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

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

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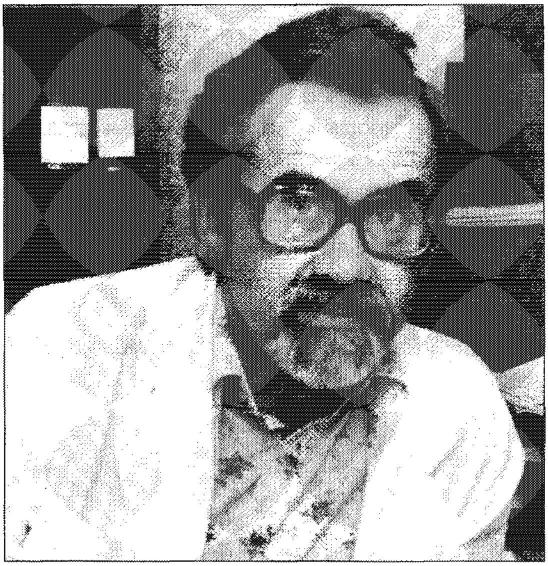

Magnus Nordkvist
Sweden's first reindeer veterinary surgeon

Magnus Nordkvist, who died on 26th June 1997 aged 73 years, was born on 19th September 1923 at Skara in southern Sweden. In 1945, after graduating from Skara high school, he matriculated at the Royal Veterinary College, Stockholm, from where, in turn, he graduated in 1955. Already before this, as a student, he was employed for a time at the College's Department of Ruminant Medicine besides which he had been temporarily engaged as veterinary practitioner in several different parts of the Sweden. Upon graduation he accepted a position at the National Veterinary Institute (Statens Veterinärmedicinska Anstalt) in Uppsala where from 1971 until his retirement in 1988 he was Government Veterinary Officer with special responsibility for reindeer diseases.

Though chiefly remembered as a pioneer in this branch of reindeer husbandry science, Nordkvist's interests were wide ranging. He worked hard to build links between reindeer herders and scientists in different biological disciplines both in Sweden and throughout the Nordic countries.

Nordkvist was a champion of the importance of research for improving reindeer husbandry. He used his sober manners and his mild voice – 'soft as a summer evening's breeze' it was once said – to great effect in increasing reindeer research in Sweden. His own work concentrated on the pathology of several important parasites, notably the warble fly (*Oedemagena tarandi*), the nasal bot fly (*Cephenemyia trompe*) and the brain worm (*Elaphostrongylus tarandi*). His desire to achieve results that would yield concrete benefits for reindeer husbandry is reflected in the fact that Ivomec was registered in Sweden for use on reindeer before it was registered for any other species of domestic mammal.

Nordkvist's scientific production (bibliography: *Rangifer* Special Issue No. 4, 1990: 6–9) reflected the breadth of his interests and his ability to work with scientists in many different disciplines. He was a tireless supervisor and a loyal colleague. He took great trouble with young scientists who wished to work with reindeer and he was eager that people who worked within reindeer husbandry – reindeer herders and agricultural advisers – should benefit from the results of research: consequently, he was a keen advocate of popular science.

Reindeer husbandry underwent large changes during his time as a reindeer veterinarian. Nordkvist watched the process of mechanisation and rationalisation and the change from subsistence to market economy and devoted considerable time to ameliorating some of the undesirable aspects of these developments. He was widely respected by herders and scientists alike. His popularity was due in large part to his pleasant manner, his gentle humour and his genuine concern for people around him. His popular lectures from the period 1969-1977, some of which were published in the SVA house journal, demonstrate his fine style and contain pearls of his subtle wit.

Magnus Nordkvist's career was clouded by two events. He considered the closure of the reindeer unit at the SVA shortly after his retirement a personal defeat. He also regretted that he was unable to carry on analysis of material he had collected with the Swedish Environmental Protection Agency during a large investigation of calf mortality in Umbyn reindeer area. The preliminary results seemed to show that predators took principally strong animals and not, as was widely supposed, only the weak ones. Several years after retiring he attempted to resume the analysis but illness prevented him from completing the work.

Those of us who knew Magnus Nordkvist as a colleague at SVA, as a companion in field expeditions, or as a fellow scientist will deeply miss a friend with an unusually warm personality and a rich sense of humour.

Claes Rehbinder *Lars Anders Bær* *Bengt Westerling* *Sven Skjenneberg*

The Second International Arctic Ungulate Conference,
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Rangifer population ecology: a Scandinavian perspective

Eigil Reimers

University of Oslo, Department of general physiology, P.O.Box 1051, Blindern, 0316 Oslo, Norway.

Abstract: Population ecology is concerned with measuring changes in population size and composition, and identifying the causes of these fluctuations. Important driving variables include animal body size and growrh rate, and their relationship to reproduction and mortality. Among wild and domestic reindeer (*Rangifer tarandus tarandus*), reproductive performance, calving time, calf birth weight and neonatal mortality are strongly correlated to maternal weight. Heavy females enjoy higher pregnancy rates, calve earlier, and give birth to heavier calves which have a higher neonatal survival rate than light females. Most studies indicate that both weaning weight of a calf and mature body weight correlate to its birth weight. Calf body weight and composition influence the rate of attainment of sexual maturity. Females which breed as calves suffer reduced growth and give birth to smaller calves, which suffer higher neonatal mortality and lower rates of postnatal growth. A yet unresolved question is whether reindeer body weight, and hence reproductive performance and neonatal mortality, are more strongly influenced by winter than by summer grazing conditions. This paper reviews population ecology studies on wild and domestic reindeer and promotes the view that body size in *Rangifer* is determined primarily by grazing conditions during the summer.

Key words: *Rangifer,* reproduction, mortality, growth.

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Introduction

Although regulated in number primarily through hunting or herding practices, most populations of wild and domestic reindeer (*Rangifer tarandus tarandus*) are also influenced by predation, climatic extremes, insects, and food limitation. These factors may act directly or indirectly through increased mortality or through reduced reproduction. In a comprehensive lirerarure review, Eriksson *et al.* (1981) demonstrated that lichens, when available, constitute a significant portion of the winter diet of *Rangifer.* Constraints on winter food availability, particularly lichens, has generally been accepred as the main factor responsible for poorer condition, increased mortality of young and reduced reproduction among reindeer (e.g. Skogland, 1983; 1984; 1985; 1988). Consequently, management of wild reindeer populations in Norway is based primarily on lichen biomass in the various areas (Gaare & Skogland, 1980). This principle also applies to management of domestic herds in most places. Nonetheless, reindeer also thrive in environments without lichens or with low lichen biomass provided there is access to alternative food, *e.g.* Russia (Syroechkovskii, 1984), Svalbard, (Reimers, 1982; Tyler, 1987) East Greenland (Reimers, 1980a) and South Georgia (Leader-Williams, 1988).

The body weight cycle in *Rangifer* with rapid growth in summer and slow growth or weight loss in winter appears to be endogenous and independent of the seasonal variation in the food supply (McEwan 1968; Skjenneberg & Slagsvold, 1968; Dauphiné, 1976; Reimers *et al.*, 1983; Suttie & Webster, 1995). The adaptive significance of this cyclic pattern of growrh is that it allows weight reduction in winters when food is scarce and of low quality and compensatory growth and a rapid restoration of body condition during rhe lush summer. Different populations of teindeer are characterized by different body sizes (Movinkel & Prestbakmo, 1969; Reimers *et al.*, 1983). Body weight influences pregnancy rates (Reimers, 1983a; Lenvik, 1988), calving time (Reimers, 1983b), birth weights (Skogland, 1984) and calf survival (Skogland, 1984; 1985). This paper reviews population ecology studies on wild and domestic reindeer and promotes the view that body size in *Rangifer* is determined primarily by grazing conditions during the summer.

Material and methods

Body condition and growth rates are based upon measurements of total body weight (TBW) and dressed or carcass weight (DW = TBW minus viscera, head, skin and lower legs). As the fetus and its associated tissues and rumen fill vary substantially with season (*e.g.* Adamczewski *et al.*, 1987), DW is a bettet index of condition than TBW. For comparative purposes, the TBW was estimated from dressed weight according to the equation: $TBW = 5.9 + 1.66 * DW$; $N = 189$; $r^2 = 0.958$ (Reimers, unpubl. data).

Growth rates were estimated from linear regression analysis. Summer growrh rates of calves were calculated from birth weights estimated from fetal growth rates (Reimers, unpubl. data) and known calving dates (Table 2), and calf body weights sampled through the hunting season from 20 August to 25 September. Summer growth rare of adults was estimated on basis of animals sampled in June/July and during the hunting or the slaughter season. Weights obtained during the hunting season were assumed to reflecr the weight of the animals 1 September.

Winter weight loss was assumed to occur from 1 December to 1 May, after which males and barren females start regaining weight. Pregnant females, however, continue to loose weight until calving.

Winter pasture quality was assessed on the basis of lichen availability according to Gaare and Skogland (1980) and Skogland (1985). Plant growth was assumed to srart on 1 June.

The animals were aged on basis of tooth development and weat or from cementum annuli (Reimers & Nordby, 1968).

Results

Pregnancy rates

Pregnancy rates are reported to range from 75–100% among 2 1/2 year or older wild or domestic reindeer (Table 1; see appendix for all tables). There is a significant positive relationship between catcass weight (DW) at the onset of rutting and pregnancy rate (Reimers, 1983a; Lenvik *et al.*, 1988). Pregnancy has not been recorded in animals weighing less than 21 kg at breeding. All wild reindeer females with an estimated pre-rut TBW 69 kg were pregnanr. In the Kaamanen experimental herd in Finland average pregnancy rate was only 79% even though the mean TBW was above 70 kg. Pregnancy rate in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) in Nordenskiøld Land, based upon the proportion of females ≥1 year old with antlers two to three weeks before calving, was annually highly variable and ranged from 26 to 82% in 1980–82 (Tyler, 1987).

Calving time

Plant phenology (Skogland, 1989a), predation and insect harassmenr (Bergerud, 1975) are suggested as the main factors explaining birth synchrony and calving time in *Rangifer*. Most calves are born within 14 days (*e. g.* Nowosad, 1975; Eloranta & Nieminen, 1986) in spring. Calving midpoint date (the day when 50% of the pregnant females have given birth) is highly variable within and between subspecies. Extreme midpoint values in reindeer vary from 15 April in the Mackenzie Delta herd (Godkin, 1986) to the first week of June in Svalbard reindeer (Kastnes, 1979; Tyler 1987). In southern Norway the calving midpoint varies from 6 to 27 May (Table 2) and is strongly cotrelated to pre-rut dressed weights in females (Fig. 1).

Birth weight

Bitth weight varies among various herds (Table 3). Birth weight is positively correlated with maternal weight immediately prior to calving (Espmark, 1980; Rognmo *et al.*, 1983; Eloranta & Nieminen, 1986) and at mating (Eloranta & Nieminen, 1986).

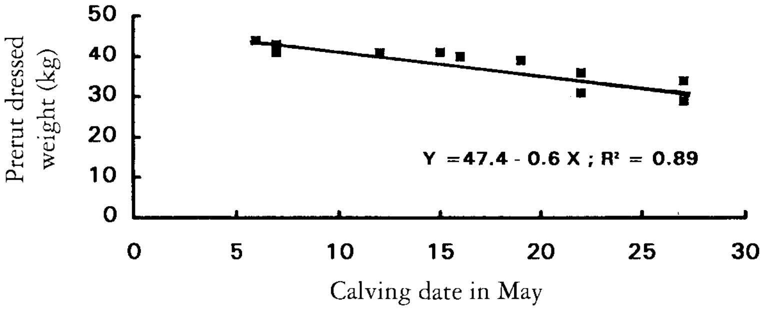

Fig. 1. The relationship between pre-rut dressed weights of adult (> 2 yr) reindeer females and calving dates (the date when 50% of the pregnant females have given birth) in 11 wild reindeer areas in southern Norway. (See Table 2 for references).

Calf mortality

Calf mortality during the first 5 months following birth varies from almost zero in Knutshø in 1984 (Skogland, 1985) to 44% in a semi domesticated herd (Rognmo *et al.*, 1983) (Table 4). A calf's chance of survival appears to be strongly influenced by its mother's body weight at the time she gives birth (Skogland, 1984; 1985). Females with small body weights give birth to small calves which suffer higher mortality than calves born from well fed and heavy females. Tyler (1987) recorded mortality of Svalbard calves aged 0–4 months during 1980–82 and found that it was negligible all three years.

Weight loss during winter

Average dressed weight loss among wild reindeer from January to April ranged from 11 to 21 g/day among calves and from 18 to 70 g/day in females aged ≥ 1 yr (Table 5). Applying these values to the entire weight loss period 1 December to 1 May, the estimated weight loss ranged from 1.7–3.2 kg among calves to 2.7–10.6 kg among 1 1/2 year or older females.

Weight increase during summer

Growth rates of wild reindeer calves in Hardangervidda and in Rondane were 70 and 82% respectively of the growth rates of calves in North Ottadalen decreasing to 29 and 72% respectively in yearling males (Table 6). The growth rate differences are reflected in the increasing carcass weight differences between male calves and yearlings (Table 7). Summer growth rates among semi domesticated reindeer were comparable to those in Hardangervidda, which were 80–90% of the growth rates in Rondane and 50–70% of those in North Ottadalen. Based upon the recorded growth rates, the estimated increase in total body weight from 1 June to 1 September varies between 25 and 36 kg among calves and between 13 and 38 kg among older animals. This corresponds to a dressed weight increase of 12–25 kg among calves, 10–22 kg among yearling males and 13–23 kg among lactating females ≥ 2 year.

Discussion

Pregnancy rates, calving time, birth weight and calf mortality

Pregnancy rates in reindeer are strongly related to autumn body weight (Table 1). Pregnancy rates in yearling semi domesticated reindeer increased from close to zero to about 90% as body weight increased from 40–50 kg (Lenvik *et al.*, 1988). In some semi domesticated and wild herds, calves reach 40 to 50 kg in autumn and conceive in their first year of life (Reimers, 1972; 1983a; Ropstad *et al*, 1991). In semi domesticated herds the consequences of early breeding has been high mortality among calves born from calves and reduced maternal gain in weight (Ropstad *et al.*, 1991; Lenvik & Aune, 1988). We have been unable to record corresponding data in wild populations. It appears maladaptive to breed, loose the calf and suffer a growth set back, and so presumably management conditions, under which a yearling looses its calf, are unfavorable.

Although female weight has a strong predictive power, number, age and body weight of the breeding males also affect the pregnancy rate (Lenvik *et al*, 1988). Males present after the hunting season were few, young and in poor condition during the sampling years (Reimers, 1975), and may well be the reason for lower pregnancy rates in Snøhetta than predicted from the TBWs (Reimers, 1983a).

Caribou are reported to mature later and reach lower pregnancy rates than reindeer (Dauphiné, 1976; Miller, 1976; Parker, 1983; Skogland, 1989b). However, nutrition and body weight are evidently also key factors among these subspecies.

For example, Quellet *et al.* (1991) found that 68 out of 69 caribou (*Rangifer tarandus groenlandicus*) including 15 yearlings, were pregnant on Southampton Island. This introduced herd of caribou were in prime physical condition judging from back fat thickness and kidney fat index.

Timing of births reflects both nutritional and genetic influences (Tables 2–3; Fig. 1). The timing of rut (Lenvik, 1988) and calving time (Reimers, 1983b) are related to the pre-rut body weights of females. Heavy females presumably ovulate earlier and so give birth earlier than light females. Calving time may change with changing environmental conditions (Nowosad, 1975; Skogland, 1990b). The midpoint of calving in the Knutshø area is 16 May (Fig. 1). These reindeer originated in the neighbouring Snøhetta and possibly Rondane North areas, from where they migrated in the 1950-60s and where midpoint of calving occurs on 27 and 22 May, respectively. Calving in Snøhetta presently appears to occur 5 days earlier, following reduction in population size and increase in body weight, while calving in North Ottadalen occurs 5 days later following a population increase and a decrease in body size (Flydal & Reimers, unpubl. data). According to Skogland (1990b), calving in Hardangervidda has advanced 10 days from 1983 to 1989, parallel to improvement in the animals' physical condition.

The birth weight of calves is related to the weight of females just prior to calving (*e.g.*, Varo, 1972; Skogland, 1984; Eloranta & Nieminen, 1986). Calves born from mothers weighing more than 90 kg total body weight, weighed 40-70% more than calves born to females weighing less than 60 kg (Rognmo *et al.*, 1983; Eloranra & Nieminen, 1986). However, as emphasized by Eloranta & Nieminen (1986), the birth weights of the calves in their study related equally significantly to female body weights in autumn. Consequently, the birth weight of a calf may be determined by the body weight of the female in autumn.

Early mortality of calves is clearly related to birth weight which is itself influenced by maternal body weight (*e.g.* Varo, 1972; Rognmo *et al.*, 1983; Eloranta & Nieminen, 1986). Lenvik & Aune (1988) were able to reduce calf mortality from 19-24% to 5-6% by selecting for high maternal body weight. In one of the experimental herds the calf mortality rate up to 2 months of age was 48% among calves born from females with 55 kg body weight and 2% among females of 70 kg or more.

Weight loss during winter

The average winter weight loss (DW) among 1 1/2 year and older females in the poor areas (Table 5) was 53±10 g/day, with a range from 16 g/day in Hardangervidda in 1983 to 72 g/day in Snøhetta around 1960. In Snøhetta, the reindeer population reached a maximum of some 15,000 animals (4 animals/km^2) in the summer 1963 (Reimers, 1968), at which time the winter pastures were heavily overgrazed (Gaare, 1968). A reduction harvest brought the population down to about 2,000 animals towards the end of the 1960s. In Hardangervidda, the reindeer population reached a maximum of about 32,000 animals (4 animals/km^2) in summer 1965, with pasture detoriation comparable to that in Snøhetta (Skogland, 1990a). Increased harvest reduced the population to about 7,000 animals in 1971. Concerned with this rapid reduction in numbers, the game administration (Direktotatet for vilt og ferskvannsfisk) protected the herd from hunting the following 2 years. Hunting was reopened in 1973, and in 1983 when the reindeer population was approaching a second maximum (24,000 animals summer 1984), the loss in dressed weight during winter (16 g/day) was the lowest on record. The winter pastures were at this time still heavily overgrazed (Skogland 1990a), calves were born small in 1983 (Skogland, 1984) and female body weights were all time low (Table 8). We have no indications of favorable snow conditions in winter 1982-83. Consequently, the high population size and the heavily overgrazed lichen pastures, should, according to the accepted management hypothesis, have resulted in rapidly decreasing body weights through the winter 1982–83. However, weight loss was relatively small (mean 16 g/day; Table 5) and female body weights were maintained reasonably well throughout that winter. In two of the areas (Forelhogna and North Ottadalen), body weight loss during winter was remarkably high. This occurred in spite of high quality winter pastures (Skogland, 1983). These results support the earlier view (Reimers, 1983) that winter range quality or lichen biomass does not explain reindeer body weight development through winter and the McEwan (1968) winter dormancy hypothesis.

Summer growth rates

The summer growth rates (TBW) among calves and yearling males in North Ottadalen were close to 400 g/day (Table 6). This is the maximum growth rate recorded among free-grazing reindeer, but higher rates of growth have been recorded among penned reindeer fed on a high plane of nutrition (Luick *et al.*, 1980; Ryg & Jacobsen, 1982; see Reimers 1983b). In Hardangervidda, the average summer growth rate in calves was 277 g/day, which is in the lower end of the scale for calf growth rate among free-ranging reindeer (*e.g.* Krebs & Cowan, 1962; Haukioja & Salovara, 1978; Nieminen & Petterson, 1990).

The differences between the areas in calf growth rates may relate to birth weights and lactational conditions during the first month. Both are strongly related to the female's body weight. Calves in Hardangervidda are born small from small mothers. Small mothers may produce less milk of poorer quality and hence raise calves of smaller body size by 1 September than better fed mothers. Female body condition has not been reported to influence milk composition (Luick *et al.*, 1974; Jacobsen *et al.*, 1981; Rognmo *et al.*, 1983). Restricted feed during late pregnancy may reduce milk volume (Jacobsen *et al.*, 1981). With the method used (milking after a 4-hour separation of mother and calf) they found a significantly higher milk production 2 weeks postpartum in the group fed supplements during pregnancy. Judging from calf growth rates, Rognmo *et al.* (1983), nonetheless concluded that milk yield, within certain limits (undefined by the authors), is independent of female nutrition during pregnancy. This apparent contradiction may relate to differences in feed quality during lactation. Rognmo *et al.* (1983) fed the lactating females a high quality diet during the first three weeks of lactation, while Jacobsen et al. (1981) added lichens to whatever the reindeer could find on a fenced-in natural pasture.

As shown by White (1983) and White & Luick (1984) milk production and calf growth rate appear to be strongly influenced by food quality in summer. Calves born from reindeer kept on a high plane of nutrition in winter and spring and then given a low plane of nutrition (dwarf birch and sedges) following peak lactation in early summer had a 24% lower growth rate than the calves given a high plane of nutrition (willows and sedges). The poorer summer range condition reduced milk production and therefore the calf growth rate. Although the reindeer calves in Jacobsen *et al.* (1981) and White (1983) were unable to compensate for lower milk intake by greater intake of forage, Hudson & Adamczewski (1990) noted that elk calves (*Cervus elaphus*) receiving less milk may compensate by eating more solid food and attain the same growth rate as those consuming more milk. In a study of captive woodland caribou (*Rangifer tarandus caribou*), Lavigueut & Batette (1992) found that growth rates of calves from birth to 45 days of age were positively correlated with suckling rate (suckles/hour) during the first 35 days. From 46 to 100 days, growth rates were positively correlated with time spent feeding on pelleted ration and on hay. They suggest that metabolic weaning (the time when the offspring should be able to satisfy all its nutritional requirements by itself) could begin at around 15–20 days and end at about 40–45 days.

The low growth rate in summer recorded among Hardangervidda calves suggests food limitation in summer. At the start of their second growing season, the initial effects of later calving time and possible milk quantity shortages should be absent. Furthermore, the ability for compensatory growth (Wilson & Osbourne, 1960; Allden, 1970) should be present. Apparently, it is not. Yearling males in Hardangervidda grow during their second summer at a lower rate than they did as calves. The difference in dressed weights towards the end of the growing season (1 September) increased 8 kg, from 14 kg as calves to 22 kg as yearlings in Hardangervidda compared with North Ottadalen (Table 7). The corresponding difference between North Ottadalen and Rondane increased 3 kg, from 9 kg as calves to 12 kg as yearlings.

The reason why Reindeer in Snøhetta, Hardangervidda and Rondane do not attain the body size of the animals in North Ottadalen, Forelhogna and Knutshø is not explained by poor winter nutrition. The winter pastures in Rondane are excellent (Skogland, 1983) and weight loss in winter is small but the animals are apparently unable to grow at a maximum rate during the summer. Nevertheless, weight loss is moderate even on the heavily overgrazed winter pastures in Snøhetta and Hardangervidda. There are two possible explanations: (1) pre- and postnatal food limitation have reduced the skeletal frame and thus the animals will grow to smaller overall size; and (2) summer conditions in terms of range quality or grazing conditions prohibit growth at a maximum rate. Allden (1970) in his review on food deprivation on cattle and sheep, found no evidence to show that a calf subjected to nutritional deprivation from an early age of suckling will eventually become a cow of smaller stature. There were indications that restricted nutrition in late prenatal or early postnatal life may affect the ultimate size in sheep (Allden, 1970). The evidence is by no means conclusive, however, because the experiments that have shown persistent residual effects have been of too limited duration. In field experiments with sheep, differences at maturity have been small (Allden, 1970). Profound nutritional stress applied to breeding ewes during early or late pregnancy have resulted in reduced birth weights. With a normal diet restored at birth, however, the weight difference was small or no longer evident.

Compensatory growth

Compensatory growth in summer following food restriction in winter is well documented in cervids. Suttie (1980); Suttie *et al.* (1983); Suttie *et al.* (1984) and Milne *et al.* (1987) reported that red deer (*Cervus elaphus*) subjected to nutritional deprivation during winter showed a remarkable compensatory growth during summer. but failed to compensate fully for the previous under nutrition. In a comparable study on yearling elk stags (*Cervus canadensis*), Wairimu *et al.* (1992) reported that the group of elk wintered on medium-quality hay attained similar weights and frame measurements in July as the group wintered on a high-quality diet.

Although no long term controlled feeding experiments comparable to the red deer and elk studies have been carried out, compensatory growth following food restriction apparently also occurs in reindeer. Kumpula & Nieminen (1992) noted that calves were capable of compensating for a low birth weight if summer conditions (temperatures, rainfall and insects) were favorable. In yearling males fed a submaintenance diet through winter, Jacobsen *et al.* (1977) reported compensatory summer growth rates (TBW) upon realimentation of 114-180 *vs.* 96–114 g/day, and Ryg & Jacobsen (1982) 352 *vs.* 209 g/day. Espmark (1980) measured a summer growth of 194 g/day among lactating females food restricted during the month before calving, compared to 134 g/day in the unrestricted group. Calves born from mothers given restricted feed during late pregnancy, however, had a lower growth rate than calves born from supplementary fed females (Espmark, 1980; Jacobsen *et al*, 1981). Rognmo *et al.* (1983) reported the opposite result; calves born from food restricted females grew at a faster rate than calves born from supplementary fed females. It is important in this context to note that male calves have a more rapid growth rate than female calves (*e.g.* Petersson & Danell, 1993). There were 7 male vs. 2 female calves in the fast growing group, and 2 male *vs.* 7 female calves in the slower growing group in the growth study of Espmark (1980) and therefore the nutritional effect may be confounded. The same may apply to Jacobsen *et al.* (1981) and Rognmo *et al.* (1983); neither of them stated the sex composition for the two groups of calves.

Summer grazing conditions - pasture quality and insect harassment

Since Klein (1968) suggested summer range quality as the main factor effecting growth rate and body size in reindeer, several workers have published reports in support of this. (*e.g.* Movinkel & Prestbakmo, 1969; Reimers, 1980b, 1983b; Huot, 1989; Kojola & Helle, 1993; Crete & Huot, 1993). As the reindeer in Snøhetta, Hardangervidda and Rondane fail to grow as rapidly as the reindeer in North Ottadalen, Forelhogna and Knutshø, focus needs to be on the summer grazing conditions. All of these areas except Rondane are rated as good summer ranges (Reimers *et al*, 1983; Skogland, 1983). Although ranges are rated as good, the quality of them as reindeer habitat most certainly vary. Insect harassment is an additional and frequently overlooked component of summer habitat quality. It is conceivable that the harassment effects will vary between years and between areas due to variations in summer climate, population size and topography and insect relief areas (high mountains and snowbeds). Insects keep animals moving about and hence increase energy expenditure and reduce grazing time (*e.g.* Kelsall, 1968; White *et al*, 1975; Thomson, 1977; Reimers, 1980b; Helle & Tarvainen, 1984; Russell & Nixon, 1990; Kojola, 1991; Helle & Kojola, 1994). Fancy's (1986) simulation of the energy budget of a lactating caribou, showed the animal in negative energy balance for 12 days in July, implying a carcass weight loss of 4 kg, resulting from insect harassment. Observations of reindeer and caribou during summer in a variety of locations indicated that the harassment effects arises from attacks from warble (*Hypoderma tarandi*) and nose bot flies (*Cephenemyia trompe*) rather than from mosquitoes (Culicidae) (Reimers, unpubl. data). The flying activity of these two species increases with increasing air temperature and the number of flies present (Folstad *et al*, 1991; Nilssen & Haugerud, 1994). The number of flies present is also a function of *Rangifer* population size.

In conclusion: a large amount of data indicate that pregnancy rate, calving time, calf birth weight and early calf survival among reindeer are strongly related to the maternal body weight. As the winter weight loss in reindeer is moderate even on severely overgrazed winter pastures, it appears that growth rates and ultimate body size in reindeer are primarily a function of summer grazing conditions. Maximum growth rate in summer of about 400 g/day (TBW) is recorded in feeding experiments with semi domesticated reindeer and in a few wild reindeer areas. In most other situations, wild as well as domestic reindeer show summer growrh rates far below the maximum. This suggests a closet look at the summer grazing conditions, including pasture diversiry and quality and insect harassment from primarily warble and nose bot flies. High quality summer pastutes are of limited value to the reindeer if harassing insects (or extensive human activity) prevent them from feeding effectively.

Winter pastutes are important in providing energy and small amounts of protein, but they will generally be incapable of meeting maintenance requirements and should be viewed as holding areas for the animals until summer ranges become available (Torbit *et al.,* 1985). It is probably of adaptive significance to allow loss of body weight in times of scarcity and a rapid build up in times of plenty. The Svalbard reindeer convincingly exemplify this strategy (Reimers, 1982).

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Appendix: Tables 1–8

Table 1. Estimated pre-rut body weights (TBW) and mean rates of pregnancy in domestic and wild reindeer herds. The TBW of wild reindeer was estimated from the regression TBW = 5.9 + 1.66*DW.

Area/herd	Period	Pre-rur TBW (kg)	Mean pregnancy rate (%)				Reference
Age at breeding		2+ yr	0–1 yr	1–2 yr	3+ yr	*n*	
Domestic reindeer							
Lødingen, Norway	1960–63		6	61	77		Skjenneberg & Slagsvold (1968)
Kaamanen, Finland	1970–84	71	0	38	79		Eloranta & Nieminen (1986)
Arvidsjaur, Sweden	1981–82		27	60	93	210	Mossing & Rydberg (1982)
Riast/Hylling, Norway	1976–79	57		63	91	1114	Lenvik *et al.* (1988)
Essand, Norway	1976–79	59		67	94	581	Lenvik *et al.* (1988)
Trollheimen, Norway	1976–79	59		94	92	1038	Lenvik *et al.* (1988)
Mackenzie Delta Herd, Canada[1]	1976–81				99		Godkin (1986)
Wild reindeer, Norway							
Forelhogna	1983	77		100	100	22	Skogland (1984)
Norrh Ottadalen	1967–72	79		50	100	10	Reimers (1983a)
South Ottadalen	1967–72	69	75	75	100	21	Reimers (1983a)
Norefjell-Reinsjøfjell	1992–94	74			97	240	Reimers (unpubl.)
Knutshø	1983	75			100	23	Skogland (1984)
Rondane North	1970–72	66	0	63	94	53	Reimers (1983a)
Snøhetta	1951–59	64	0	23	75	132	Reimers (1983a)
Snøhetta	1963–65	62	0	0	80	19	Reimers (1983a)
Hardangervidda	1948–58	57	0	50	79	48	Reimers (1983a)
Hardangervidda	1970	54	0	33	84	46	Reimers (1983a)
Hardangervidda	1973	57	0		91	25	Reimers (1983a)
Hardangervidda	1983	54	0	80	88	69	Skogland (1984)

[1] Twin fetuses occurred in from 0.4 - 26.2% of the females.

Table 2. Midpoint calving date (the day when 50% of the pregnant females have given birth) in semi-domesticated and wild reindeer herds. Values are multi-year means.

Area	Midpoint calving date	Reference
Semi-domesticated reindeer		
Kautokeino, Norway	8 May	Skjennebetg & Slagsvold (1968)
Kaamanen, Finland	20 May	Eloranta & Nieminen (1986)
Mackenzie Delta Herd, Canada	15 April	Godkin (1986) Nowosad (1975)
Wild reindeer, Svalbard	1st week of June	Kastnes (1979), Tyler (1987)
Wild reindeer, Norway		
Forelhogna	7 May	Skogland (1984)
North Ottadalen	6 May	Holthe (1975)
South Ottadalen	12 May	Holthe (1975)
Norefjell-Reinsjøfjell	7 May	This wotk
Knutshø	16 May	Reimers (1983b)
Rondane North	22 May	Reimers (1983b)
Rondane South	15 May	Reimers (unpubl.)
Setesdal West	22 May	Reimers *et al.* (1980)
Setesdal East	19 May	Engen (1991)
Snøhetta	27 May	Holthe (1975)
Hardangervidda	27 May	Skogland (1984)

Table 3. Mean total body weights (kg) of females and newborn calves in semi-domesticated and wild reindeer.

Area/Herd	Maternal pre-calving (April) weights	Maternal autumn (Aug.-Sept.) weights	Calf birth weights			Reference
			Males	Females	M + F	
Semi-domesticated reindeer						
Kaamanen, Finland		< 50			4.2	Eloranta & Nieminen (1986)
Kaamanen, Finland		51-90			4.5-6.1	Eloranta & Nieminen (1986)
Kaamanen, Finland		> 90			6.6	Eloranra & Nieminen (1986)
Finland, domestic reindeer					5-6	Timisjärvi *et al.* (1984)
Finland, domesric reindeer	62		6.0	5.7		Varo (1972)
Lødingen, Norway	62–75				4.7	Espmark (1980)
Lødingen, Norway	56				3.7	Rognmo *et al.* (1983)
Lødingen, Norway	68				4.5	Rognmo *et al.* (1983)
Lødingen, Norway	68				4.5	Rognmo *et al.* (1983)
Lødingen, Norway	82				5.8	Rognmo *et al.* (1983)
Mackenzie Delta Herd, Canada			7.3	6.9	7.1	Nowosad (1975)
Wild Reindeer, southern Norway						
Snøhetta/Hardangervidda 1950-73	50 (27)[1]	55 (30)[2]			4.3	Reimers (unpubl.)
Hardangervidda 1983	46 (23)	54 (29)			3.7	Skogland (1984)
Rondane North	56 (30)	65 (36)			5.3	Reimers (unpubl.)
Forelhogna/Knutshø/ N. Ottadalen	72 (39)	76 (42)			6.0-7.0	Skogland (1988), Reimers (unpubl.)

[1] Mean dressed weight in parenthesis.

[2] Mean dressed weight in parenthesis.

Table 4. Rates of calf mortality (%) in semi-domesticated and wild reindeer herds during the first 5 months after calving.

Area/Herd	Sampling years	% Mortality first 3-5 months	% Mortality first month	Reference
Semi-domesticated reindeer				
Kaamanen, Finland	1970–71	35	12	Eloranta & Nieminen (1986)
Riast/Hylling, Norway	Before 1977		19-24	Lenvik & Aune (1988)
Riasr/Hylling, Norway	1981		7-8	Lenvik & Aune (1988)
Riast/Hylling, Norway	1984		5-6	Lenvik & Aune (1988)
Semi-domesticated reindeer, Norway			10-20	Skjenneberg & Slagsvold (1968)
Lødingen, Norway			33-44	Rognmo *et al.* (1983)
Mackenzie Delta Herd, Canada	1969–71	31-46	10	Nowosad (1975)
Wild reindeer, Norway				
Hardangervidda	1983	55	42	Skogland (1984)
Forelhogna/Knutshø	1984	0.3	0.3	Skogland (1984)
Hardangervidda	Average of 7 years	47	38	Skogland (1985)
Snøhetta	Average of 5 yeats	43	38	Skogland (1985)
Hallingskarvet	1982	72	23	Skogland (1985)
Brattefjell-Vindeggen			14	Skogland (1985)
Knurshø	Average of 6 years		5	Skogland (1985)

Table 5. Mean winter weight loss (gDW/day; DW = dressed weight) in reindeer calves (males and females) and females 1 1/2 year or older. The error term (SD) in the wild reindeer calculated from regression analyses including animals weighed during February-April. Number of animals in parenthesis. Weight loss among semi-domesticated reindeer are means of estimates based upon three studies in which the end weight is subtracted from the start weight and the result divided with the number of days.

	Weight loss (gDW/day) in winter (January–April)		
Herd/Area	Calves	Females >1 yr old	
Semi-domesricated reindeer Norway[1]	21 ± 6		
Wild reindeer, Norway[2]			
North Ottadalen			
Forelhogna & Knutshø	13±24 (8)	70±27 (57)	32 -101[3]
Rondane North	11±11 (49)	18±31 (24)	
Hardangervidda & Snøhetta.	11±12 (77)	53±10 (213)	16 - 72[3]

[1] From Reimers (1983b).

[2] From Reimers (1983b), Skogland (1984), Reimers (unpubl. data).

[3] Range of regression coefficients.

Table 6. Mean summer growth rates (gTBW/day ± SD; TBW = total body weight) in reindeer. Growth rates in wild reindeer are from the respective calving dates in May (male and female calves) and from June (male yearlings and 2 year or older lactating females) to September. Growth rates in semi-domesticated teindeer are mean estimates based upon several studies in which the end weight is subtracted from the start weight and the result divided with the number of days. Number of studies in paranthesis.

	Growth rates in summer (gTBW/day)		
Herd/Area	Calves	Male yearlings	Females 1 1/2 yr+
Semi-domesticated reindeer[1]			
Finland, Russia, Norway	274±42 (22) 206 - 350[4]	183± 34 (4) 151 - 231[4]	152±24 (5) 134 - 194[4]
Alaska[2]			136
Wild reindeer, Norway[3]			
North Ottadalen	396	397	412
Rondane North	326	285	234
Hardangervidda	277	115	211

[1] From Reimers (1983b).

[2] White (1983).

[3] From Reimers *et al.* (1983).

[4] Mean range.

Table 7. Male reindeer dressed weights (DW) (SD in three wild reindeer areas in southern Norway. Number of animals weighed in parenthesis.

Area	Sampling years	September dressed weighrs (kg) Calves	Yearlings
Hardangervidda	1969–74	15.5 ± 2.3 (29)	26.9 ± 5.1 (58)
Rondane North	1970–74	19.8 ± 3.8 (9)	37.0 ± 6.1 (103)
North Ottadalen	1967–74	29.3 ± 3.8 (35)	49.1 ± 6.8 (175)

Table 8. Background information about the wild reindeer populations under study in southern Norway. Number of animals weighed in paranthesis.

Area	Sampling years	Grazing quality[4] Summer	Winter	Female 1+ yr dressed weights (kg) in February
North Ottadalen	1966–74[1]	Good	Good	45.4±8.3 (3)
Fotelhogna	1984[2]	"	"	46.8±5.0 (7)
Knutshø	1984[2]	"	"	41.4±2.6 (7)
Rondane North	1972–74[1]	Medium	Good	31.4±4.9 (14)
Snøhetta	1950–67[3]	Good	Poor	28.0±5.4 (19)
Hardangervidda	1955–58[3]	"	"	30.1±4.2 (30)
	1970[3]	"	"	28.1±3.2 (7)
	1973[3]	"	"	31.6±4.6 (8)
	1983[2]	"	"	25.7±5.8 (17)

1 From Reimers *et al.* (1983).

2 From Skogland (1984). Animals were sampled during February, March & April.

3 From Reimers (1983a). Dressed weights from January.

4 From Skogland (1985).

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Brief communication

Ultrasonic Imaging of Reproductive Events in Muskoxen

Emma K. Hoare, Sarah E. Parker, Peter F. Flood & Gregg P. Adams

Department of Veterinary Anatomy, Western College of Veterinary Medicine, University of Saskatchewan, 52 Campus Drive, Saskatoon, Saskatchewan, Canada S7N 5B4. e-mail: Peter.Flood@usask.ca

Key words: ovary, corpus luteum, *Ovibos moschatus*, ultrasound, follicle.

Rangifer, 17 (3): 119–123

Introduction

Patterns of ovarian follicular development have been well described in horses (Ginther, 1992), cattle (Ginther *et al.*, 1989; Knopf *et al.*, 1989), sheep (Ravindra *et al.*, 1994), goats (Ginther & Kot, 1994), llamas, alpacas (Adams *et al.*, 1990) and, more superficially, in several non-domestic species (Adams *et al.*, 1991) using transrectal ultrasonography. The technique allows the identification of follicles >2 mm. in diameter though analysis is usually restricted to follicles >4 mm. In all the species mentioned above, antral follicles appear in the ovaries in small groups or cohorts, and continue to grow in parallel for the next few days, before the majority degenerate. Such a group is known as a follicular wave. Each wave is initiated by a surge of follicle stimulating hormone from the pituitary which precedes wave emergence (Adams & Pierson, 1995). Follicular waves occur during the breeding and non-breeding seasons as well as during pregnancy. It is not known whether follicular waves are affected by nutrition.

Transrectal ultrasonography has recently been used in muskoxen to characterize the corpus luteum of pregnancy (Rowell *et al.*, 1993) and to examine the accessory genital glands of males (Tedesco, 1996) but the behaviour of ovarian follicles has not been studied. Follicular and luteal dynamics are of particular interest in muskoxen because their reproduction is very sensitive to nutritional (Adamczewski *et al.*, 1997) and photoperiodic (Gray, 1987; Tedesco, 1996; Tener, 1965) effects.

The objectives of this study were to determine the feasibility of daily transrectal ultrasonography of the female reproductive tract, and to characterize ovarian follicular and luteal dynamics during the breeding and non-breeding seasons. Here we report on the technique and preliminary results obtained during the breeding season. A full account will appear elsewhere.

Materials and methods

Female muskoxen at the University of Saskatchewan – Goodale Research Station were examined weekly or daily, by transrectal ultrasonography during selected periods in 1992 and 1995. In 1992 the animals (n=4) ranged in age from 6–10 years and weighed 222±9 kg; in 1995 all the animals (n=6) were two years old and weighed 171±6

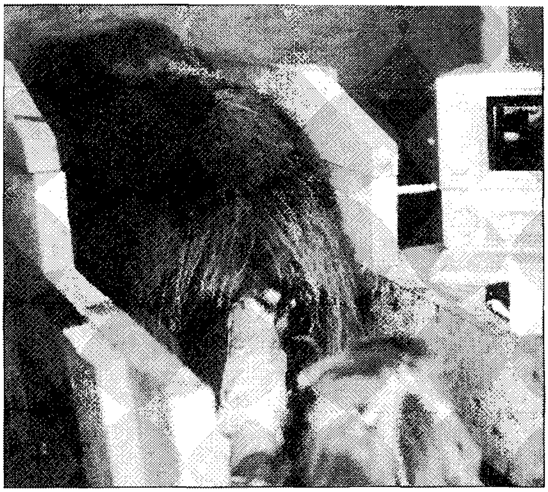

Fig. 1. Ultrasound examination of a muskox showing the animal, the instrument, the examining stall and the operator (who is crouching to give a clear view).

kg. The longest period of continuous daily observation was 35 days.

The muskox cows were normally maintained on pasture with at least one male. With the onset of the rut, the cows were separated from the bulls by a wire fence until one oestrous cycle had been completed. The muskoxen were accustomed to entering a central feeding pen daily, and were halter-tied in individual stalls while feeding. The study animals were led into a raised tie-stall that was enclosed and darkened so the ultrasound screen could be seen (Fig. 1). The side of the stall was adjustable to minimize lateral movements. The animals were fed during the procedure and could be easily restrained without tranquilization or anesthesia. After manual removal of the feces, the reproductive tract was examined as in horses (Ginthet, 1986), using a B-mode scanner with a 7.5 MHz linear-array transducer (Aloka SSD 500, Overseas Monitor Corp. Ltd., Richmond, B.C.). On each occasion, the ovaries were sketched to record the size and location of the follicles and the corpus luteum.

As in cattle, individual follicles could be identified and monitored (Knopf *et al.*, 1989). The diameter of the largest follicle was recorded from the day at which it was first identified (4 to 5 mm.) to the day on which its identity was lost (regression to ≥4 mm.). The daily diameter profile was then related to the total number of follicles >4 mm detected each day. Follicular development was accepted as wave-like if the number of new follicles detected each day peaked at regular intervals. The largest follicle of a follicular wave was defined as a dominant follicle, and the next largest follicles were defined as subordinate if they appeared within one day of the dominant follicle and increased in size for at least one day after detection (Ginther *et al.*, 1989). Waves in which the size of the dominant and subordinate follicles diverged markedly were defined as major waves. If the largest follicle was only a little larger than its companion follicles, the wave was referred to as a minor wave (Bergfelt & Ginther, 1993). Successive follicular waves in an oestrous cycle (Day 0 = day of ovulation) were designated as Wave 1, Wave 2, Wave 3 and Wave 4 regardless of whether they were major or minor. The day of wave emergence was determined in retrospect as the day on which the dominant follicle was 4 to 5 mm in diameter.

The significance ($P\geq0.05$) or tendency ($P\geq0.1$) of fluctuations in the number of follicles detected per day was tested by analysis of variance for repeated measures and confirmed by split-plot analysis of variance. An indication of a day effect in the number of follicles detected per day was followed by a normalization procedure in which the data (follicle number and diameter, corpus luteum diameter) were adjusted to the mean day of wave emergence for each successive wave, and to the mean interovulatory interval.

Results and discussion

Within a week of commencing daily examinations, all of the muskoxen had adjusted to the procedure and could be handled by one person with minimal coaxing (Fig. 1). The animals remained standing when examined and rarely kicked. There was some resistance (restless movement) during the initial period of habituation but very little effort was made to avoid being handled. No signs of learned aversion were observed. On the contrary, the muskoxen became more eager to enter the stall as the study progressed.

The rectum of all the muskoxen ($n=10$) was large enough to permit the insertion of a gloved hand and an ultrasound probe. The part of the procedure that was most resented was initial insertion of the examiner's hand into the anus. The muskoxen particularly resented the guard hairs around the perineum being pulled and the short tail was clamped tightly over the anus at the start of the examination. Clipping the hair covering the tail and perineum greatly facilitated access and minimized discomfort. The anus was more restrictive than the rectum and operators with small hands (glove size, <7) were most successful. Once the anus was passed, both the tail and the anal sphincter relaxed. Standard methyl-cellulose gel was satisfactory as both a lubricant and contact medium. Insertion of the hand into the rectum was an improvement over an earlier technique in which the transducer was fitted with a stiffened handle manipulated from the exterior, because it allowed controlled pressure on the rectal wall and greater subtlety of movement. Typical images are shown in Fig. 2.

Follicular waves were apparent during the oestrous cycles of all 4 muskoxen examined during the ovulatory season ($P<0.1$); one animal had 3 waves per cycle and the remaining 3 animals had 4 waves. Only the dominant follicle of the last wave of the cycle ovulated; the dominant follicle of other waves regressed slowly over a period of a few days. Intervals and follicle growth characteristics for 3- and 4-wave animals are summarized in Table 1 and Fig. 3. Dominance was clearly manifest in the first and last follicular waves in each of the 4 animals (major waves), whereas the other waves in all but one instance appeared to be minor waves. In cattle and llamas, the largest follicle of a wave consistently suppresses its subordinates, growing in diameter while its subordinates regress (Adams *et al.*, 1990; Adams *et al.*, 1992; Ginther & Kot, 1994; Ravindra, 1994). In sheep (Ravindra *et al.*, 1994), goats (Ginther & Kot, 1994) and horses (Bergfelt & Ginther, 1993), follicle dominance is not seen in some waves and apparently muskoxen show the same phenomenon.

The first ovulation of the breeding season was detected in 2 of the 4 muskoxen. The subsequent interovulatory intervals were 6 and 7 days, and included only 1 follicular wave and a short-lived corpus luteum. Growth characteristics of the dominant follicle and corpus luteum of this initial short cycle are given in Table 1.

Corpora lutea were detected soon after ovulation (Day 0.6±0.2). They first appeared as brightly echogenic structures but became less echogenic as the cycle progressed; they remained visible throughout the interovulatory interval and attained a maximum diameter about 5 days after ovulation

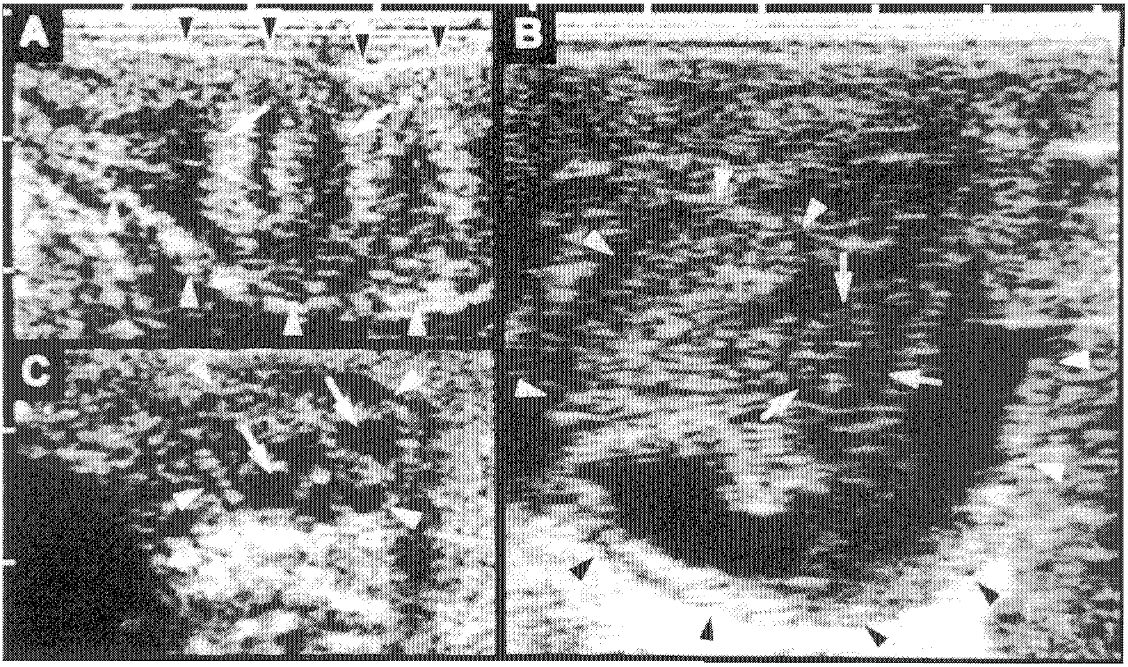

Fig. 2. Ultrasonographic images of the female reproductive tract of the muskox. One cm. scale divisions are shown at the top of each image and cranial is to the right. A) The cervix. The arrows indicate cervical folds and arrow heads the outline of the cervix. B) The female reproductive tract at 25 days gestation. The arrow heads show the greater curvature of the uterus.and the arrows show the outline of the corpus luteum within the ovary. The black area inside the uterus is allantoic fluid. C) An ovary with many follicles. The arrows show follicles of about 4 mm diameter. The arrows heads indicate the outline of the ovary.

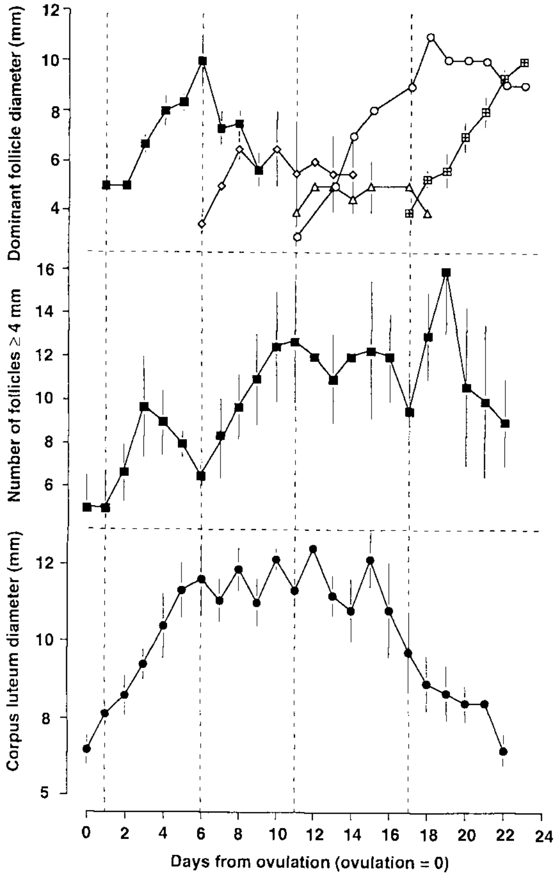

Fig. 3. The diametet of the largest follicle (upper panel), number of follicles >4 mm in diameter (middle panel) and diameter of the corpus luteum (lower panel) throughout the second oestrous cycle (interovulatory interval = 22.8±1.1 days) in 3 muskoxen with a 4-wave cycle (means±SEM; vertical dotted lines show the day of emergence of a follicular wave). Wave 1 (solid squares) and Wave 4 (boxes) were all major waves and Wave 2 (open diamonds) was all minor. In Wave 3, 1 animal (open circles) had a major wave and the other 2 (open triangles) had minor waves; these are shown separately.

Table 1. Follicular and luteal characteristics of the first and second cycles of the breeding season.

	First cycle	Second cycle
Number of muskoxen	2	3 or 4
Inrerovulatory		
Interval (days)	6.5±0.5	22.8±1.1
Interwave Interval (days)	–	5.4±0.2
Day of wave emergence*		
Wave 1	0.5±0.5	1.3±0.3
Wave 2		6.0±0.4
Wave 3		11.5±0.3
Wave 4		17.3±0.3
Dominant Follicle		
Number of observations	2	11 or 12
Emerging diametet (mm)	4.5±0.5	4.5±0.4
Growth rate (mm/day)	0.9±0.1	0.9±0.1
Maximum diametet (mm)	10.5±0.7	9.1±0.9
Days to maximum diameter	5.0±1.0	6.0±1.1
Regression rate (mm/day)	–	0.6±0.1
Corpus Luteum		
Number of observations	2	4
Day of first detection	0.5±0.5	0.6±0.2
Diametet at first detection (mm)	6.5±0.5	7.2±0.4
Days to maximum diametet	5.0±0.0	4.7±0.4
Maximum diameter (mm)	14.5±3.5	13.5±1.9
Days retained	> 6	23.5±3.5

*Day of ovularion = Day 0.

(Table 1 and Fig. 3). The corpus luteum of the first cycle of the season was also seen soon aftet ovulation and was visible throughout the interovularory interval (Table 1).

Conclusion

These results show the applicability of transrectal ultrasonography to the study of reproduction in muskoxen. The animals wete easily examined daily for 5 weeks without apparent stress. The technique could also have been used to assess the reproductive status of immobilized muskoxen in the field. The ovaries of well fed tame muskoxen show regular follicular waves during rhe breeding season and probably during the non-breeding season, though the latter data are, as yet, incomplete. Each oestrus cycle included 3 or 4 follicular waves at about 6 day intervals. The short cycle at the onset of the breeding season consisted of a single follicular wave.

To our knowledge, this is the firsr detailed teport of ovarian follicular dynamics in a wild species. It seems that the pattern in muskoxen, with major and minor waves and a short first cycle, is similar to that in goats. Insight of this kind is important in the design of appropriate artificial breeding systems and in this tespect, the muskox may provide a useful model for the endangeted takin (*Budorcas taxicolor*). A detailed knowledge of ovarian events may also be critical to the interpretation of the response of wild populations to environmental srress.

Acknowledgements

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Brief communication

Progesterone during the breeding season and pregnancy in female muskoxen on different dietary regimens

Janice E. Rowell, Robert G. White & William E. Hauer

Institute of Arctic Biology, University of Alaska Fairbanks, AK 99775-7000, USA. e-mail: fnjer@aurora.alaska.edu

Abstract: Previously, we documented lowered calving success in caprive muskoxen raised for 6 years on a low nutritional plane. In an effort to identify causes of lowered calf production, we looked at serum progesterone during the breeding season in muskoxen raised on either a high (HP) or low (LP) nutritional plane. Complete cessation of estrous cyclicity in 2 parous cows was the only irregularity identified. Aborrion and/or embryonic loss occurred in both HP and LP cows. We also compared progesterone during pregnancy between the 2 nutritional planes and lactating and non-lactating cows. The timing of the rise and fall of the mid-pregnant progesterone peak was consistent with stage of gestation and apparently independent of time of breeding, diet or lactational status.

Key words: estrous cycle, body condition, embryonic loss, aborrion.

Rangifer, 17 (3): 125–129

Introduction

There is now good evidence that habitat quality from mid-Augusr to mid-October affects the ability of female muskoxen to regain sufficient body weight fot successful reproduction (White *et al.*, 1989; Parker *et al.*, 1990; Adamczewski *et al.*, 1992; White *et al.*, 1997). Under good conditions muskoxen can calve annually and produce their first calf at 3 years of age (Latour, 1987; Rowell, 1991). Calving as a 2-year-old does occur, both in the wild and captivity, but is less common (Jingfors & Klein, 1982; Rowell *et al.*, 1987).

Under captive conditions, the probability of a cow calving falls below 50% when autumn body weight is less than 180 kg and body condition score (on a scale of 3-15) is less than 6 (White *et al.*, 1997). These authors recorded calving success in 2 groups of muskoxen maintained for 6 years on either a high (HP) or a low (LP) nutritional plane and were able to document a clear depression in calving success among LP cows. We, rherefore, wanted to know if there were differences between the 2 groups in estrous cycle length or evidence of repeat cycles, establishment of ptegnancy or indication of embryonic loss. In 1992, in conjunction with the study on calving success, we began collecting weekly blood samples during the bteeding season from the most tractable animals within each nutritional group. In addition, plasma samples were collected throughout pregnancy (1993/94) in 3 HP and 3 LP cows to compare the pattern of progesterone secretion over mid to late pregnancy in both lactating and non-lactating females. This brief report is a summary of these results.

Methods

As part of a long term nutritional study in muskoxen, females ranging in age from 2.5-7.5 years-old at the time of breeding, have been maintained on either a high plane or a low plane of nutrition since 1987. High plane animals were allowed to graze pasture, had year-round access to brome-grass hay and were supplemented with a pelleted ration twice weekly (Quality Texture, Fisher Mills, Seattle; Alaska Mill and Feed, Anchorage) to give a daily pellet dry matter intake of 14 $g/kg^{0.75}$. Low plane cows were given slightly restricted grazing during the summer and allowed free access to brome-grass hay. They did not receive the pellet supplement and, in winter, had access to hay only. Body weight (BW) was measured weekly during the mating season (August 1-October 31) and body condition score (BCS) was assessed twice-monthly in August and September. Body condition score, a subjective index of subcutaneous fat and tissues, was determined from three regions on the animal: 1) the back (immediately caudal to the withers), 2) the ribs and 3) over the tuber coxae (pins) (Gerhart *et al.*, 1992; Gerhart *et al.*, 1995). Each region was evaluated on a scale of 1-5, where 1=hide only and 5=maximum subcutaneous fat and other tissues (Gerhart *et al.*, 1995). Details on the nutritional regimen and condition scoring are given in White *et al.*, 1997.

An experienced breeding bull (> 4-years-old) was placed with each harem. The bulls were periodically exchanged between the HP and the LP group. Harems were set up in late Sept. in 1992, Aug. 17, 1993, and Aug. 22, 1994. All harems remained together until mid-late October. Throughout the breeding season weekly blood samples were collected by jugular venepuncture from a subset of HP and LP muskox cows (Table 1).

Table 1. Number of female muskoxen sampled weekly in each breeding season, at the Large Animal Research Station, Fairbanks AK. The females were divided between a high (HP) or low (LP) nutritional plane.

	1992	1993	1994	TOTAL
HP	1	3	4	8
LP	5	4	4	13

Jugular blood samples were collected from 3 HP and 3 LP pregnant muskoxen throughout the winter of 1994/95. Three of these cows (2HP, 1LP) were lactating and in 3 cows (1 HP, 2 LP) lactation had ceased before or during the breeding season. Plasma samples were collected at 1-2 week intervals after the breeding season. The plasma was harvested within 2 hours of collection and remained frozen until assayed.

Progesterone was determined by RIA. In 1992 samples were assayed by Reproductive Endocrine Labs, Colorado State University, Fort Collins, Colorado (Niswender, 1973). Assay sensitivity was 0.05 ng/ml. In 1993 and 1994 samples were assayed with commercial radioimmunoassay kits (Diagnostic Products Corporation; Los Angeles, CA). Sensitivity of the assays was 0.03 ng/ml. Intra-assay CV's were 4.9% (low) and 6.3% (high) in 1993 and 2.2% and 8.1% (low) and 9.5% and 16.2% (high) in 1994. All samples for each year were run in a single assay. The use of RIA to successfully assay steroids from muskox plasma has been demonstrated (Rowell & Flood, 1988; Rowell *et al.*, 1993). To validate the immunoassay kits, a subset of duplicate aliquots spanning the expected period of the progesterone rise and decline during pregnancy were submitted to Reproductive Endocrine Labs in Colorado for separate analysis. The results from the independent lab and the immunoassay kits corroborated very well.

The care and handling of the animals (and all study protocols) were approved by an independent animal welfare committee.

Results and discussion

Progesterone during the breeding season

Among the sampled females, all HP cows calved in 1993 and 1994 but only 3 of 4 calved in 1995. Two of 5 LP cows did not calve in 1993, one failed to calve in 1994 and again in 1995. Failure to ovulate (progesterone never rose above 0.5 ng/ml throughout the breeding season) was the mechanism employed by the 2 LP cows that failed to calve in 1993. One of these cows was not lactating while the other was suckling a yearling calf. The September BCS of both cows was 4 and we consider it probable that the cessation of estrous activity was associated with their very poor body condition. A similar situation was identified in field collections where the ovaries of 2 parous, female muskoxen had no corpora lutea or other indications of cyclic activity at the end of October (Rowell *et al.*, 1987). Reduced or absent courtship activity in the breeding season following a severe winter could also reflect the absence of estrous cycles (Gray, 1987).

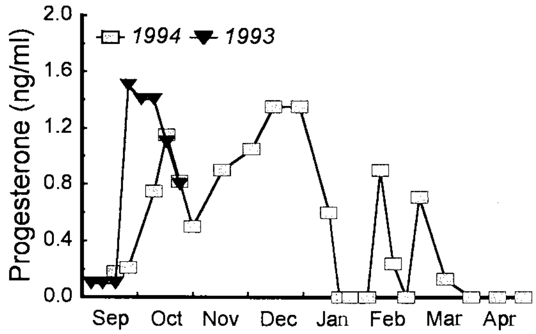

Fig. 1. Progesterone profiles for a female muskox that underwent abortion/embryonic loss in 2 consecutive breeding seasons. In 1993 sampling stopped shortly after harems were broken up. At this point the cow's (Sine) progesterone had remained elevated for 5 consecutive weeks but she failed to calve the following spring. In 1994 physical signs of an abortion were apparent at the end of December when progesterone returned to baseline. Following the abortion Sine resumed cyclic activity which continued into March.

It has been suggested that early embryonic loss/abortion may be a mechanism for controlling female productivity among muskoxen (Adamczewski, 1995) and in this study abortion and/or embryonic loss occurred on 3 occasions in 2 cows, 1 LP and 1 HP. In the LP cow (Sine), elevated progesterone levels (>0.5 ng/ml) were noted for 5 consecutive weeks in 1993 and for 10 consecutive weeks in 1994 (Fig. 1). In November, 1994, ultrasound corroborated the interpretation of pregnancy. Physical evidence of abortion was only evident in 1994 although no fetus was recovered. This cow had not calved since 1991. Her fall BW was above 180 kg (207 kg-1993, and 225 kg-1994) but in both years her BCS was around the threshold value of 6 (5.6 - 1993 and 7.4 - 1994).

There are 2 equally plausible interpretations for the early embryonic loss, ecological or pathological:

Ecological - Sine's body condition in 2 consecutive autumns was marginal (BCS at threshold, BW above threshold). She was able to conceive but body condition did not improve and/or was not adequate for mid-winter conditions and somewhere between November/December she aborted or reabsorbed her fetus.

Pathological - This cow has a subclinical condition inhibiting adequate placental formation. Endometrial scarring has been observed in captive muskoxen (Blake, unpubl. obs.). This condition does not produce overt clinical symptoms but can seriously impair placental establishment. We know that the muskox corpus luteum of pregnancy regresses completely by December (Rowell *et al.*, 1993), and, if at this time the placenta is small and underdeveloped, the risk of abortion would be very high. The fact that this cow is 12 years old and has aborted in consecutive years also supports a pathological interpretation.

We cannot discriminate between the 2 explanations. This cow died of unrelated causes before the issue could be resolved.

The HP cow showing signs of early embryonic loss (Unni) had elevated progesterone for an estimated 6 weeks in 1994 and it is assumed she was pregnant. By early November progesterone had declined to baseline, ultrasonography indicated she was not pregnant and a large preovulatory follicle was visible on one ovary. Early pregnancy loss in Unni, a HP cow, is harder to explain in terms of a controlling mechanism for female productivity. Both BCS (12.3) and BW (239 kg) were increasing from August to October and remained above theoretical thresholds for successful breeding. This cow is 11 years old and, in her case, we could hypothesize an age effect or possibly a subclinical condition. She calved successfully the following year.

Early pregnancy loss occurs in all species and is associated with a complex interaction of physiological and genetic elements (Austin, 1972). These preliminary data can neither support nor refute the suggestion that early pregnancy loss is a mechanism controlling female productivity. However, it does emphasize some of the variables that should be considered when invoking controlling mechanisms and the need for a reasonably large sample size before conclusions can be drawn. It is interesting to note that following pregnancy termination both cows apparently resumed estrous cycles (Fig 1). Continuous cyclic activity into March has been observed before in well conditioned, non-pregnant, captive muskoxen (Rowell, 1991) and the occasional report of a very late born calf suggests that it must also happen in the wild (Alendal, 1971). However, this would not be an expected result if poor body condition had precipitated the abortion.

Progesterone during pregnancy

In all 6 muskoxen progesterone began to rise at 10-12 weeks gestation to levels 2-3 times those normally found during the estrous cycle. Progesterone then dropped suddenly between 19-22 weeks gestation, returning to levels typical of the estrous cycle

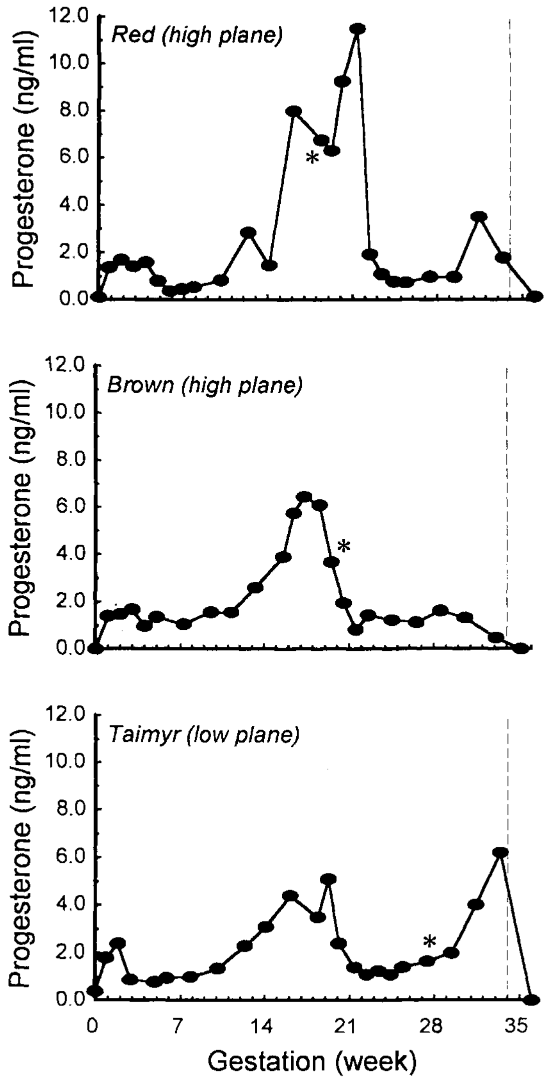

Fig. 2. Progesterone profiles from 3 individual muskoxen throughout pregnancy. All cows (2 HP and 1 LP) were lactating during the first half of gestation. Weaning is indicated by the asterisk and calving by the dotted line.

(Figs. 2 and 3). This pattern of progesterone secretion has been previously described (Rowell *et al.*, 1993) but its uniqueness among ruminants makes it important to demonstrate repeatability of the profile in different muskoxen under different conditions.

The mid-pregnant peak of progesterone occurred at the same stage of gestation (19-22 weeks) in both HP and LP cows regardless of whether or not they were lactating (Figs. 2 and 3). This unusual profile was first documented in captive, non-lactating

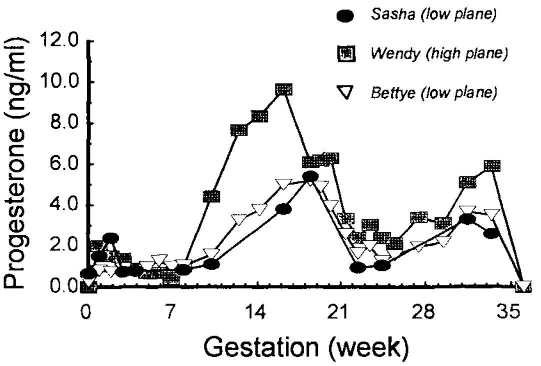

Fig. 3. Individual progesterone profiles throughout pregnancy from 3 non-lactating muskoxen (1 HP and 2 LP).

muskoxen on a high nutritional plane Rowell *et al.*, 1993). Because natural weaning tends to occur at approximately the same time as the mid-pregnant progesterone peak, we were looking for a temporal association between the two events. The timing of weaning did not show any consistent relationship with the peak or decline of progesterone. The time of the progesterone peak in relation to the stage of gestation was consistent in both studies regardless of the date of breeding. This implies a physiological event related to the fetus and/or placenta.

We report here some of our observations on the characteristics of the estrous cycle in muskox cows that have been reared for over 6 years on either a high or low nutritional plane. We found a complete cessation of estrous cyclicity during the breeding season in 2 mature, parous cows in very poor body condition. No other irregularities of the estrous cycle were evident in our limited sample. We have documented abortion and early embryonic loss in both a HP and LP cow, although the role this may play in regulating productivity remains unclear.

Progesterone profiles during pregnancy support and expand previous documentation of a completely unique pattern. The timing of the progesterone rise and fall is remarkably consistent with stage of gestation and apparently independent of timing of breeding, diet or lactational status. This suggests an endocrine event that is a reflection of fetal/placental development rather than the maternal environment.

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Brief communication

Seasonal Patterns in Growth Hormone, Insulin and Insulin-like Growth Factor-1 in Female Muskoxen

Jan Z. Adamczewski[1]*, Susan C. Tedesco[1], Bernard Laarveld[2] & Peter F. Flood[1]

[1] Department of Veterinary Anatomy, 52 Campus Drive, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5B4, Canada. (*Present address: c/o Sahtu Renewable Resources Board, P.O. box 490, Norman Wells, Northwest Territories X0E 0V0, Canada).

[2] Department of Animal & Poultry Science, 72 Campus Drive, Universiry of Saskatchewan, Saskatoon, Saskatchewan S7N 5B5, Canada.

Abstract: Over a year, mean serum growrh hormone concentrations ranged from 0.5 to 3 ng/ml in tame muskoxen with the lowest values and fewest pulses between October and January. Serum insulin ranged from 0.25 to 0.92 ng/ml, with minima in summer. There were marked seasonal changes in serum insulin-like growth factor-1 in both tame and wild muskoxen but the late summer peak was higher and more distinct in the tame animals with levels reaching 160-250 ng/ml in September.

Key words: *Ovibos moschatus, nutrition*, weight.

Rangifer, 17 (3): 131–134

Large annual changes in weight and body composition of female muskoxen (*Ovibos moschatus*) are partly due to lactation and decreased nutrient availability in winter (Thing *et al.*, 1987; White *et al.*, 1989). However, tame well-fed non-bteeding muskoxen also lose weight in late winter and gain weight in autumn and early winter (Groves, 1992; Adamczewski *et al.*, 1994), suggesting an effect of photoperiod, independent of nutrition. Growth processes in ruminants are regulared by hormones such as growth hormone (GH), insulin-like growth factor-1 (IGF-1) and insulin (Pearson & Dutson, 1991). To investigate the seasonal regulation of weight change in muskoxen, we measuted seasonal patterns in GH, IGF-1, and insulin in muskox cows offered a dier of constant medium quality, and IGF-1 in hunter-killed wild muskoxen. A summary of preliminary IGF-1 data was presenred previously (Adamczewski *et al.*, 1992).

The tame muskoxen wete part of a research herd kept near Saskatoon, Saskatchewan, Canada (52°N), and were offered brome-alfalfa hay [9–12% crude protein (CP)] and a pelleted supplement (13–14% CP; 20% of diet; Adamczewski *et al.*, 1994) during each blood-sampling period and for at least 12 days previously, in 1990 and 1991. We studied 3 cows which bted annually and 2 non-breeding hysterectomized cows with intact ovaries, all ≥ 4 years old. Jugular catheters were installed 36-48 hours prior to sampling, using local anaesthetic and mild sedation (Tedesco, 1996). During sampling, the muskoxen wete kept loosely tied in shaded outdoor stalls with access to hay and water or snow. Blood samples of 5-10 cc were taken every 15 min fot 24 h

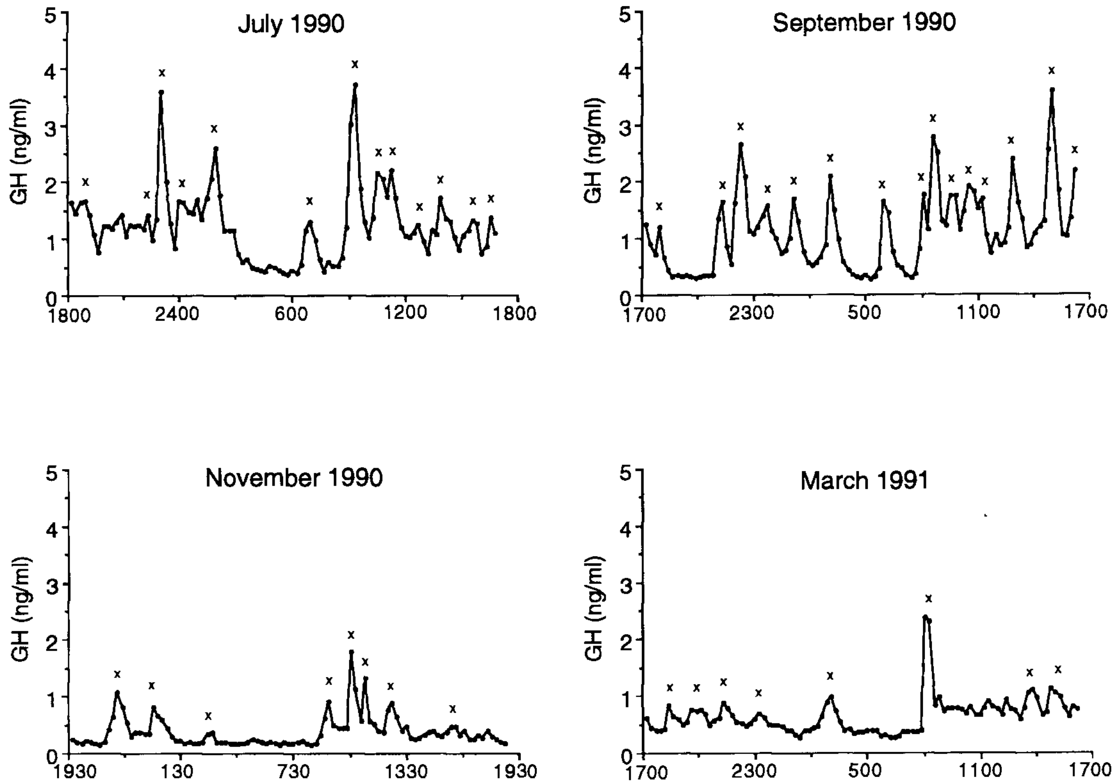

Fig. 1. Selected 24-h growth hormone profiles for Athabasca, a non-breeding muskox cow in Saskatoon. Pulses identified by PULSAR are denoted by x's.

Table 1. Seasonal changes in serum concentrations (ng/ml) of growth hormone and insulin in tame muskox cows offered a constant-quality diet in Saskatoon, Saskatchewan, 1990-1991. Samples were taken from the same animals throughout. Means with standard errors in parentheses.

	Growth hormone		Insulin	
Month	Intact Cows (*n* = 3)	Hysterectomized Cows (*n* = 2)	Intact Cows (*n* = 3)	Hysterecromized Cows (*n* = 2)
May	-	1.10 (0.45)	-	0.55 (0.01)
July	2.01 (0.85)	2.02 (0.79)	0.24 (0.04)	0.27 (0.48)
Sept.	1.12 (0.20)	2.62 (1.50)	0.46 (0.09)	0.92 (0.06)
Nov.	0.53 (0.05)	1.33 (0.95)	0.43 (0.08)	0.40 (0.05)
Jan.	0.99 (0.31)	1.46 (0.97)	0.69 (0.02)	0.69 (0.02)
Mar.	1.38 (0.30)	2.48 (1.83)	0.31 (0.03)	0.41 (0.08)
May	2.37 (1.30)	-	0.52 (0.05)	-

under ambient light augmented by dim ted lights at night. Cortisol analysis of samples taken periodically showed that the muskoxen were unstressed at these times (Tedesco, 1996). Wild muskox cows ≥ 3 years old were shot by Inuit hunters near Cambridge Bay during 15 hunts in April, May, July, August, September and November from 1989 to 1993 (Adamczewski, 1995). Blood was collected just aftet death from a jugular vein.

Serum GH, IGF-1 and insulin were assayed by radioimmunoassays described by Van Kessel (1992). The GH assay was developed for ovine serum and validated for muskox serum by showing parallelism to the standard curve in a serial dilution of a concentrated sample. GH was assayed in representative 24-h sequences from 5 muskox cows, and GH pulsatility was analysed using the pulse-detection algorirhm PC-PULSAR (J. Girzen and V. Ramirez, Univ. Illinois), following Merriam & Wachter (1982). The IGF-1 assay was developed and tested fot sera from various species and validated for muskox serum as above. The insulin assay was developed for bovine and ovine serum, and similarly validated. IGF-1 and insulin were assayed in samples pooled from 24-h profiles from tame muskoxen, and IGF-1 was assayed in individual samples from wild muskoxen. Monthly values from tame muskoxen were compared for all three hormones by splir-plor analysis-of-variance (ANOVA) and values from wild muskoxen by one-way ANOVA, using season as the main effect.

Setum GH was pulsatile in the tame muskoxen (Fig. 1), with highly individual profiles. Mean GH ranged from 0.5 to 3 ng/ml and GH pulse frequency ranged from 6 ro 18 pulses/24 h. Both the frequency of pulses and mean GH were lowest between October and January, with significant (P=0.04) ot near-significant (P=0.06) monthly variation, respectively (Table 1). Serum insulin means ranged from 0.25 to 0.92 ng/ml, with significant monthly variarion (P<0.001) and the lowest concentrations in June and July. Individual variation in insulin was high and a clear seasonal progression was not apparent. Thete was a srrong seasonal progression (P<0.001) in serum IGF-1 in the tame muskox cows, with mean concentrations increasing during summer, a clear peak in September (160–250 ng/ml) and lowest concentrations in November (60–120 ng/ml) (Table 2). There was a strong (P<0.001) but different seasonal pattern in serum IGF-1 in wild muskoxen, with a plateau of high values (80–120 ng/ml) in July, August and Septembet, and the lowest values (30–50 ng/ml) in November. Serum IGF-1 was lower throughout the yeat in wild muskox cows than in tame ones.

Table 2. Seasonal changes in serum concentrations (ng/ml) of insulin-like growth factor-1 (IGF-1) in tame muskox cows offered a constant-quality diet in Saskatoon, Saskatchewan, 1990-1991 (repeated samples from the same animals) and from wild muskox cows on Victoria Island, NT (single samples from individual animals). Means with standard errors in parentheses.

Month	Tame Muskoxen (n = 5)	Wild Muskoxen	n
March	82.1 (8.9)	-	-
April	-	45.1 (3.2)	47
May	79.7 (6.0)	54.7 (5.1)	38
July	122.8 (13.8)	106.5 (8.6)	8
August	-	116.5 (14.4)	18
Sept.	191.9 (28.7)	93.7 (10.3)	12
Oct.	94.5 (25.9)	-	-
Nov.	85.3 (20.1)	50.9 (3.5)	40
Jan.	72.3 (5.1)	-	-

These endocrine patterns are consistent with the tendency of muskox cows to gain weight in autumn and early winter, and with a large seasonal variation in intake and diet quality in free-ranging muskoxen. Although the insulin values varied widely in tame muskoxen, they were lowest in early summer, a period when fat deposition is limited (White *et al.,* 1989; Adamczewski, 1995). The autumn peak in IGF-1 in tame muskox cows, despite a diet of constant quality, is also consistent with lean tissue growth at this time of year (Adamczewski, 1995) and may account for the high IGF-1 in August and September in wild muskox cows at a time of decreasing forage quality. The proximate cause of this peak is unknown but may include seasonal changes in melatonin secetion (Tedesco, 1996) or increased estrogen due ro reproductive cycling (cf. Sauerwein *et al.,* 1992). These results are consistent with the strong seasonality in growth and intake of temperate and arctic cervids (Suttie *et al.,* 1993) but suggest that the effects of season on growth are subrly different in muskoxen and caribou, as has been shown for the effects of season on reproduction in muskoxen (Tedesco, 1996). The late IGF-1 peak, in particular, appears to contrast with the earlier peak of IGF-1 in red deer (Suttie *et al.,* 1992) and reindeer (Suttie *et al.,* 1993), where the IGF-1 rise appears to anticipate lean growth. Female muskoxen appear predisposed to an apparently simultaneous surge in growth of lean and adipose tissue toward the end of summer, well past the period of peak forage quality (White *et al.,* 1989; Adamczewski 1995). This timing underscores the association of weight gain in female muskoxen with reproductive events, as suggested in reindeer by Tyler (1987). The elevared IGF-1 and insulin in the autumn also suggest that serum concentrations of these hormones, intimately involved in ovarian physiology (Spicer & Echternkamp, 1995), influence the highly variable productivity of female muskoxen.

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Brief communication

Seasonal changes in metabolic rates in muskoxen following twenty- four hours of starvation

James P. Lawler & Robert G. White

Institute of Arctic Biology, Univ. of Alaska Fairbanks, AK 99775-7000 USA.

Abstract: Timing of seasonal trends in post-prandial energy expenditure (EE) was measured in muskoxen (2 males and 1 female) given a standardized meal followed by a 24-26 h starvation during 10 months over the course of a year. EE was significantly lower in winter than summer. CH_4 production (E_{CH4}) was reversed with winter highs and summer lows. Ratio of E_{CH4}:EE indicates a change in dietary efficiency but this difference was not associated with a seasonal shift in RQ which was constant. The main increase in EE from winter ro summer occurred between April and May and the summer to winter decrease between August and Septembet.

Key words: *Ovibos moschatus,* energy expenditure, seasonality, methane.

Rangifer, 17 (3): 135–138

Introduction

A seasonal lowering of resting metabolic rate typifies a north temperate adaptation to limiting winter food supply in a cold environment (Wood *et al.*, 1962; Feist & White, 1989). Nilssen *et al.* (1994) documented a significantly lower resting metabolic rate for ad. lib. fed and starved muskoxen (*Ovibos moschatus*) during the winter compared ro summer. However, timing of the down regulation in winter and up regulation in summer was not determined. The objective of this study was to determine the timing of seasonal trends in metabolism of muskoxen given a standardized meal followed by a 24-26 h starvation.

Materials and methods

Energy expenditure was measured in two intact males and one intact non-pregnant female muskoxen during 10 months over the course of a year. All were 3 year olds and had been used in similar metabolic trials since yearlings. Animals were calm during metabolic trials. Before and after each trial, animals were maintained in a brome pasture (*Bromus inermus*) with *ad. lib.* access to brome hay. Twice a week, animals were offered high-protein pellets (Quality Texture, Alaska Mill and Feed, Anchorage) fed at a daily rate of 14 g (DM) per kg $BW^{.75}$. At the start of an experiment each animal was brought into an unheated barn, offered 1 standard meal of 50% chopped brome hay and 50% pellets fed at 10 g (DM) per kg $BW^{.75}$ and then starved for 24-26 h. Each was then placed in an open circuit metabolic chamber (White *et al.*, 1984) to measure oxygen consumption, and carbon dioxide and methane production at 2 min intervals over a 2 h period. Temperature and barometric pressure was

Table 1. Comparison of winter with summer mean standardized energy expenditures, methane production and RQ of three 3 year muskoxen.

	Summer[1]		Winter[2]		
	mean	*SEM*	*mean*	*SEM*	*p*
Daily Energy Expenditure[3]	447	8.5	370	5.6	<0.001
Energy Expenditure (W/kg)	1.40	0.03	1.20	0.02	<0.001
CH_4 Energy	17.0	1.16	24.0	0.92	0.001
CH_4 Energy / Energy Expenditure	0.038	0.003	0.063	0.002	<0.001
RQ	0.88	0.01	0.90	0.01	NS

[1] June (*n*=3: Where *n* is the number of trials per month), July (*n*=3) and August (*n*=3)

[2] November (*n*=3), January (*n*=15), February (*n*=14) and March (*n*=19)

[3] kJ per kg $BW^{0.75}$

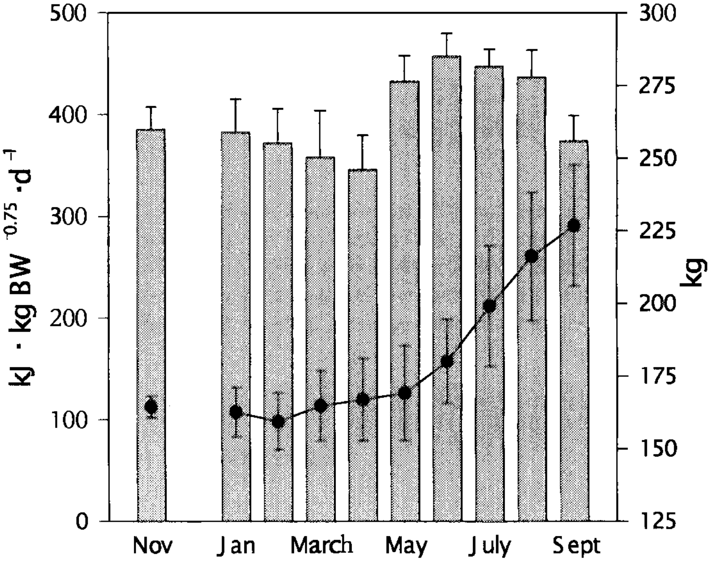

Fig. 1. Seasonal trends in mean energy expenditure and mean body weight of 3 muskoxen following a standardized meal and 24 hours of starvation. Seasonal patterns of summer highs and winter lows in energy expenditure and body weight were not synchronized.

logged by computer. Energy expenditure (EE) and methane energy loss (E_{CH4}) was calculated from gas concentrations, and flow rates (Kokjer, 1981). Calculations were performed using the entire 2 h interval. Therefore, differences in EEs associated with different activities were not calculated. Respiratory quotient (RQ) was calculated as CO_2 expired/O_2 consumed. Differences in energy expenditure were assessed by a two-factor analysis of variance. Sources of variance for the analysis were season, animal, and animal by season. Significance was determined at a 5 percent confidence level.

Results and discussion

EE was significantly lower in winter (November through March) than summer (June, July, August) (Fig. 1 and Table 1, $P<0.001$). Mean EE ($n=3$) was lowest in April at 343 ± 15 (SEM) kJ per kg $BW^{.75}$ (1.11 ± 0.03 W per kg) and highest in June at 457 ± 16 kJ per kg $BW^{.75}$ (1.45 ± 0.05 W per kg). The 33% difference was significant ($P=0.006$) but less divergent than the seasonal values for 7-10 h starved animals reported by Nilssen *et al.* (1994) who found winter and summer metabolic rates of 0.86 ± 0.10 and 1.74 ± 0.27 W per kg respectively (a 49% difference). The difference in winter-summer extremes more closely resemble the 30% difference recorded by Nilssen *et al.* (1994) for 6 d starved animals (winter values of 0.62 ± 0.07 W per kg and summer values of 0.77 ± 0.03 W per kg). Values reported for our muskoxen, represent both lying and standing-active animals, whereas those for Nilssen *et al.* (1994) are for the lying period. Low EEs occurred when body mass was at maintenance (November through April) and highest values during a period of weight gain (June through September) (Fig. 1). Summer and winter mean values were 53% and 27% respectively above the predicted BMR using the Kleiber equation (Kleiber, 1975).

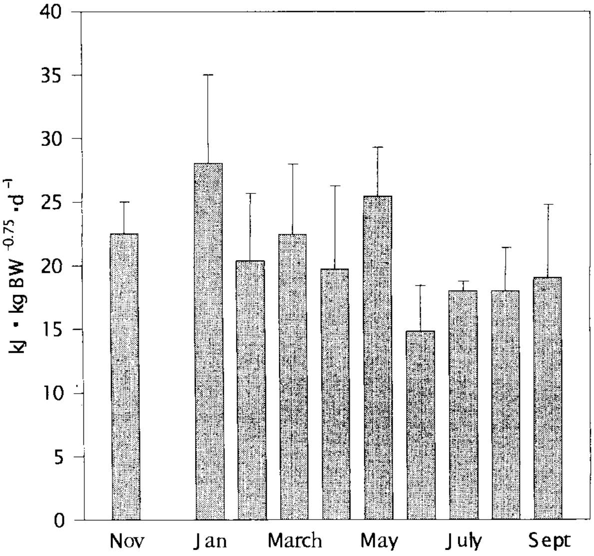

Fig. 2. Trends in mean CH_4 energy loss of 3 muskoxen following a standardized meal and 24 hours of starvation. Methane energy loss was higher in winter than in summer.

CH_4 production showed a significant but reverse seasonal pattern wirh winter highs and summer lows (Fig. 2 and Table 1, P=0.001). Mean daily E_{CH4} loss after the standardized starvation was lowest in June at 15 ± 2.6 kJ per kg $BW^{.75}$ and highest in Januaty at 28 ± 2.1 kJ pet kg $BW^{.75}$ (P=0.02) (Fig. 2). Ratio of E_{CH4}:EE indicates a change in dietary efficiency (Fig. 3) but this difference was nor associated with a seasonal shift in RQ which was constant at 0.88.

Variation exists between individuals and between seasons in voluntary levels of dietary intake, passage rate, and digestibility in muskoxen (Holleman *et al.*, 1984; White *et al.*, 1984; Adamczewski *et al.*, 1994). Each of these factots altet the heat increment of feeding and make it difficult to determine when a ruminant animal will reach a posr-absorptive state (Blaxter, 1962). Usually methane production would be low or non-exisrent when ruminants are truly post absorprive, thus out estimate of significant production shows heat increment is ptesent. However, in some species, starving an animal to the point that it teaches a post-absorptive state has been shown to cause hyperacrivity and restlessness (Robbins, 1994). These factots and those imposed by new animal welfare concerns make it difficult to achieve the conditions required ro directly measure BMR in large ruminants.

An alternative approach to long-term starvation is to measure EE under standardized conditions (Blaxter & Boyne, 1982), with the realization that some effects of heat increment may be carried over to add an indeterminate contribution to the variability in EE. As depicted by trends in body weight (Fig. 1), muskoxen were at maintenance levels in winter, but in positive energy balance in the summer. Thus rhe seasonal pattern in EE for these 24 h starved muskoxen, even when preceded by a standardized meal, undoubtedly reflect some residual heat increment and other merabolic effects associated with body weight gain and food intake. Howevet, the 33% shift in seasonal extremes in this study closely resembles that for long-starved muskoxen (Nilssen *et al.*, 1994) which suggests that endogenous tegulations could partially conttibute to these seasonal EEs. Nilssen *et al.* (1994) argue that the 30% decrease in EE in long starved muskoxen is a down regulation and not due to heat increment.

For the first time, we report on the timing of seasonal changes. The main increase in EE from winter to summer occurred between April and May and the summer to winter decrease

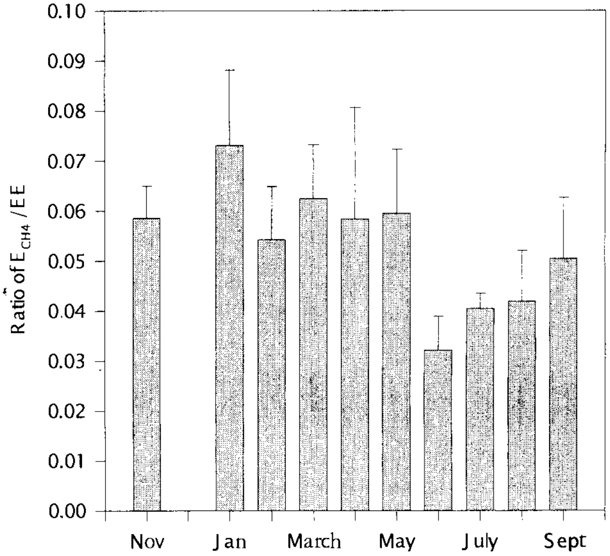

Fig. 3. Ratio of monthly mean methane energy loss to monthly mean energy expenditure indicating changes in dietary efficiency. Animals were more efficient in summer then in winter.

between August and September (Fig. 1). Possible cues rhat initiate seasonal shifts include seasonal photoperiod and forage quality and quantity. Under rhe conditions of this study in Fairbanks, Alaska (laritude 65° N) the month of April provides a summer cue, while the month of August provides that for winter, the month after and the month before equinox respecrively. From a natural history viewpoint, it is significant that the initiation of calving occurs in April, and initiation of the rutting season, and a shift of nutrient partitioning in adult females from milk production to body reserves, occurs in early August (White *et al.*, 1989), precisely when we observe significant shifts in seasonal EE.

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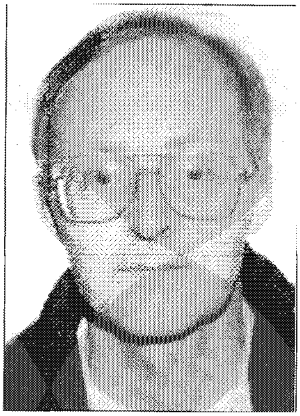
Manuscript accepted 26 February, 1997

Dissertation

Terje Domaas Josefsen defended his thesis: «Influence of diet on the forestomach mucosa in reindeer calves (*Rangifer tarandus tarandus*)» for the degree of *Doctor scientiarum* of the Norwegian College of Veterinary Medicine (NCVM), Oslo, on May 29, 1997. The title of his lecture was: «Diseases of the gastrointestinal tract of reindeer». The opponents were Dr. Timo Soveri, Univ. of Helsinki, Helsinki, and Prof. Inge Bjerkås, NCVM, Oslo.



Terje D. Josefsen was born in Tromsø in 1959. He finished his veterinary education at the NCVM in Oslo in 1984. After some years in general veterinary practise he was employed by the former Centre of Veterinary Medicine in Tromsø (now Department of Arctic Veterinary Medicine, NCVM) in 1991, on a research project concerning rumen pathology in reindeer. Important co-operating institutions on this project were Dept. of Pathology at the NCVM, Oslo, and Dept. of Arctic Biology at the University of Tromsø. The project was funded by the Norwegian Research Council.

Terje D. Josefsen is currently employed at the National Veterinary Institute in Tromsø.

The thesis is based on four papers:

Josefsen, T. D. and Landsverk, T. 1996. T cell subsets and Langerhans cells in the forestomach mucosa of adult sheep and sheep foetuses. *Vet. Immunol. Immunopathol.* 51: 101–111.

Josefsen, T.D., Aagnes, T. H. and Mathiesen, S. D. 1996. Influence of diet on the morphology of the ruminal papillae in reindeer calves (*Rangifer tarandus tarandus* L.). *Rangifer* 16: 119–128.

Josefsen, T. D., Aagnes, T. H. and Mathiesen, S. D. 1997. Influence of diet on the occurrence of intraepithelial microabscesses and foreign bodies in the ruminal mucosa of reindeer calves (*Rangifer tarandus tarandus*). *J. Vet. Med. A* 44: 249–257.

Josefsen, T. D. and Landsverk, T. Increase in γδ T cells in the ruminal mucosa of reindeer calves (*Rangifer tarandus tarandus* L.) induced by baled grass silage. (*Vet. Immunol. Immunopathol., accepted*).

Abstract: The study investigated the influence of diet on morphological aspects of the forestomach mucosa in reindeer calves. Three approaches were used: Morphometric measurements on ruminal papillae, pathological examination of the forestomach mucosa and immunohistological staining for leukocytes in the forestomach mucosa. An immunohistological study on leukocytes in the forestomach mucosa of sheep was included as a basis of the corresponding study in reindeer.

Reindeer forestomach samples were obtained from 4 groups of 3 free-ranging reindeer calves (Sept.-April), and 11 groups of 3 reindeer calves used in feeding trials with silage, pelleted feed or lichen. Sheep forestomach samples were obtained from 5 adult ewes and 7 sheep foetuses.

Results of morphometric measurements on reindeer ruminal papillae (Paper II) were expressed as group means of an "overall value" (the mean of 4 sample sites), and ranged from 2.3 to 3.4 mm for papillar length, 2.2 to 3.5 mm for cross-sectional perimeter, 85 to 189 papillae/cm^2 for papillar density and 5.8 to 18.6 for ruminal surface enlargement factor (SEF). Papillar size and density were larger in late summer compared to winter, and larger in animals fed low-fibre silage, high in easily digestible carbohydrates, compared to high-fibre silage, low in easily digestible carbohydrates. The SEF was highest in *atrium ruminis* and lowest in the caudodorsal blind sac.

Histopathological examination of the forestomach mucosa (Paper III) showed the occurrence of intraepithelial microabscesses (IEMAs) and foreign body lesions (FBLs). Both IEMAs and FBLs occurred more frequent in animals fed silage or pelleted feed compared to free-ranging and lichen-fed animals. FBLs occurred more frequently in animals with high numbers of IEMAs, and it is suggested that both IEMAs and FBLs are caused by plant particles penetrating the forestomach epithelium. The lesions did not seem to be associated with the nutritional value of the diet, nor influence animal health.

The immunohistological studies in sheep (Paper I) and reindeer (Paper IV) showed that MHC-II+ dendritic cells, interpreted as Langerhans cells, were present in the forestomach mucosa of both species. CD4+ T cells, CD8+ T cells and γδ T cells were demonstrated in sheep, while, due to lack of cross-reacting antibodies, only the γδ T cell subset was demonstrated in reindeer. All leukocytes were mainly located either within or immediately below the epithelium. The number of T cells differed between different sample sites in the forestomachs and between dietary groups, while the number of Langerhans cells showed less fluctuations.

It is concluded that morphometric measurements on ruminal papillae reflects ruminal function, while no functional changes were associated with increased frequency of epithelial lesions and increased mucosal γδ T cell density.

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Proceedings of rhe 2nd International Arctic Ungulate Confetence, Fairbanks, Alaska, 13–17 Aug. 1995: Issue No. 3

Information

NOR-CONFERENCE 1998
AT KAUTOKEINO/GUOVDAGEAIDNU, FINNMARK, 13–15 March.

NORs 10. Nordiske Reinforskningskonferanse. Tema: Reindriften i de nordiske land.

10th NORDIC CONFERENCE ON REINDEER RESEARCH.
Theme: Reindeer husbandry in the Nordic countries.

The next NOR-conference will be held at Guovdageaidnu (Kautokeino), Norway, 13-15 March, 1998 in cooperation with the Saami College. There are some possibilites for travel grants. The deadline for grant application is 10 **January**, 1998, and for registration 25 **January**, 1998. See separate announcements.

Deadline for grant application: 10 January, 1998

NORDIC COUNCIL FOR REINDEER RESEARCH
Travel Grants 1998

The 1998 NOR travel grants will be allocated primarily for participation at the 1998 NOR-meeting in Guovdageaidnu (Kautokeino) 13-15. March (10th Nordic Conference on Reindeer Research). There are also some funds set aside for other occasions. The grants are to be used in 1998 and are paid retrospectively. Successful applicants must submit an expenses report to NOR within 1 November, 1998 before reimbursement will be made. Grants will be paid through the applicants institution (university, research centre, etc.).

Applications will be considered for:
- participation in conferences, symposia, scientific meetings, etc.;
- shorter stay for study/research;
- arrangements of meetings for small groups of researchers to discuss particular subjects.

To be considered the application has to include the following information:
- applicant's name, university/college address, current position (student, researcher, other) and type of engagement (salaried, stipend, no financial support);
- the purpose of the proposed activity, more detailed information;
- destination, means of travel, purpose for journey, budget (cheapest maintenance and travel);
- other grants applied for;
- presentation if conference (oral/poster, abstract)
- publishing if applicable (proceeding article, ordinary scientific paper).

The main purpose for the NOR grant is to support participation at the NOR-conference in Guovdageaidnu/Kautokeino. Participants presenting lectures/posters are given priority.

Deadline for applications is 10 **January**, 1998. Applications (enclosed form in this Rangifer issue) must be sent to the Nordic Council for Reindeer Research, c/o NVH, Institute of Arctic Veterinary Medicine, N-9005 Tromsø, Norway.

Deadline for registration: 25 January, 1998

10th NORDIC CONFERENCE ON REINDEER RESEARCH

This conference will convene in Guovdageaidnu (Kautokeino), Norway, March 13-15, 1998. Organizers are the Nordic Council for Reindeer Research, Tromsø, and the Saami College, Kautokeino. The conference is aimed at researchers, students, and others involved in reindeer husbandry and its management and administration. Deadline for registration is 25. January, 1998.

NOR will use the meeting to present an overview of the Nordic reindeer husbandry and its management through presentations by invited speakers. Participants are invited to present research information on posters within any topic and in agreement with the organization committee, lectures within the main theme.

The conference will be conducted in Scandinavian and Finnish. NOR will try to use simultaneous translation, possibly also in north-Saami language.

1) Abstracts of posters and lectures in English and the presentation language, i.e. Scandinavian or Finnish, must be ready before the meeting. A Rangifer Report or Rangifer Special Issue with abstracts/summary/expanded abstracts will be issued for the conference. Abstracts must be received by NOR at the latest on February 20, 1998.

2) Manuscripts in Scandinavian/Finnish for a proceedings issue are to be given to the Editor of Rangifer during the conference.

3) Scientific manuscripts in English from either oral or poster presentations can be considered for publication in ordinary issues of Rangifer. These should then be given or submitted to the Editor for peer review and publication as original articles or brief communications respectively.

Programme and registration form (enclosed in this issue of Rangifer) are available at request. **Registration (deadline January 25, 1998)** is to be sent to, and further information is available from, NORs secretariate (see address below).

Please inform colleagues and other interested parties of the upcomming NOR conference.

Nordic Council for Reindeer Research, c/o NVH, Institute of Arctic Veterinary Medicine, N-9005
Tromsø, Norway. Att: NORs secretary Rolf Egil Haugerud.
Phone +47 776 84310, fax +47 776 84411. E-mail: Nor.Rangifer@veths.no

Rangifer
Nordic Council for Reindeer Research,
c/o NVH,
Institute of Arctic Veterinary Medicine,
Stakkevollvn. 23 B,
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NORs REINDEER RESEARCH CONFERENCE 13–15 March, 1998

NORs 10. Nordiske Reinforskningskonferanse. Tema: Reindriften i de nordiske land.
10th NORDIC CONFERENCE ON REINDEER RESEARCH.
Theme: Reindeer husbandry in the Nordic countries.

See separate announcements, pages 142 and 143.

This edition of **Rangifer** closes volume 17.

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