish as one needs and taking special care of the catch is also important. You can borrow fishing luck from others but you cannot lend it. If I have bad fishing luck I can borrow yours and fish in your name and in your place. Then perhaps I will catch many fish. I can borrow it when I need it and so can others. I don't need to ask permission, I just think that I am borrowing your fishing luck and it is done. You can't lend it and neither can I. Nor can I spoil your fishing luck while I am borrowing it. I can only spoil my own. Fishing luck is seen as a resource and a blessing which can be used for common benefit.

Those who have dog luck have good and talented dogs which can perform all types of reindeer work: gathering, driving, fetching, separating and guarding the herd. A clever dog can anticipate problems and take measures to protect the herd on its own. A herder may not realise until later what the good dog has done. It doesn't need commands or discipline. It works independently and uses its own judgement. For a dog to become a good herder is, of course, dependent on how it is raised. But it isn't enough just to train a dog showing interest and treating the dog with care are necessary to have good dog luck. Some people have good dog luck and it is said about them that they have dog luck in their armpit (*beanalihku gidavuolli*) and this is considered a personality trait.

Fishing luck comes from how you treat fish and lakes and dog luck comes from your treatment of dogs. Reindeer luck doesn't just come from how you treat reindeer although that is included. Reindeer luck is dependent on how you live your life and it cannot be lent or borrowed. Whoever has reindeer luck can stabilise their herd, increase it and eventually become tich in reindeer. But a large herd is not enough, it must also be beautiful. Normally a large herd is beautiful, but not because it is large. If there are too many calves in relation to cows, and too many young cows in relation to adult cows, a herd is ugly both aesthetically and morally. You have not bred your own herd but scraped it together somehow. You can slaughter many reindeer, have plenty of food, be generous and be well supplied in many ways. The herd does not become smaller through slaughtering. Your reindeer survive and are healthy even if they do not grow in number. Then you have reindeer luck. Numbers alone cannot determine reindeer luck. Not evetyone rich in reindeer has reindeer luck. The reindeer may have been inherited, received as wedding gifts, or stolen and re-marked. To determine good reindeer luck the reindeer must survive over time. On the other hand not everyone who has a small number of reindeer has bad reindeer luck. Both the number of reindeer and the degree of reindeer luck can vary over time usually in relation to age. A child usually has few teindeer and herd size is reduced as old age comes but neither are any reflection on reindeer luck. Whether your number of reindeer means that you have reindeer luck today is not a meaningful question. In the first place you should not attempt to determine the exact number of reindeer. Determining the exact number of animals in a herd can spoil reindeer luck and can lead to bad reindeer luck (*guorzuluvvot*). I know approximately how many reindeer I have and sooner or later I will know how many survive. You shouldn't challenge your reindeer luck with accounting.

To speak about exact numbers of reindeer is seen as being confused and half asleep but that doesn't mean you should be so ignorant that you don't recognise your own reindeer or fail to notice if any are missing. People who may be good at recognising reindeer and remembering each reindeer as an individual but that is different from keeping exact accounts. Our humanity does not require us to be rich in reindeer and richness in reindeer is not a sign that we are honest, just and honourable. A large herd is good but not a moral obligation and not a sign of our moral stature.

In addition everyone has their lot in life. That lot is usually though not necessarily consistent because it can only be measured when the herd experiences a catastrophe. When you experience a catastrophe that reduces your herd considerably and it is usually said that the herd flowed out beyond your lot in life. It is rare to experience more than one large reindeer catastrophe in a lifetime.

Number of reindeer is not synonymous with the good life. A person rich in reindeer can be unhappy and a person with few reindeer can be happy. Unhappiness can take the form of not having a spouse or children. Reindeer luck does not in itself mean a good life but is an ingredient of a good life. Reindeer luck can get improve or worsen. It can be ruined but not improved for the sake of improving it. It improves if you live a value-driven life. You should be humane, honest, fair and honourable but these values do not automatically belong to everyone with a large and beautiful herd. How your reindeer luck develops depends on how you live as a person, not just how you handle reindeer.

You should not overwork draught reindeer, frighten them or force them to work but be observant and patient especially when they are tired. You should always keep in mind that when a draught reindeer cannot work it is not because it is lazy but because it has over exerted itself and is exhausted. In general you should handle the sled reindeer with kindness. To not feed draught reindeer properly is seen as insulting them.

The herd should not be thought of or treated as a means. It has a value in itself. It is considered in bad taste to point out a reindeer as fat or thin or point out an animal as a means to an end, such as a future meal or clothing. This insults the reindeer. The hide belongs to the animal whereas the clothing made from it belongs to people. These should be kept separate. It is acceptable to remark on how large the reindeer is and whether it is fatter or thinner than before. This is not insulting since you are comparing it with itself and not in relation to some external purpose. You may castrate a reindeer with a view to taming it as a draught reindeer or to fatten it up but a castrated reindeer is still a reindeer and should never be treated as transportation or a walking larder. Such behaviour would be less than human. You should always hold your own herd in awe and never disparage or devalue it. Therefore you never say that you have too few reindeer since that would belittle it, or that you have too many, for that would challenge reindeer luck. This would dishonour both the herd and yourself as a human. One way to honour the herd is to put on better clothes when seeing the reindeer corralled for the first time in autumn or when milking the cows the first time after the rut.

Reindeer Sami know that the survival of reindeer depends on how well you get along with others. It is important to know people not as just individuals but also their family line and their situation and to grasp situations quickly and negotiate without either being presumptuous or unfocussed. It is believed to be impossible to drive someone out of reindeer business if they have reindeer luck. But that doesn't mean that all sociable people have reindeer luck.

Being honest, just and honourable means that you can get along with others but you must also get along with places - pastures, migration routes, calving places - anywhere that can be considered a home to the herd. Such places have protective spirits which you must also get along with somehow. An appropriate way is to ask for permission from the land and to make requests of the land.

Both the reindeer and the reindeer Sami have strong ties to grazing land. Ancestors, memories, stories and conversations in general would be empty without reference to their particular setting. There is little to remember or tell without including the landscape which gave form to these events. It is not an accident that wishes and enquiries are addressed to the grazing land and that a place is remembered through *yoik*, embellished, made happy and invoked like an old and loyal friend.

You can come into communication with a *sieidi* (a sacred place in nature), persuade and prevail upon it. In addition you can make an agreement with the *sieidi,* idolise it and build up a trusting relationship with it. One way to get a large and beautiful herd is to make such an agreement with a *sieidi* and serve it. A grazing land is not the same as a *sieidi* but it may contain several *sieidi.* But this is not a good way because even though you will get a large and beautiful herd you will not get reindeer luck. There are two types of arguments against idolising and serving a *sieidi.*

The first atgument is that the herd of such a person will not last longer than the lifetime of that person and barely that. The descendants will be without reindeer and the herd will disappear when the server dies. The other argument is that serving a *sieidi* is to worship it. It becomes an idol and worshipping idols is a sin. Both Johan Turi and Lars Hætta (1836-1897) mention both arguments, Turi emphasised the first and Hætta the second. Indignantly, Hætta reported that the reason Rasmus Andersen Spein (1819-1894) stopped serving a *sieidi* was not because of any feeling of sin but because the *sieidi* had become too headstrong. Spein maintained that he hadn't done anything wrong but it was the *sieidi* who had done something wrong. (Hætta & Bær, 1982). Johan Turi makes a fine distinction between serving a grazing land as if it were a *sieidi* and making requests of it. Turi rejects serving a *sieidi* but richly describes getting along with a grazing land. Turi's description of coming to terms with the grazing land goes beyond making wishes and comes close to making agreements. One gives gifts, returns gifts and pays tax to the protective spirits to ensure that they take care of the herd. But to Turi this is not the same as giving gifts to and making agreements with a *sieidi*. Turi's distinction is perhaps better expressed in implying that the grazing land takes rent, rather than that we pay rent to the grazing land. Even if you do not serve or idolise a *sieidi* you should still not insult, ridicule or tease it. To act respectfully, humble and polite toward the *sieidi* is not the same as worshipping it as an idol. Normal politeness indicates that you should greet it and wish it well in your thoughts when passing by. It is unheard of to argue with a *sieidi* or enter into conflict with it. It is best to wish it peace and leave it in peace.

Another way to get a large and beautiful herd is to steal reindeer, either to avoid slaughtering your own or to increase the size by re-marking another person's reindeer. The same arguments apply against stealing: it is a sin and the herd will not survive the thief's lifetime nor will there be any reindeer luck to pass on to descendants. Reindeer luck belongs to an individual and cannot be lent or borrowed. It can, however, be inherited. Reindeer thieves and *sieidi* servers can ruin reindeer luck for their descendants but reindeer luck from someone who has been honest, just and honourable in their life can go in inheritance for up to three generations. You can ruin reindeer luck by stealing reindeer but not every form of stealing is just as bad, and can be looked at from three perspectives: as sinful, as immoral and as a spoiler of reindeer luck.

Part of being human is to ask for permission and make wishes. In some situations it is a desirable way to get along with grazing lands. To do this to a grazing land is to show respect. When you migrate, for example when moving from winter pasture to the calving area, from the calving area to the summer pasture, or from the summer pasture to the autumn pasture you should wish that the migration is free of problems. When moving around inside one area this is not necessary. When you arrive you should wish that the herd lives healthily and safely and when you leave you thank the grazing land for taking good care of the herd. There is no hierarchy, or one all powerful grazing land. There is not just one mother nature but many small mothers. You must relate to each and every grazing land. The grazing lands are neither good nor bad; it depends upon how you relate to them. You do not 'serve' the grazing lands but seek to be in agreement with them. To serve them would be to worship an idol and turn life's purpose into honouring grazing land. You should not speak of your own reindeer luck either to complain about it or to celebrate it. If others speak about it in my presence, I should neither confirm nor deny what they say. Individual occurrences I can describe as lucky but reindeer luck is not dependent upon individual occurrences. Reindeer luck is not the only measure of a good life. How we get along with others, primarily in our *siida,* has much to say.

Children are taught to make a wish when they bring bones and food scraps outside. They should wish for many reindeer. It is important to teach them to use a slaughtered animal fully, since that brings reindeer luck. You should really gnaw the bones well.

Another way to get along well with the landscape is to ask for permission, for example, to camp or sleep overnight even if not setting up a tent. You wish not to disturb anyone and you wish to be left in peace. To ask for permission and to make wishes is part of our humanity and it improves our reindeer luck. But we should do it as part of our humanity and not just to improve our reindeer luck.

What is the path to reindeer luck and what world view is implied in its understanding? In reindeer herding society you should not deny the world by fleeing from it or by trying to dominate or control it. You should not conquer the world but try to get along with it and come to an understanding with it. The relevant stance to the world is not mastery of or flight from it. The way of ascertaining the world is not secured in a passive manner of contemplation or in a manner of affirmation of the world by one-sided adjustment to it. The path to reindeer luck is through a conciliatory spirit and the ability to get along with the world. You cannot justify actions simply to improve your reindeer luck. Good actions should be done naturally, as a habit.

What may we learn by studying the type of culture presented here? Does it possess a 'primitive ecological wisdom'? Sometimes the distinction between nature and culture is inappropriate for describing Sami reindeer herders' understanding of factors they invoke to account for society and the terms they accept to explain human agency and nature. If it is a difference between nature and culture then it is not possible to explain this difference or to resolve it into a single dichotomy.

What we may learn by studying reindeer herding cultures among Samis in regard to ethics and morality is a different range of possibilities of making sense of human life and that can give us a new sense of what constitutes human satisfaction and well-being. This does not mean that it is possible to adapt and emulate the practices and worldview of other cultures. I would conceive that as lacking intellectual credibility. Nor does it imply an appeal for a change in the practice of natural science. It makes claims on us, indeed, only to investigate our own ways of making sense of our lives without adopting ready-made solutions.

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STATUTES

for

ARCTIC UNGULATE SOCIETY (AUS)

§ 1

The AUS was founded in Tromsø, Norway, 1999 to foster studies of Arctic Ungulates, particularly reindeer/caribou and muskoxen, through the continuation of the quadrannual Arctic Ungulate Conference (AUC).

§ 2

The AUS is governed by an Executive Committee, consisting of one representative from Canada, Finland, Greenland/Denmark, Norway, Russia, Sweden and USA, elected by the respective delegations at the first day of each AUC.

§ 3

The Executive Committee shall, in a closed meeting on the day before the closing of each AUC appoint a chairman, and, by simple majority, choose the organizer of the next AUC from among those member nations which at the said meeting put forward an offer to do so.

§ 4

The organizer-elect will be responsible for the archives of the AUC until a new organizer is elected.

These statutes may be amended at any meeting of the Executive Committee, provided the proposal carries a two-thirds majority vote.

Tromsø, 11 August 1999

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Ö. Danell (sign.)
Sweden

M. Nieminen (sign.)
Finland

M. Magomedova (sign.)
The Russian Federation

A.S. Blix (sign.)
Norway

Information

Dissertations

Monica Alterskjær Olsen (b. 1966) defended her thesis; **'Microbial digestion in reindeer and minke whales'** for the degree of Doctor Philosophiae at the University of Tromsø, Norway, April 2000. Olsen completed her Cand. Scient. degree at Department of Arctic Biology, University of Tromsø in 1992. She conducted her doctoral work at the same department, where she is currently employed as an associate professor.

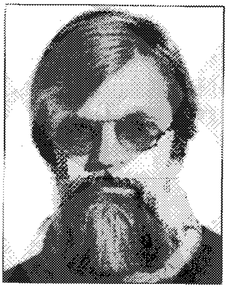
Her doctoral thesis was based on the following seven papers:

1. Olsen, M. A., Aagnes, T.H. & Mathiesen, S. D. 1995. Failure of cellulolysis in the rumen of reindeer fed timothy silage. – *Rangifer* 15: 79–86.
2. Olsen, M. A., Aagnes, T. H. & Mathiesen, S. D. 1997. The effect of timothy silage on the bacterial population in rumen fluid of reindeer (*Rangifer tarandus tarandus*) from natural summer and winter pasture. – *FEMS Microbial Ecol.* 24: 127–136.
3. Olsen, M. A. & Mathiesen, S. D. 1998. The bacterial population adherent to plant particles in the rumen of reindeer (*Rangifer tarandus tarandus*) fed lichen, timothy hay or silage. – *Rangifer* 18: 55–64.
4. Moen, R., Olsen, M. A., Haga, Ø. E., Sørmo, W., Utsi, T. H. A. & Mathiesen, S. D. 1998. Digestion of timothy silage and hay in reindeer. – *Rangifer* 18: 35–45.
5. Olsen, M. A., Aagnes, T. H. & Mathiesen, S. D. 1994. Digestion of herring by indigenous bacteria in the minke whale forestomach. – *Appl. Environ. Microbiol.* 60: 4445–4455.
6. Olsen, M. A. & Mathiesen, S. D. 1996. Production rates of volatile fatty acids in the minke whale (*Balaenoptera acutorostrata*) forestomach. – *Brit. J. Nutr.* 75: 21–31.
7. Olsen, M. A., Blix, A. S., Aagnes, T. H., Sørmo, W. & Mathiesen, S. D. 2000. Chitinolytic bacteria in the minke whale forestomach. – *Can. J. Microbiol.* 46: 85–94.

Abstract: Both reindeer and minke whales have multichambered stomach systems with a non-glandular forestomach allowing retention of digesta and growth of anaerobic bacteria. The objective of this study was to explore the microbiota of these two systems in relation to diet and function. Whales and ruminants had common ancestors about 60 million years ago, and the forestomach fermentation of the prey in whales is probably a remnant from their terrestrial herbivorous ancestors maintained to utilise complex nutrients such as chitin. Reindeer rely on a complex system of symbiotic rumen microorganisms to digest the cell wall carbohydrates of the forage plants that they eat, resulting in microbial protein and volatile fatty acids (VFA). The thesis demonstrates that the numbers and composition of the rumen bacterial population in reindeer change in response to diet. Furthermore, the extent of cellulose degradation was found to be higher in rumen fluid from reindeer on a natural pasture in northern Norway, both summer and winter, as compared to previous results from Svalbard reindeer, indicating a positive effect of the energy-rich lichen in winter on mainland Norway. Viable numbers of bacteria adherent to plant particles in the rumen of reindeer fed lichen were high ($26.5\text{x}10^9$ – $53.0\text{x}10^9$), while numbers of cellulolytic bacteria adherent to the rumen particles were low. Depression of cellulose degradation after prolonged feeding with lichen alone could result from nitrogen deficiency due to the low nitrogen contents in the lichen. Starvation during the winter season greatly influences both numbers and composition of rumen microorganisms with a resultant depression in rumen cellulolysis. Loss of some of the synergistic bacterial species in the complex rumen ecosystem may cause problems when food is again available. Transfer of rumen fluid from sheep appears to help restore rumen function in such situations. Depressed rate of rumen cellulolysis was demonstrated in individual reindeer even 4 – 5 weeks after being re-fed on timothy silage. Slow ruminal fibre degradation was associated with low ruminal VFA concentrations, a high pH and an increase in relative rumen fill compared to other animals eating the same food. Overall *in vivo* cellulose degradation was, however, unchanged indicating that depressed rate of rumen cellulolysis was compensated for either by a longer ruminal retention time and/or by increased hindgut degradation. Numbers of bacteria adherent to the rumen plant particles was significantly lower in reindeer fed timothy prepared as silage compared to hay from the same crop. Likewise, timothy silage appeared to depress numbers of cellulolytic bacteria both in the rumen fluid and adherent to the plant particles. Supplement of easily digestible carbohydrates to the timothy silage seems to stimulate not only food intake but also ruminal cellulose digestion and production rates of

VFA in reindeer. It is recommended that leafy timothy rich in easily digestible carbohydrates and proteins preserved as hay is used as emergency feed for reindeer in winter.

Olsen's studies were supported by grants from the Norwegian Reindeer Husbandry Research Council under the auspices of the Norwegian Ministry of Agriculture, from the Norwegian Research Council, from the University of Tromsø, the Roald Amundsen Centre of Arctic Research, and from Kjellfrid and Helge Jakobsens Foundation at the University of Tromsø.



On June 22, Cand. Agric. Jan Åge Riseth successfully defended his dissertation "Sámi reindeer management under technological change 1960-1990: Implications for Common-Pool Resource Use Under Various Natural And Institutional Conditions. A comparative analysis of regional development paths in West Finnmark, North Trøndelag, and South Trøndelag/Hedmark, Norway." for the degree Dr. Scient. at the Agricultural University of Norway (AUN), Dept. of Economics and Social Sciences.

His supervisor has been Professor Arild Vatn (AUN). The evaluation committee consisted of Prof. Daniel Bromley, University of Wisconsin, Madision, USA, Prof. Carl Erik Schultz, Univetsity of Tromsø and Assoc. Prof. Olvar Bergland, AUN.

The dissertation is a monography, and aims to explain *why the development paths of reindeer management in Finnmark and Trøndelag have been so different* in the period studied. *While Trøndelag during the 1980s has prospered, most of Finnmark at the same time developed an accelerating overgrazing of vulnerable lichen pastures.*

Riseth's basic approach is the multidisciplinary "Institution and Development (IAD) Framework". The framework analyses both ecological and socio-economic factors, and is developed in the research environment around Workshop in Political Theory and Policy Analysis, Indiana University, Bloomington, USA. For the ecological factors Riseth has developed a new herbivore-pasture model for grazing seasonally at lichen winter pastures and "green" summer pastures. The main ecological factors analysed are pasture balance and landscape structure, while hypotheses are developed for a series of socio-economic factors.

The empirical analysis is comparative contrasting West-Finnmark (denoted North) with Trøndelag (denoted South). Riseth finds that under technological change (motorization) in the North both ecological factors are in favour of herd-expanding strategies, while they in the South support herd-stabilising strategies. In the North both (1)summer-pasture limitation and (2) a relatively open landscape with weak natural borders between season pastures, facilitate a gradual out of season grazing from the midst of the 1970s and throughout the century.

For the socio-economic factors Riseth finds that the more extensive exposure to the pressure from the expanding Norwegian farmer society and the resulting Sámi organisation efforts from early in the 20th century, made South herder leaders better prepared for the changes from the 1960s than their fellows in the North. South herders have developed trust and co-operation with the extension service. In accordance with this the main adaptation strategy in the South seems to have been herd stabilisation and production increase, while the main strategy in the North seems to have been competitive herd expansion. In the North the influence of groups being the relative winners of the pasture competition also seems to have been an obstacle for the herder society to take action against the overgrazing.

Riseth was born in 1953 in Snåsa, North Trøndelag. He earned his master degree in natural conservation management at AUN in 1979 with a thesis within vegetation ecology and conservation. He also has studied land use planning, law history and public management. He was a co-worker of the Norwegian Reindeer Husbandry Administration (Reindriftsforvaltninga), Alta, for practically the whole 1980s as "Statskonsulent i reindrift" (Vice Director of Planning, Extension and Information Services) and editor of the Norwegian information journal of reindeer husbandry "Reindriftsnytt". He has worked on many fields related to reindeer management. Most of his writings on the subject is reports, notes and case documents filed in Alta. In 1992 he published the textbook "Reindriftsforvalting" (Management of reindeer husbandry).

In 1990-1992 Riseth was a land use planner of Narvik municipality. Since 1992 he has been an Assistant Prof. at the University College of Narvik. From 1998 he has headed the Division of Environmental Engineering. Riseth has published on issues of waste management. His dissertation research was included in the Norwegian part of the UNESCO research program "Man and Biosphere" (MAB), where he had a scholarship (The Norwegian Research Council, NFR) for the period 1994-1997. In 1996 Riseth was a Visiting Scholar at Indiana University, Bloomington, USA. Since 1999 he has been a member of the working committee of Circumpolar PhD Network in Arctic Environmental Studies (CAES Network) and one of the organisers and lecturers of the interdisciplinary and travelling Ph.D.-course "Reindeer as a keystone species of the North" arranged in Finland, Norway and Russia.

Riseth continues his work in Narvik as an associate professor lecturing ecology, land use planning and resource economics. He is planning further research on reindeer management both oriented towards traditional ecological knowledge and towards property rights issues.

Contact address:
e-mail: jar@hin.no
Narvik University College
Department of Technology
Division of Environmental Engineering
P.0. Box 385
N-8505 Narvik
Norway
Ph. +47-76966134, Fax. +47-76966812

Rangifer
Nordic Council for Reindeer Research, c/o NVH,
Department of Arctic Veterinary Medicine,
Stakkevollvn. 23 B,
N-9292 Tromsø, Norway
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