

Overview of key note presentations

Lectures Monday-Thursday

Monday 9th August

- Lecture 1 Quantifying the free living energy exchanges of Arctic ungulates with stable isotopes.
Dr. Paul Haggarty
- Lecture 2 Functional and comparative digestive system anatomy of Arctic ungulates.
Prof. R.R. Hofmann
- Lecture 3 Viral diseases of northern ungulates.
Dr. Kai Frölich

Tuesday 10th August

- Lecture 4 Rangifer and human interests.
Dr. David Anderson
- Lecture 5 On nature and reindeer luck.
Dr. Nils Oskal

Wednesday 11th August

- Lecture 6 Multi-scale habitat selection and population dynamics of Arctic ungulates: a unifying theory.
Dr. Francois Messier
- Lecture 7 Wild and semi-domesticated reindeer in Russia: status, population dynamics and trends under the present social and economic conditions.
Prof. Eugene Syroechkovsky
- Lecture 8 Biological rhythms in Arctic vertebrates.
Bob van Oort

Thursday 12th August

- Lecture 9 Aspects of the ecology of mat-forming lichens.
Dr. Peter Crittenden
- Lecture 10 Equilibrium and non-equilibrium models of livestock population dynamics in pastoral Africa: their relevance to Arctic grazing systems.
Dr. Roy Behnke

Key note abstracts

NB. The Abstracts of the papers by Dr. David Anderson and Professor Eugene Syroechkovsky have been prepared by the Programme Committee on the basis of submitted manuscripts of the full papers and have not been reviewed by the authors.

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

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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 is important in assessing both their nutritional needs and their ecological relationships. 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 mobilisation 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 the iterative calculation of unknown parameters, have produced a methodology suitable for use in species under truly free ranging conditions. 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 ^2H 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 ungulates.

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Functional and comparative digestive system anatomy of Arctic ungulates

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This review paper addresses the question of dietary niche, feeding type classification and seasonal strategies of *Rangifer tarandus* and *Ovibos moschatus* in relation to what is known on 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. Both Eurasian mountain reindeer / North American barren-ground caribou and Svalbard reindeer / Victoria island caribou is 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.

Viral diseases of northern ungulates

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This paper documents the relevant viral diseases that have been reported in holarctic ungulates, or which could be of potential risk 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 hemorrhagic disease of deer and bluetongue disease, rabies, respiratory syncytial virus infection, adenovirus infection, hog-cholera, Aujeszky's disease, and equine herpesvirus infections. The author found no significant difference 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 a unique position of this roe deer strain within the BVDV group I. This study indicates that distinct BVDV strains might circulate in free-ranging roe deer populations in Germany and that the virus transmission is independent from domestic livestock. Similar results were obtained in a serological survey about alpha-herpesviruses in deer in Germany. In a study about MCF in deer in Germany the seroprevalence and positive PCR results detected in sheep samples, which originate from the same area as the antibody-positive fallow deer (*Cervus dama*), might indicate that in this case sheep are the main reservoir animals. Contagious ecthyma (CE) is a common disease in domestic sheep and goats caused by the orf virus. CE can, furthermore, affect several wild ungulates of the holarctic regions including Rocky Mountain bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), Dall sheep (*Ovis dalli*), chamois (*Rupicapra rupicapra*), musk-ox (*Ovibos moschatus*), and reindeer (*Rangifer tarandus*). Most parainfluenza type 3 virus infections are mild or clinically inapparent. Serological surveys in wildlife have been successfully conducted in a lot of species. In 1985, a new disease was identified in Swedish moose, designated as Älvsborg disease. This wasting syndrome probably has a multi-factorial etiology. Foot-and-mouth disease virus (FMDV) can infect deer and many wild cloven-hoofed animals. In the former Soviet Union, apart from moose and roe deer, the saiga antelope was the main host of FMDV. In addition, serological evidence of a FMD infection without clinical disease was given in red deer in France. Epizootic hemorrhagic disease of deer (EHD) and bluetongue (BT) are acute non-contagious viral diseases of wild ruminants characterized by extensive hemorrhage. Culicoides insects are the main vectors. EHD and BT only play a subordinate role in Europe. However, in North America both diseases are widespread.

Rangifer and human interests

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The reindeer or caribou occupies a special place in the minds of scholars and hunters alike. To a great extent, anthropologists, biologists, local hunters and ecological activists build their nations, disciplines and identities through thinking about Rangifer and, conversely, all the talk and action surrounding Rangifer by different human communities constitutes a significant part of the ecology of the species. Consequently, the literature in biology and anthropology on Rangifer from the middle of the 19th Century to the present day shows that biologists, anthropologists and local 'aboriginal' hunters have identified common interests in the study of Rangifer. People, moreover, influence the ecology of the animals and the size and nature of populations through the modification of habitat - of which the people are an integral part. Controversies and anomalies in the biological literature indicate that the analysis of data is not always tidy, and there is room for the discussion of fundamental concepts. For example, indigenous knowledge includes the notion that there is no clear difference between domestic, semi-sedentary and migratory Rangifer; likewise, the migratory behaviour, movements and behaviour Rangifer are best described by adjectives that ascribe intention and a certain subjectivity rather those which imply that these attributes of the animals' biology are solely physical entities. By reviewing the history of scholarly interest in Rangifer it is evident, first, that although Rangifer has a universal interest for all circumpolar communities, there has been a growing reticence to acknowledge and incorporate the models of indigenous thinkers in academic study. Even recent attempts to recognise 'traditional ecological knowledge' (TEK) or 'local knowledge' pale before the quality of collaboration between reindeer peoples and scholars at the start of the century. Second, published analyses reflect more the interests of state administrations, in a region that has increasingly become an arena of political tension, than the interests of local peoples. Academic models need to be 'revitalised' so that they reflect the interest of local communities in Rangifer. Scientific interests can be calibrated to reflect general circumpolar interests be they those of nation-states, local communities, or various definitions of economic development. What is required is more discussion of what exactly are the

common human interests in reindeer/caribou instead of assuming that 'TEK' and 'science' are two mutually exclusive bodies of thought. Use of 'TEK' is merely as one technique of many in the collecting of data to describe the nature of reindeer and caribou.

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On nature and reindeer luck

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This paper describes the reindeer Sami understanding of a worthy life expressed in qualitative distinctions centred around the term 'reindeer luck'. This theme is discussed in regard to what we may learn from relations to nature.

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Multi-scale habitat selection and population dynamics of Arctic ungulates: a unifying theory

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Ecological studies are increasingly focusing on population interactions which operate at different scales. Hierarchy theory is now an integral part of most resource selection studies on ungulates. In Arctic environments, however, foraging decisions by large herbivores are best viewed as a multi-scaled problem integrating effects of forage distribution, snow cover, and predation risk. Resource selection and population dynamics studies cannot be dissociated because the ultimate challenge is to understand how animals maximize their fitness under different ecological constraints. Decisions about space-use and foraging must reflect limiting factors affecting individuals within a population. The ability to avoid the factors that are most limiting at each scale (from population range to feeding sites) will maximize an individual's fitness. Recent studies on caribou and muskoxen exemplify the connection between resource selection and population limitation at various scales. Caribou are particularly vulnerable to wolf predation, representing the most important limiting factor at the large scale and long time frame. Barren ground and mountain caribou have responded by migrating over large distances and, thus, avoid contact with wolves during the calving season. In contrast, woodland caribou in the boreal forest have responded to the same limiting factor by adopting relatively small home ranges in climax habitats (peatlands, black spruce forests, open jackpine forests) and, thus, avoid contact with moose, an alternate prey associated with wolves. At finer scales and shorter time frame, food limitation becomes the next most important limiting factor for caribou. Hence, we should expect that decisions at such fine scale be oriented toward nutrient acquisition. For muskoxen, living in groups is an effective adaptation against wolves. Predation is a minor limiting factor for muskoxen even at large scale and long time frame. At smaller scales, for example for selecting winter ranges and multi-day foraging areas, decision making of muskoxen is often directed toward minimizing the limiting effect of snow cover. However, at the smallest scales, such as feeding craters and forages selected, forage distribution becomes most important. For Arctic ungulates, at least, multi-scale habitat selection can serve as an 'unifying theory' for the two (on-going) paradigms of 'food limitation' and 'predator limitation' that ecologists continue to debate.

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

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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 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 the 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 Nenets region in the north-west of Russia. Successful sympatric existence 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 been lost in recent years. There are approximately 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 leading 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 but there are signs of improvement in the situation among those peoples which have retained reindeer herding culture following the gradual restoration of private 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 the genetic diversity.

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Biological rhythms in Arctic vertebrates

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Temporal organisation is fundamental to every process in life, from the transcription of DNA to patterns of behaviour, and many biological processes show regular cyclical fluctuations that persist throughout an organism's life. These 'biological rhythms' are regulated by endogenous oscillators and are recognised on at least three time scales: ultradian ($\ll 24$ h), circadian (~ 24 h) and circannual (~ 1 year). Proper synchrony and phase-relationships among the different physiological rhythms within the organism and between these rhythms and cyclical fluctuations in the environment is achieved by the entrainment of the oscillators by external time cues, or 'zeitgebers', such as the daily light-dark cycle which varies in an entirely predictable manner throughout the year. Photic (day length) information is conveyed to the animal via the neuroendocrine axis and is translated into the rhythmic production of the pineal hormone melatonin which is thought to act as the principal mediator of photoperiodicity. At least three levels of control of behavioural rhythms are recognised in vertebrates: (1) weak or strong self-sustained endogenous oscillators, (2) non-self-sustained oscillators ('hourglass' control) and (3) environmental and/or motivational control. Animals living at high latitudes are of special interest because they receive only very weak zeitgeber information for much of the year owing to the absence of the daily light-dark cycle during the polar night and the polar day. In humans and in seasonal migrants to the Arctic such as snow buntings (*Plectrophenax nivalis*) and green finches (*Carduelis chloris*), circadian rhythms of behaviour persist throughout summer implying their control by strong endogenous oscillators. In organisms resident in the Arctic all year round like the Svalbard ptarmigan (*Lagopus mutus hyperboreus*) and Eurasian mountain reindeer in Norway (*Rangifer tarandus tarandus*), by contrast, the circadian rhythms of behaviour observed in spring and autumn disappear completely in summer. Likewise, Svalbard ptarmigan and Svalbard reindeer (*R. t. platyrhynchus*) lose their behavioural circadian rhythmicity during the polar night and, instead, feed opportunistically around the clock as conditions permit. Two inferences can be drawn from this. First, circadian rhythms of behaviour in reindeer and ptarmigan must be controlled by weak self-sustained or non-self-sustained endogenous oscillators. Second, the circadian regulation of behaviour in these sub-species is insensitive to the photic information provided by the weak daily cycle in the quality of light which persists throughout the polar day and the polar night. Notwithstanding these observations, ultradian rhythms of activity persist in reindeer at all times of the year reflecting the motivational control characteristic of ruminant digestion.

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Aspects of the ecology of mat-forming lichens

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Lichen species in the genera *Cladonia* (subgenus *Cladina*), *Cetraria*, *Stereocaulon* and *Alectoria* are important vegetation components on well-drained terrain and elevated micro-sites in peatlands in boreal-Arctic regions. These lichens often form closed mats in which the thalli 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 assess critically the importance of these processes are

required. Mat-forming lichens can constitute in excess of 60% of the winter food intake of reindeer and caribou. Accordingly there is a pressing need for data on lichen growth rates, measured as mass increment, to help determine the carrying capacity of winter ranges of these herbivores and to predict recovery rates following grazing. Trampling during the snow-free season fragments lichen thalli but mat-forming lichens regenerate very successfully from thallus fragments provided the trampling does not re-occur. Frequent recurrence of trampling creates disturbed habitats from which lichens will rapidly become eliminated consistent with Grimes' CSR strategy theory. Such damage to lichen ground cover has occurred where reindeer are unable to migrate away from their winter range such as on small islands or where political boundaries have been fenced. Mat-forming lichens are sensitive indicators of atmospheric deposition partly because they occur in open situations in which they intercept deposits directly with minimal modification by vascular plant overstoreys. Data from both the UK and northern Russia are presented to illustrate relationships between acid rain and lichen chemistry. Species of *Stereocaulon*, and other lichens 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 system in which to investigate the role of lichens in nitrogen cycling. The ecology of mat-forming lichens remains under-researched and there are good opportunities making significant contributions to this field including areas that relate directly to the management of Arctic ungulates.

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

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Equilibrium grazing systems are characterised by climatic stability that results in predictable primary production. Non-equilibrium grazing systems 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 to determine what stocking rate is optimal. The correct stocking rate for a grazing system will vary depending on the production strategy and the social and economic circumstances of the rangeland user – there is no single, biologically predetermined optimum density. Variable rainfall complicates 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 systems hinges on the reliability of rainfall. In northern latitudes, at least three primary variables important for plant growth and the survival herbivores must be considered: rainfall, snow cover and temperature. It is probably not useful to consider Arctic grazing systems 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.