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Information

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Are arctic ungulates physiologically unique?

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Abstract: Reindeer/caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) are the arctic ungulates. Few studies have been carried out to directly compare their level of physiological uniqueness with similar species in the same family. The approach adopted in this review has been to compare data within family for physiological parameters including reproduction, nutrition and growth, to attempt to place the adaptations of reindeer/caribou and muskoxen in context. It is concluded that both species have unique adaptations to their environment which are likely to be specific to the Arctic. An hypothesis is advanced that some adaptations are constrained not only by the long intense winters, but also by the need to exploit the brief summers. The review has highlighted considerable gaps in understanding of some key physiological parameters for many species. This incompleteness in some ways mitigated the original goal of the project, but provisional conclusions are presented.

Key words: *Rangifer tarandus, Ovibos moschatus,* adaptation, reproduction, nutrition, growth.

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Introduction

Although the range of several species of ungulates extends into the Arctic, muskoxen (*Ovibos moschatus*) and reindeer/caribou (*Rangifer tarandus*) are the only truly permanent resident species. There are nevertheless differences in distribution; muskoxen are high arctic while reindeer/caribou are found from high arctic well into temperate regions and live in as divergent habitats as mountains, forests and barren tundra. Very few comparative physiological studies exist of reindeer/caribou and muskoxen. Also comparisons of the different arctic subspecies of Rangifer and their con-subspecies further south are sparce. Dave Klein, in his paper at the first Arctic Ungulate Conference in Nuuk, compared morphological, ecological and behavioural adaptations of the two species, although many of these adaptations are supported by physiological characteristics (Klein, 1992). Muskoxen are heavier than reindeer/caribou, have a shorter chest height and have smaller hooves (Table 1). The weight distribution pattern also differs, muskoxen have more weight distributed over the forelegs whereas reindeer/caribou have a nearly even weight distribution. The larger body size of muskoxen gives this species a lower surface area/volume ratio than the reindeer/caribou resulting in an advantage in energy efficiency, but also affects locomotive speed and predator avoidance strategies. Longer legs in the reindeer/caribou give advantages in deep snow both for locomotion and digging. The pelage also differs; in the muskoxen the underwool is dense and thick

Table 1. Comparative morphological measurements of muskoxen (*Ovibos moschatus*) and reindeer/caribou (*Rangifer tarandus*); from Klein (1992) – different sources.

Measurements		Muskoxen	Reindeer/caribou
Total weight (kg)		218–266	87–99
Chest height (mm)		484	730
% body length		25	41
Hoof size (mm^2)			
Fore	Male	125	185
	Female	97.5	146
Hind	Male	98.3	170
	Female	92.4	138
Ratio of fore/hindfoot			
	Male	1.60	1.09
	Female	1.25	1.06
Foot loading (g/cm^2)			
Hard surface		770	184
Soft snow		570	125

and is covered with long guard hairs while in contrast the reindeer/caribou depends on straight hollow hair with minimal underwool for insulation. Both sexes of both species have cranial appendages, horns in the muskoxen and antlers in reindeer/caribou. The uniqueness of the antlers in reindeer/caribou will be examined later. The morphology of the digestive tract overwhelmingly supports the conclusion that the muskoxen is a high bulk, low quality roughage feeder while the reindeer/caribou is primarily adapted to a quick turnover of nutrients and consequently must select more concentrated food supplies. Ecological studies in Greenland by Staaland & Olesen (1992) emphasised that when caribou are forced to eat grass species they cannot compete with muskoxen. Parker *et al.* (1990) examined the differences in growth rate patterns between neonatal muskoxen and caribou. Whereas caribou grow maximally in summer while fed concentrated milk during a short lactation period, muskoxen grow relatively slower and drink less concentrated milk for longer. This reflects the very different anti-predator and migration strategies of the two species. In general the above-mentioned differences between the two species demonstrate that although both are well adapted to the arctic habitat, they differ appreciably in their strategies to cope with it.

To effectively answer the question 'Are arctic ungulates unique?', it is necessary to go beyond of studies limited to arctic ungulates. Consequently, the approach which has been adopted here is to draw heavily on studies of temperate and boreal ungulates in order to place the physiological adaptations of arctic ungulates in context. The aim of this paper is to compare these physiological adaptations, with a reasoned explanation for each set of adaptations in an attempt to assess their uniqueness. This comparative approach means that many adaptations of arctic ungulates which have received considerable attention fall outside the scope of the review. Such adaptations as the hormonal control of lipolysis and lipogenesis in reindeer adipose tissue (Larsen *et al.*, 1984; 1985a; b), the vascular anatomy of the reindeer head to cool the general body or the brain selectively (Johnsen *et al.*, 1985a; b; 1987; 1988; Blix & Johnsen, 1983) and rumen microbial adaptations in reindeer (Mathiesen *et al.*, 1984; 1987) were fully reviewed by Tyler & Blix (1990) at an earlier Reindeer/Caribou Symposium. These adaptations may well be unique, but as no comparison can be made with temperate and boreal ungulates, they are not considered in this review.

The Arctic is a zone of climatic extremes (Potter & Gates, 1984). It is typical to consider that the Arctic is dominated by the long dark winters but these are balanced by intense summers with illumination throughout the 24 h period. If latitude is plotted against temperature change, from summer to winter then it can be seen that arctic latitudes are the most highly seasonal environment as well as being the coldest (Fig. 1). This is shown by the fact that annual temperature range is highest at the highest latitude. Thus species inhabiting the Arctic must not only have adaptations for the long winter

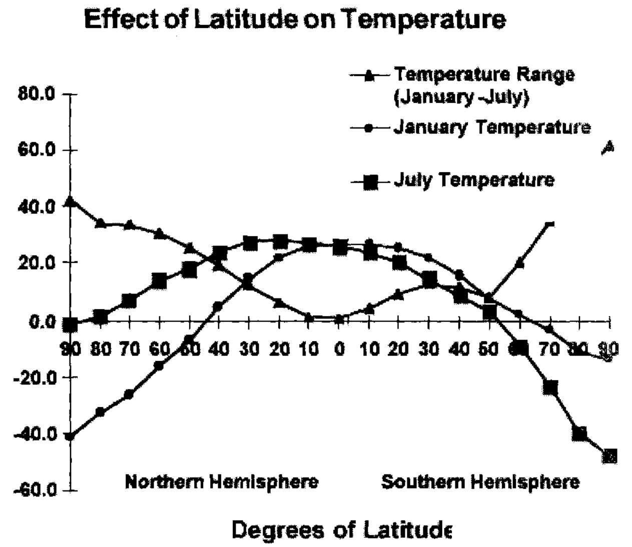

Fig. 1. Effect of latitude on the January and July average temperature, with the range in temperature between January and July (after Potter & Gates, 1984).

but they must also have adaptations to take full advantage of the brief summer. In terms of considering the unique adaptation to the Arctic both of these environmental extremes are relevant.

We have drawn our data from a wide variety of sources and in some cases this has required recalculation and, where possible, standardisation of units. The literature search has not been completely exhaustive and in some cases, for brevity, not all relevant references have been used. Rather comparative data has been taken in a representative manner. There are relatively few truly comparative studies and we have evaluated data from diverse experimental designs and data collection systems. We have interpreted the word 'physiological' somewhat literally. Many variables exist both between populations, and within species and where possible we have chosen representative data. Likewise between studies there are many variations due to age, sex, season, location and data collection methods. For the remainder of the paper muskoxen will be compared with other Bovidae and reindeer/caribou with other Cervidae.

The physiological topics for which we could find sufficient comparative data fall into six categories, each of which is treated separately, where relevant, for Bovidae and Cervidae. The topics are: - Reproduction, Photoperiod information transduction, Antlers, Energy metabolism, Digestion and Comparative growth.

Reproduction

Comparative reproductive data on oestrus cycle length, presence of short luteal phases prior to the onset of breeding, the timing of the breeding season if present and the gestation length were sourced for muskoxen, both bison species (*Bison bison* and *B. bonasus*), domestic Asian buffalo (*Bubalis bubalis*), cattle (*Bos taurus*) and sheep (*Ovis aries*) (Table 2). The oestrus cycle of the muskoxen is similar to other bovids in length and the presence of a short luteal phase of progesterone secretion prior to the onset of breeding is consistent with sheep and cattle. The breeding season may be slightly later in muskoxen compared with bison but this is countered by the shorter gestation length of muskoxen. In view of the fact that muskoxen are considerably smaller than cattle, the shorter gestation is not surprising. Published studies of breeding seasonality in muskoxen reveal some discrepancies, leading to a wide range of dates and could be investigated further.

A further feature of muskoxen reproduction which is of interest is the source of progesterone during pregnancy (Table 3). In domestic species of Bovidae, the *corpus luteum* produces progesterone throughout pregnancy and in the case of the goat (*Capra hircus*) is the sole producer of this hormone which is vital for the maintenance of the pregnancy. In the muskoxen not only does the *corpus luteum* regress about half way through pregnancy but the plasma levels of progesterone show a unique pattern, the function of which is not clear.

Rowell & Flood (1988) have shown that luteal regression in the muskoxen is accompanied by a fall in progesterone. This gives a tri-phasic pattern during pregnancy characterised by a 12 week period of low progesterone 12 weeks of high progesterone and a further 10-12 weeks of low progesterone. Whether this pattern of progesterone is unique to muskoxen or whether other wild bovids demonstrate such a pattern is unknown, but intriguing. The abrupt change in source of progesterone could be a mechanism to permit the termination of pregnancy if the nutritional environment was unsuitable.

The oestrus cycle length of caribou and reindeer is similar to those of other deer, but there is a trend that the Odocoilids (*Odocoileus virginianus* and *O. hemionus*), moose (*Alces alces*) and reindeer/caribou

Table 2. Comparison of reproductive characteristics in Bovidae.

Species	Oestrus cycle Length in days*	Source	Short luteal phases	Source	Timing of breeding season	Source	Gestation Length in days*	Source
Muskoxen (*Ovibos moschatus*)	19.6 (0.96)	1	Yes	1	Sept-Oct Aug-Oct	1 2	235 (4)	3
American bison (*Bison bison*)	23.1 (0.76)	4			Aug-Sept	4	285	5
European bison (*Bison bonasus*)	18-22				Aug-Sept			
Asian buffalo (*Bubalis bubalis*)	21.6 (0.23)	6			Variable		310-315	6
Domestic cattle (*Bos taurus*)	21.3 (0.06)	6	Yes	6	-		285	6
Domestic sheep (*Ovis aries*)	16	7	Yes	7	Dependant on breed		150	7

Sources: 1. Rowell & Flood (1988); 2. White *et al.* (1989); 3. Rowell *et al.* (1993); 4. Kirkpatrick *et al.* (1991); 5. Hauge (1994); 6. Dobson & Kamonpatana (1986); 7. Austin & Short (1972). * SD in parenthesis.

Table 3. Comparison of reproductive characteristics in Bovidae. Source of progesterone during pregnancy.

Species	Source of Progesterone	Source
Muskoxen (*Ovibos moschatus*)	*Corpus luteum* regresses completely at 20-22 weeks of gestation. This is accompanied by an abrupt fall in progesterone.	1
Domestic cattle (*Bos taurus*)	Progesterone produced by the *corpus luteum* throughout pregnancy, *placenta* also produces progesterone in the second half of gestation.	2,3
Goat (*Capra hircus*)	Depends solely on luteal progesterone throughout pregnancy.	3
Sheep (*Ovis aries*)	*Corpus luteum* produces progesterone throughout pregnancy but *placenta* is most important source in the second half of gestation.	3

Sources: 1. Rowell *et al.* (1993); 2. Dobson & Kamonpatana (1986); 3. Heap (1972).

appear to have longer cycles than other cervids (Table 4). All deer species appear to have short luteal phases prior to the breeding season. For their body size the gestation length of reindeer/caribou appears to be slightly short. In view of the fact that the calving season of reindeer/caribou is highly synchronised, the possibility that flexibility in the calving time due to flexibility at the implantation stage and hence length of gestation could be a source of this variation. Correspondingly, the Père David deer (*Elaphurus davidianus*) has a particularly long gestation period.

Photoperiodic information transduction

As mentioned above, the breeding of arctic ungulates is seasonal. It is critical in an environment of harsh extremes that birth takes place at the optimal time of year. It follows then that arctic ungulates will have evolved excellent systems to ensure that this is the case. In seasonally breeding domestic species such as sheep, and also in red deer (*Cervus elaphus*), the way in which seasonal breeding is controlled is well understood. It is believed that ungulates have an innate endogenous rhythm of reproduction which has a period of about 365 days - a

Table 4. Comparison of reproductive characteristics in Cervidae.

Species	Oestrus cycle Length in days*	Source	Short luteal phases	Source	Timing of breeding season	Source	Gestation Length in days*	Source
Caribou (*Rangifer tarandus*)	24	1	Yes	2	October	2	216	1
Reindeer (*Rangifer tarandus*)	20-24	1,2	Yes	2	Late August September	2 3	208 220	1 3
Red deer (*Cervus elaphus*)	18.3	4	Yes	5	[October]	5	234	6
Wapiti (*Cervus elaphus*)	21.2	7			October	7	255	7
Fallow (*Dama dama*)	22.4 (13.8)	8	Yes	8	[October]	8	234 (5)	9
Moose (*Alces alces*)	25	10	Yes	10	October	10	235	10
Père David (*Elaphurus davidianus*)	19.5 (0.6)	11	Yes	11	August	11	283	12
White tailed (*Odocoileus virginianus*)	28 (1)	13	Yes?	13	November	14	200 (5)	14

Sources: 1. McEwan & Whitehead (1972); 2. McEwan & Whitehead (1980); 3. Rehbinder *et al.* (1981); 4. Guinness *et al.* (1971); 5. Jopson *et al.* (1990); 6. Fisher & Fennessy (1985); 7. Haigh & Hudson (1993); 8. Asher *et al.* (1985); 9. Asher (1993); 10. Markgren (1969); 11. Curlewis *et al.* (1988);12. Brinklow & Loudon (1993); 13. Plotka *et al.* (1977); 14. Plotka *et al.* (1980). [Southern Hemisphere data converted to Northern Hemisphere]. * SD in parenthesis.

circannual rhythm. This rhythm draws from the environment a precise cue which permits the timing to be accurate. The precise cue is photoperiod which determines the pattern of secretion of melatonin from the pineal gland. Melatonin is secreted only at night and thus gives the brain a neuroendocrine signal which distinguishes darkness from daylight, and consequently permits the animal to receive a signal of night length. In this way, information is transduced from environmental to physiological. How this information is actually used by the animal is not known but in temperate species it is believed that either the duration of melatonin secretion or the timing of melatonin secretion in relation to a so-called photosensitive phase may be important. Which ever way is used, among the ungulate species which mate in autumn, a short day corresponds to a long night which is a cue to begin breeding (Arendt, 1986).

Fig. 2 shows melatonin secretion at four times of the year in a mature castrated muskoxen maintained outdoors at 52°N in Saskatchewan (Tedesco *et al.*, 1992). Notice that at this latitude elevated melatonin secretion filled the night in all seasons. Studies in domestic sheep have shown that the duration/timing of this elevation of melatonin secretion is the premier cue rather than amplitude of secretion. Data such as this would suggest that the muskoxen is like other temperate ungulates in its use of melatonin to time reproduction accurately. However muskoxen, and for that matter reindeer/caribou, live at much higher latitudes than 52°N and indeed live a large part of their lives in constant light or constant dark. What effect does this have on melatonin secretion? Eloranta *et al.* (1992) and Stokkan *et al.* (1994) have studied melatonin in reindeer in the Arctic and the data shown in Fig. 3 is from the latter study. Note that under conditions of constant light in summer the reindeer appear not to secrete melatonin at all, yet under prolonged darkness in winter, melatonin is elevated continuously. As we believe dark/light rhythms every 24 hours are important to provide photoperiodic information, how do reindeer - and by inference possibly

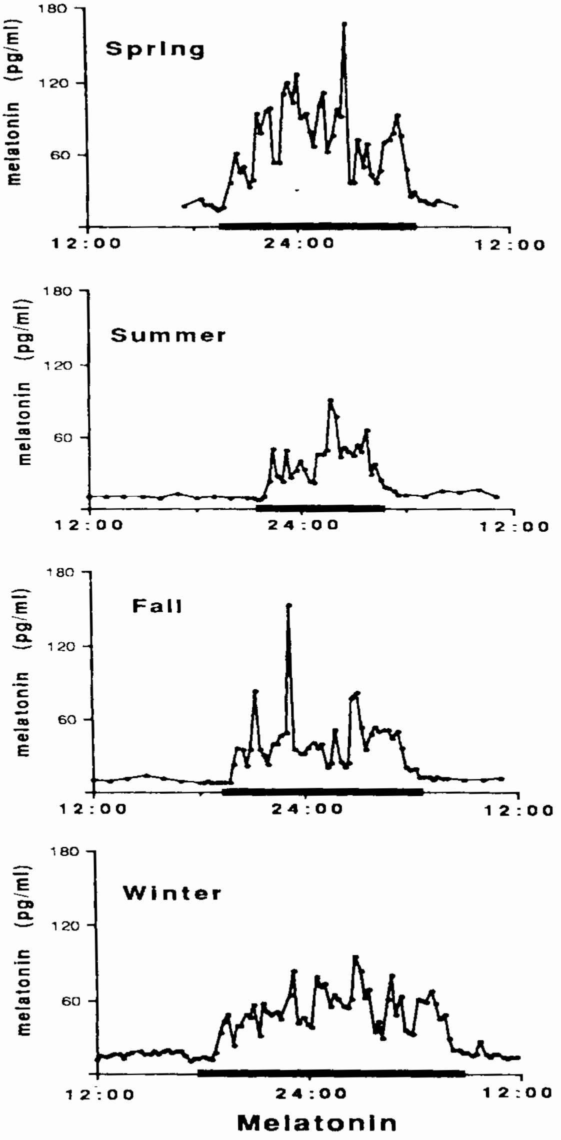

Fig. 2. Melatonin secretion during four seasons of the year in muskoxen (after Tedesco *et al.*, 1992).

muskoxen at high latitudes - respond to the lack of photoperiodic information particularly in summer to accurately time reproduction. In some cases animals must begin breeding before they perceive a short day (due to the absence of melatonin secretion during summer), the classical cue to time of breeding. The answer probably comes from a study in pinealectomised sheep, which were given infusions of melatonin representing different three month portions of the year (Woodfill *et al.*, 1994). This three month period of photoperiodic information each year was sufficient to synchronise the circannual reproductive rhythm, although not all portions of the year were equally effective. Arctic ungulates provide a real life test of this hypothesis. Because they see no melatonin from late spring to early autumn they may utilise spring information to time reproduction. We propose arctic ungulates do not need photoperiodic information during summer to time breeding as they rely on the last photoperiodic signals received during spring to maintain entrainment until the breeding season. The lack of photoperiod information in summer therefore poses no problem.

Antlers

Reindeer/caribou are unique in that it is only in this species that the female normally bears antlers, which are thought of, in other deer, as a male secondary sexual characteristics. It is assumed from the abundant behavioural/ecological data that presence of antlers provides a selective advantage for female reindeer in intraspecific competition, particularly during winter (Henshaw, 1969). Presence of antlers permits a higher dominance status than males, who lack antlers at that time (Espmark, 1964).

Two important questions relevant to this review are whether antlers in females are a unique adaptation to the Arctic and how the antlered condition in female reindeer/caribou evolved. A crucial question is 'What came first: the antlers on the females or living in the arctic environment?'. Geist & Bromley (1978) accepted the findings of Espmark (1964) and Henshaw (1969) and further pointed out that the presence of antlers in females was more common in barren ground than woodland caribou, a finding later confirmed by Reimers (1993). This may mean that 'male mimicry' is an adaptation primarily to the tree-less arctic environment, and hence is an example of a unique adaptation. With respect to the second question a hypothesis can be put forward as follows. Androgens - male hormones - play an important role in controlling the antler cycle in males however the dependence on androgens is not consistent across species (Table 5). Androgens from our studies in red deer act as the primary controllers of pedicle development - that is the permanent antler tissue grown during early puberty - and also the controller of antler cleaning and casting. Clearly in the female and castrate male reindeer, the antler cycle is complete without androgens, although Ryg (1983) has shown that treatment with testosterone can cause premature antler cleaning. This means

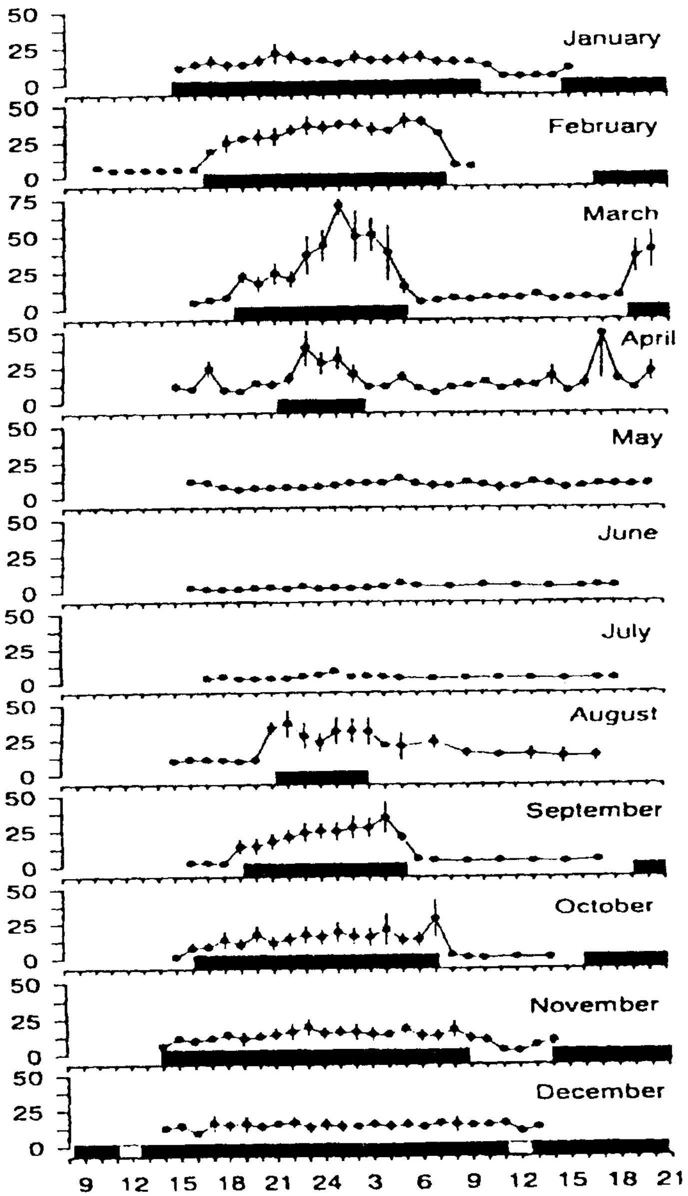

Fig. 3. Plasma melatonin in reindeer (*Rangifer tarandus*) (Stokkan *et al.*, 1994).

that the ability to use androgens as a control mechanism is retained but may be non-essential. In contrast androgens in red deer are required for all typical aspects of the antler cycle, except for cessation of antler growth in the castrate. In the roe deer (*Capreolus capreolus*), androgens appear to be required even in the castrate to stop growth of antlers. It seems that there could be a wide range of androgen sensitivities in deer species, with reindeer/caribou being the least sensitive.

It is hypothesised that after initial evolution, different species have evolved separate antler control mechanisms. Presence of antlers in female reindeer/caribou gave a selective advantage in the Arctic but their evolution depended on mechanisms that were independent from androgen control systems. This means than antlers in female reindeer are considered unique arctic adaptations. It can be speculated that an additional advantage of antlers in female reindeer/caribou could be a predator avoidance strategy. It would be of interest to know if there is selective predation on non-antlered females, particularly in winter.

Energy Metabolism

Resting and fasting metabolic rates (RMR and FMR respectively) have been measured in muskoxen, only resting metabolic rates are available for yak, American bison and domestic cattle (Table 6). Interestingly, the resting metabolic rate has been compared in bison, cattle and yak at different ambient temperatures and at different seasons. Muskox have the lowest RMR in summer and winter compared with other species. Both FMR and RMR in muskoxen are higher in summer than in winter and within summer the standing rate is higher than the lying rate. In contrast the RMR of the other bovid species do not appear to show seasonal differences but tend to increase with body size. The responses of bison to low temperatures are of interest; in contrast to yak and cattle the RMR decreases or stays the same in bison at -30 °C compared with 0 °C. It would be of interest to determine whether this metabolic action is unique to bison or if it is also found in muskoxen. Both resting and fasting metabolic rates depend to some extent on food intake. Of the wild bovids studied, only muskoxen appear to have a marked seasonal increase in food intake in summer/autumn compared with winter (Nilssen *et al.,* 1994). In terms of an adaptation to the Arctic, muskoxen appear to

Table 5. Role of androgens during antler development and the antler cycle.

Species	Pedicle	Source	Cleaning	Source	Casting	Source	Castrate	Source
Male reindeer (*Rangifer tarandus*)	Not required	1	Treatment induces cleaning	2	Low levels associated with casting	3,4	Grows cleans and casts normal antlers	1,4
Female reindeer (*Rangifer tarandus*)	Not required	1	Not required	1	Not required. Progesterone levels probably important	5	Grows clean and casts normal antlers	1
Red deer (*Cervus elaphus*)	Required	6	High levels required	6	Withdrawal causes casting	6	Grows small antlers which never clean or cast	7
Roe deer (*Capreolus capreolus*)	Required	8	High levels required	8	Withdrawal associated with casting	8	Grows antlers which form 'peruqus' and grow permanently in velvet	9

Sources: 1. Lincoln & Tyler (1991); 2. Ryg (1983); 3. Whitehead & McEwan (1973); 4. Lincoln & Tyler (1994); 5. McEwan & Whitehead (1980); 6. Lincoln (1971) 7. Lincoln et al. (1972); 8. Sempere & Lacroix (1982); 9. Bubenik *et al.* (1976).

conserve energy by having not only a lower overall RMR expressed relative to bodyweight, but an adaptation to winter is having about a 50% a seasonal reduction in RMR. It would be useful to carry out a controlled study comparing RMR in cattle and muskoxen at the same levels of feeding. Data are too few to present more in depth comparisons.

Comparisons between reindeer/caribou and other deer species reveal that RMR and FMR are similar (Table 7). The seasonal differences in RMR were considered by Nilssen *et al.* (1984) to be due to changes in the thermic effects of feeding rather than specific physiological adaptations for energy conservation. Indeed the original studies by Silver *et al.* (1969) which appeared to show seasonal differences in FMR in white tailed deer (*0. virginianus*) were refuted by Mautz *et al.* (1992) who also showed that these apparent rhythms were strongly influenced by the underlying seasonl rhthym of food intake. So, although there are no underlying cycle of resting or fasting metabolic rate, but seasonal alterations in food intake which are found in all arctic, and temperate deer might dictate an apparent cycle in some studies. It seems that changes in voluntary food intakes, which are observed in all temperate and arctic cervid species, are the principle mechanism for lowering energy metabolism in winter. Thus these do not represent a true adaptive to the Arctic, but rather represent an increase in seasonality in higher latitude species.

Digestion

Studies of digestion are greatly confounded by variability in age, sex, season and particularly diet. Drawing the data together and relying heavily on Adamczewski *et al.* (1994a), it is clear that muskoxen have high apparent dry matter digestibilities. Interestingly, both digestibility and mean retention time in the same diet in muskoxen decrease from winter to summer (Table 8). Compared with cattle, muskoxen digest low quality hay significantly better. Available data generally emphasises the muskoxen's suitability as a low quality grazer. Information on digestibility and retention time should be interpreted in relation to dry matter intake which varies seasonally in the muskoxen but in none of the other bovids reviewed. The fact that cattle (Adamzcewski *et al.,* 1994b) compensated for a low quality diet by eating more, but muskoxen digested food better is important. This strategy might be particularly relevant in a non-migrating grazer faced with a restricted standing crop of low quality forage. These data are hard to put in the

Table 6. Comparison of metabolic rates in Bovidae.

Species	Number and sex	Time of year	Resting metabolic rate W kg^{-1}	Fasting metabolic rateW kg^{-1}	Source
Muskoxen					
(*Ovibos*	2F	Summer	1.74 (0.27)	0.77 (0.03)* lying	1
moschatus)				1.19 (0.09) standing	1
	2F	Winter	0.86 (0.10)	0.62 (0.07)	
Yak	2F	January 0 °C	2.93	NM**	2
(*Bos grunniens*)	2F	January -30 °C	3.46	NM	2
Bison	1M,1F	January 0 °C	2.93	NM	2
(*Bison bison*)	1M,1F	January -30 °C	2.25	NM	2
	1M,1F	Winter 0 °C	4.30	NM	3
	1M,1F	Winter -30 °C	4.32	NM	3
	1M,1F	Spring 0 °C	5.25	NM	3
	1M,1F	Spring -30 °C	4.15	NM	3
	1M,1F	Summer 0 °C	5.87	NM	3
	1M,1F	Summer -30 °C	5.29	NM	3
	1M,1F	Fall 0 °C	6.63	NM	3
	1M,1F	Fall -30 °C	5.21	NM	3
Domestic cattle	2F	January 0 °C	4.53	NM	2
(*Bos taurus*)	2F	January -30 °C	5.76	NM	2
	2M,2F	Winter 0 °C	4.42	NM	3
	2M,2F	Winter -30 °C	5.60	NM	3
	2M,2F	Spring 0 °C	6.89	NM	3
	2M,2F	Spring -30 °C	8.59	NM	3
	2M,2F	Summer 0 °C	7.69	NM	3
	2M,2F	Summer -30 °C	8.27	NM	3
	2M,2F	Fall 0 °C	9.47	NM	3
	2M,2F	Fall -30 °C	8.76	NM	3

Sources: 1. Nilssen *et al.* (1994); 2. Christopherson *et al.* (1978); 3. Christopherson *et al.* (1979).
* SD in parenthesis. ** NM: not measured.

context of unique adaptations to the Arctic because no seasonal comparison is available for bovids other than muskoxen. One can only speculate whether bison have seasonal changes in forage digestibility. Taking the existing data at face value, it can be concluded that muskoxen appear to have a unique adaptation within the Bovidae to increase digestibility in winter by increasing the amount of time digest are retained in gastro-intestinal tract. This conclusion should be rigorously tested.

In deer, estimates of digestibility are presented using a variety of techniques, for reindeer/caribou red deer, wapiti (*Cervus elaphus*) and moose (Table 9). There were no consistent differences in digestibility between species or between seasons in the references reviewed. Interestingly, Freudenberger *et al.* (1994) showed that the lack of seasonality in digestibility in red deer was not due to level of intake and stags were not capable of increasing digestibility if feed was restricted during summer. Reindeer/caribou are similar to other deer in retaining a cycle of voluntary food intake which is higher in summer compared with winter. Another constraint on digestibility is diet selection and its seasonality because an animal conceivably can vary its percentage of browse/grass consumed. It is not possible to place this constraint in the comparative context of this review. Consequently no convincing argument can be put forward to include digestibility in reindeer/caribou as a unique adaptation to the Arctic.

Table 7. Comparison of metabolic rates in Cervidae.

Species	Number and sex	Time of year	Resting metabolic rate (RMR)	Fasting metabolic rate (FMR)	Source
			W kg^{-1}	W kg^{-1}	
«Norwegian» reindeer	3F	Winter	2.05		1
(*Rangifer t. tarandus*)	3F	Summer	2.95		1
	3F	Autumn	2.15	1.4	1
Svalbard reindeer	3F	Winter	1.55		
(*Rangifer t.*	3F	Summer	2.15		1
platyrhynchus)	3F	Autumn	2.20		1
			kJ/kg 0.75/day	kJ/kg 0.75/day	
Barren ground caribou	2F	Spring	484	404	2
(*Rangifer t. groenlandicus*)					
Moose	3M,3F	January	481	393	3
(*Alces alces*)	3M,3F	March	435	402	3
	3M,3F	July	619	557	3
	3M,3F	November	410	406	3
Moose	2F	February	272	NM*	4
(*Alces alces*)	2F	May	469	NM	4
	2F	October	376	NM	4
	2F	December/November - 3 March	430	310	5
	2F	July	940	NM	5
	2F	April		540	5
Red deer			512	NM	6
(*Cervus elaphus*)					
Red deer	4M	January	475	391	7
(*Cervus elaphus*)					
Wapiti (*Cervus elaphus*)			330-400	NM	8
Black tailed deer	7?	November	778	NM	9
(*Odocoileus*	7?	January	662	NM	9
hemionus)	7?	April	634	NM	9
White tailed deer	4F	Summer	NM	359	10
(*Odocoileus*	4F	Winter	NM	351	10
virginianus)	4F	Spring	NM	372	10

Sources: 1. Nilssen *et al.* (1984); 2. McEwan (1970); 3. Regelin *et al.* (1985); 4. Renecker & Hudson (1989); 5. Renecker & Hudson (1986); 6. Brockway & Gessaman (1977); 7. Simpson *et al.* (1978a,b); 8. Haigh & Hudson (1993); 9. Parker (1988); 10. Mautz *et al.* (1992). * NM: not measured.

Growth

The pattern of weight gain and loss in large animals follows an annual rhythm. In adult female muskoxen weight is maximal during winter but there is a large loss at parturition, partly due to weight of the foetus. During the summer little weight is recovered and it is not until late summer that the females begin to increase in weight. Young male muskoxen gain weight steadily for the first six or seven months of life, but then gain little weight during their first winter and second spring. Growth rate increases again during the second summer of life. The

Table 8. Comparison of feed digestion in Bovidae.

Species	Number and sex	Time of year	Diet	DMD[1] %	Retention time in h	Source
Muskox	8	Winter	Pellets and hay	81	53.8	1
(*Ovibos*	8	Summer	Pellets and hay	74	22.0	1
moschatus)	7F	March	Supplemented brome alfalfa hay	70.8 (1.1)[2]	114.6 (3.8)[2]	2
		July	Supplemented brome alfalfa hay	56.4 (1.3)	95.1 (4.4)	2
	1M, 4F	March	Low protein (6%) grass hay	52.5 (1.3)	NM[3]	3
Domestic cattle	3F	March	Low protein (6%) grass hay	45.0 (2.6)	NM	3
(*Bos taurus*)	4F	Spring	Alfalfa hay	57.5	NM	4
	4F	Spring	Sedge hay	76.0	NM	4
	4F	Spring	Brome fescue hay	61.8	NM	4
Bison	1M,3F	Spring	Alfalfa hay	77.5	NM	4
(*Bison bison*)	1M,3F	Spring	Sedge hay	64.3	NM	4
	1M,3F	Spring	Brome fescue hay	74.0	NM	4
Yak	1M, 3F	Spring	Alfalfa hay	72.0	NM	4
(*Bos*	1M, 3F	Spring	Sedge hay	63.0	NM	4
grunniens	1M, 3F	Spring	Brome fescue hay	70.8	NM	4
Holstein cattle (*Bos taurus*)	2F	NS[4]	Pelleted alfalfa brome hay	57.7	65.2	4
Hereford cattle (*Bos taurus*)	2F	NS	Pelleted alfalfa brome hay	49.1	68.7	5
Highland cattle (*Bos taurus*)	2F	NS	Pelleted alfalfa brome hay	49.4	65.3	5
Bison (*Bison bison*)	1M, 1F	NS	Pelleted alfalfa brome hay	50.1	78.8	5
Yak (*Bos grunniens*)	2F	NS	Pelleted alfalfa brome hay	49.3	78.2	5
Domestic sheep	8M	Summer	Lucerne hay	54.0	NM	6
(*Ovis aries*)		Winter	Lucerne hay	56.0	NM	6
Domestic goa	7M	Summer	Lucerne hay	56.0	NM	6
(*Capra hircus*)		Winter	Lucerne hay	62.0	NM	6

Sources: 1. White *et al.* (1987); 2. Adamzcewski *et al.* (1994a); 3. Adamczewski *et al.* (1994b); 4. Richmond *et al.* (1977); 5. Schaefer *et al.* (1978); 6. Domingue *et al.* (1991).

[1] DMD: dry matter digestibility. [2] SD in parenthesis. [3] NM: not measured. [4] NS: not stated.

muskoxen growth pattern is quite different from that of the caribou. Although the pattern of weight gain and loss is cyclic the female caribou gains weight during lactation. Peak seasonal weight is reached in late summer, rather than late winter as in the muskoxen. Young male caribou do not grow in winter but resume rapid seasonal growth early in spring McEwan (1968). How do these patterns compare with other species?

If the growth patterns of young male deer fed *ad lib.* over their first year of life are compared, between reindeer, rusa (*Cervus rusa*) and red deer, then it is clear that the tropical rusa deer shows no seasonality and grows constantly, while the reindeer and red deer show no growth during the first winter of life and then increase the growth rate during spring and summer (Fig. 4). The red deer differs from the reindeer in that rapid growth in spring begins about one month earlier.

In the Arctic the plant growing season is very short but is characterised by abundant forage of high quality (Klein, 1992). Animals must grow

Table 9. Comparison of feed digestion in Cervidae.

Species	Number and sex	Time of year	Diet	DMD[1] %	Retention time in h	Source
Reindeer (*Rangifer tarandus*)	2	NS[2]	Lichens and hay	NM[3]	51	1
	4	NS	Lichens and hay	NM	44	1
	1M,1F	NS	Grass and pelleted concentrate	NM	19.1/26.0	2
Reindeer (*Rangifer tarandus*)	F	Summer	Forbs Leaves	70	NM	3
			Flowers	81	NM	3
			Shrubs *Salix*	58	NM	3
			Betula	35	NM	3
			Rubus	37	NM	3
			Vaccinum	56	NM	3
			Grass leaves	39	NM	3
			Cotton grass	24	NM	3
			Lichens	38	NM	3
		Winter	Lichens	78	NM	3
Red deer (*Cervus elaphus*)	8M	Winter	Lucerne hay *ad lib*	62	NM	4
	8M	Summer	Lucerne hay *ad lib*	61	NM	4
	8M	Summer	Lucerne hay restricted to winter intake	58	NM	4
	5M	Summer	Lucerne hay	55	NM	5
	5M	Winter	Lucerne hay	57	NM	5
Moose (*Alces alces*)	1F	Winter	Lucerne hay	51.9	NM	6
	1F	Winter	Timothy brome hay	55	NM	6
	1F	Winter	Aspen twigs	48.1	NM	6
	1F	Summer	Lucerne	52.4	NM	6
	1F	Summer	Timothy Brome hay	67.9	NM	6
	1F	Summer	Aspen twigs	57.7	NM	6
Wapiti (*Cervus elaphus*)	2M	Winter	Lucerne hay	51.5	NM	6
	2M	Winter	Timothy Brome hay	64.2	NM	6
	2M	Winter	Aspen twigs	46.2	NM	6
	2M	Summer	Lucerne hay	57.7	NM	6
	2M	Summer	Timothy Brome hay	58.8	NM	6
	2M	Summer	Aspen twigs	54.7	NM	6

Sources: 1. White *et al.* (1987); 2. Valtonen *et al.* (1983); 3. White & Trudell (1980); 4. Freudenberger *et al.* (1994); 5. Dominque *et al.* (1991); 6. Renecker & Hudson (1990).

[1] DMD: dry matter digestibility. [2] NS: not stated. [3] NM: not measured.

during this period to increase reproductive success, to ensure survival, and to attain a lower surface area to volume ratio. If the animals attempted to grow when food was not available they would be metabolically stressed, thus there is high pressure to grow rapidly at the correct time. To determine if the growth of arctic ungulates is unique, growth data from the literature and unpublished sources were compared. Weight gain over the four months of shortest daylength (W) and weight gain for the month of longest daylength (S) were determined and the maximum yearling weight was recorded. The W/S ratio and the percentage of growth taking place in winter and summer was calculated. As with any review, data are inconsistent with respect to nutrition, age, genotype and other variables. We have used data from *ad lib.* experiments or where wild populations were considered to be on a high plane of nutrition. The data are restricted to yearling males, because they have a high pressure to grow and show more seasonal patterns than females.

Fig. 5 is a representative set of data. Unfor-

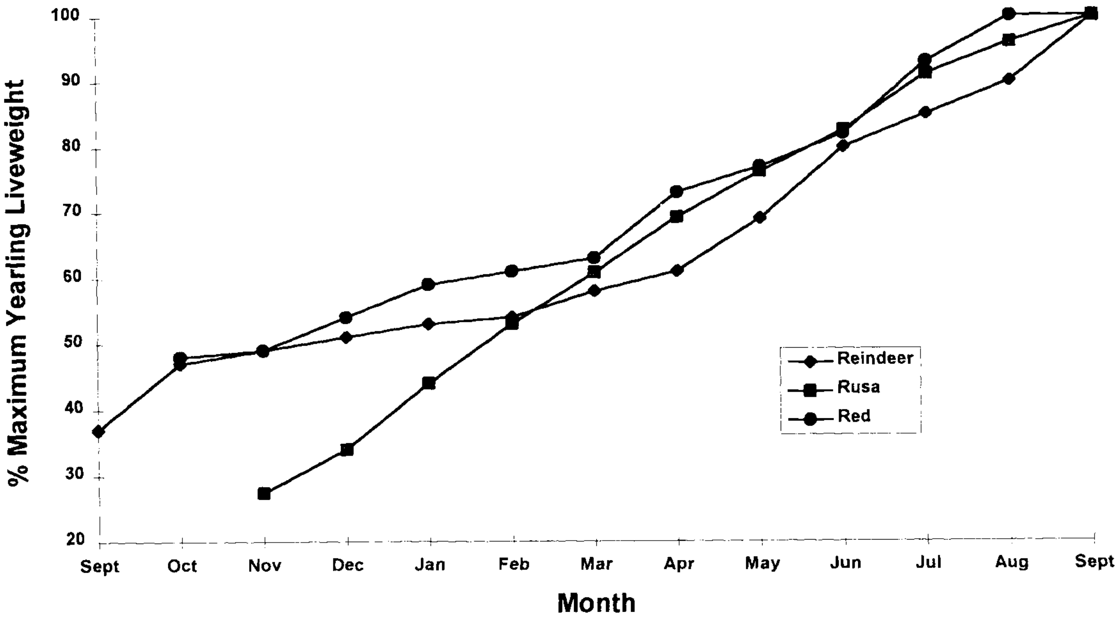

Fig. 4. The cumulative % of maximum liveweight achieved each month in yearling males of three species of deer fed *ad lib.* (Reindeer data (*Rangifer tarandus*), Ryg & Jacobsen, 1982; Red deer (*Cervus elaphus*), Suttie & Fennessy, unpubl.; Rusa deer (*Cervus rusa*), Suttie & Woodford, unpubl.).

tunately little comparative information on bovids exists so comparisons rely heavily on Cervidae. Arctic deer tend to be large and have a low percentage of growth taking place in winter, certainly compared with tropical deer in Australia. The ratio of W/S is lowest and, hence, the percentage of growth in summer is highest in arctic deer. Within a species it appears that latitude influences the W/S ratio. The muskoxen, and interestingly the Himalayan tahr (*Hemitragus jemlahicus*) (Barrell *et al.*, 1992), have a different pattern of growth than the deer in that they appear to grow more in winter and less in summer. In the muskoxen this may reflect a different growth seasonality due to their different nutritional requirements, as discussed earlier.

Young male arctic deer grow most in summer and winter growth is minimal even under *ad lib.* feeding conditions. Selection pressure probably limits growth potential to seasons of high food abundance, but the availability of food *per se* does not appear to be a controlling factor. Indeed repeated studies show that appetite in deer is voluntarily reduced during winter. Animals which have been captured at one latitude and transported to another for study appear to have a typical growth pattern, so winter energy requirements are unlikely to be the cause of the pattern. Could daylength be the cue for the diverse seasonal growth patterns? When W/S is plotted against latitude of origin, there is a strong negative relationship (Fig. 6). (Note that animals such as red deer in Australia which have been there for over one hundred years have a pattern similar to tropical rusa deer.) This means that latitude is correlated with a growth parameter. High latitudes are associated with long winter darkness and long summer daylight. If the hours of daylight 60 days from the summer solstice and the proportion of growth taking place in summer are compared, the correlation coefficient is 0.844 (Fig. 7). (The correction of 60 days is necessary to account for the fact that latitudes greater than that of the Arctic circle have the same daylength at the summer solstice). That is deer at high latitudes have the most pronounced seasonal growth pattern, which appears to be related to daylength. The causal mechanisms are outside review, but experimental studies in red deer have revealed that daylength appears to have separate effects on both the timing of seasonal growth and also its rate and insulin like growth factor (IGF-1 may be involved in this mechanism (Suttie & Webster, 1995). Clearly the seasonality of appetite must also parallel that of growth. Arctic deer may be using daylength cues not only to time seasonal growth but also to ensure the most rapid growth possible during summer. Interestingly IGF 1 is also seasonal in muskoxen but Adamczewski *et al.*

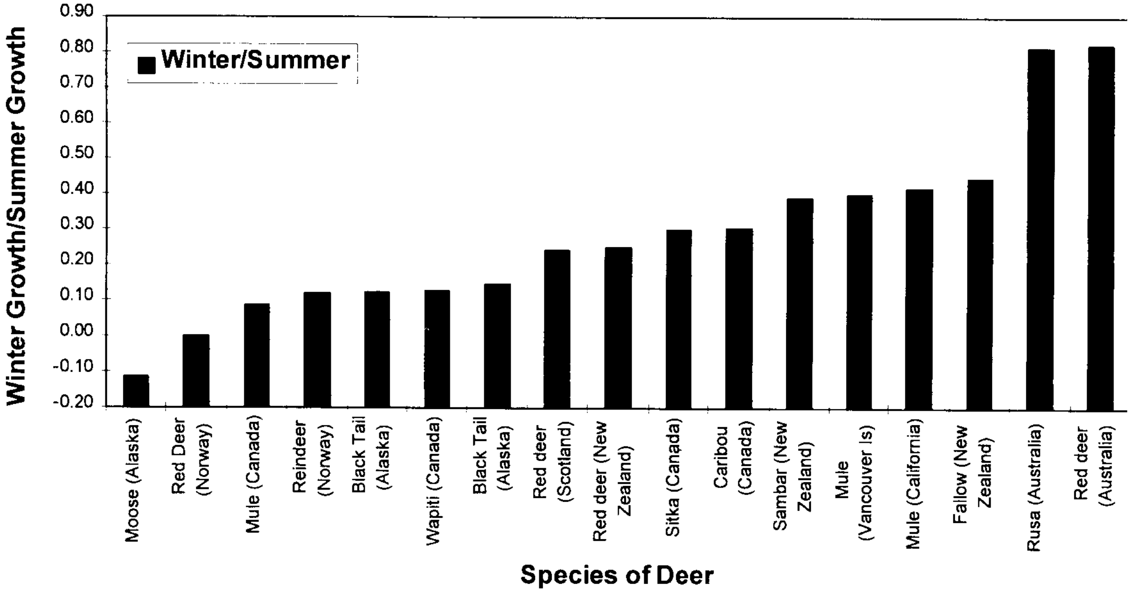

Fig. 5. Winter growth/summer growth ratios in deer species.

Moose (Alaska) (*A. alces*)	Franzmann *et al.*, 1978
Red deer (Norway) (*C. elaphus*)	Ryg & Langvatn, 1982
Mule deer (California) (*O. hemionus*)	Bandy *et al.*, 1970
Deer sitka (Vancouver) (*O. hemionus*)	Bandy *et al.*, 1970
Blacktail (Alaska) (*O. hemionus*)	Parker, 1993
Reindeer (Norway) (*R. tarandus*)	Ryg & Jacobsen, 1982
Wapiti (Canada) (*C. elaphus*)	Hudson & Haigh, 1993
Red deer (Scotland) (*C. elaphus*)	Blaxter *et al.*, 1974
Red deer (New Zealand) (*C. elaphus*)	Fennessy, unpubl.
Caribou (Canada) (*R. tarandus*)	McEwan, 1968
Sambar (New Zealand) (*C. unicolor*)	Semiadi, 1993
Fallow (New Zealand) (*D. dama*)	Asher, 1993
Rusa deer (Australia) (*C. rusa*)	Suttie & Woodford, unpubl.
Red deer (Australia) (*C. elaphus*)	Suttie & Woodford, unpubl.

(1992) have shown that the peak IGF 1 is later in the summer, and corresponds better with the seasonal growth pattern of that species.

Discussion

After reviewing the six physiological subjects (Table 10) the question can be posed again, 'Are arctic ungulates unique?'

The reproductive biology of muskoxen is undoubtedly unique in the pattern of progesterone secretion. This permits the female to delay the decision as long as possible as to whether to continue with a pregnancy or abort it to conserve energy and improve maternal survival. This can be considered a unique adaption to the Arctic environment because the costs of carrying a pregnancy in sub-optimal conditions are high and possibly life-threatening. In less harsh environments the costs are lower because the mother has a better chance of improving body condition even if the pregnancy succeeds. Reindeer/caribou may be unique if further work can examine the patterns of foetal growth and pregnancy length in more detailed. More data are required on the synchronising of birth in reindeer/caribou. To firmly establish whether this species has endured a unique adaptation to the arctic it would be necessary to understand the mechanisms triggering ovulation, conception, implantation and early foetal development better. A cohesive hypothesis linking calf survival and an adaptation during pregnancy would be considered an adaptation to the arctic environment. Whether this represents a truly 'unique' adaptation must await more complete studies on other species, for example wildebeest, which conceive and give birth during seasonal

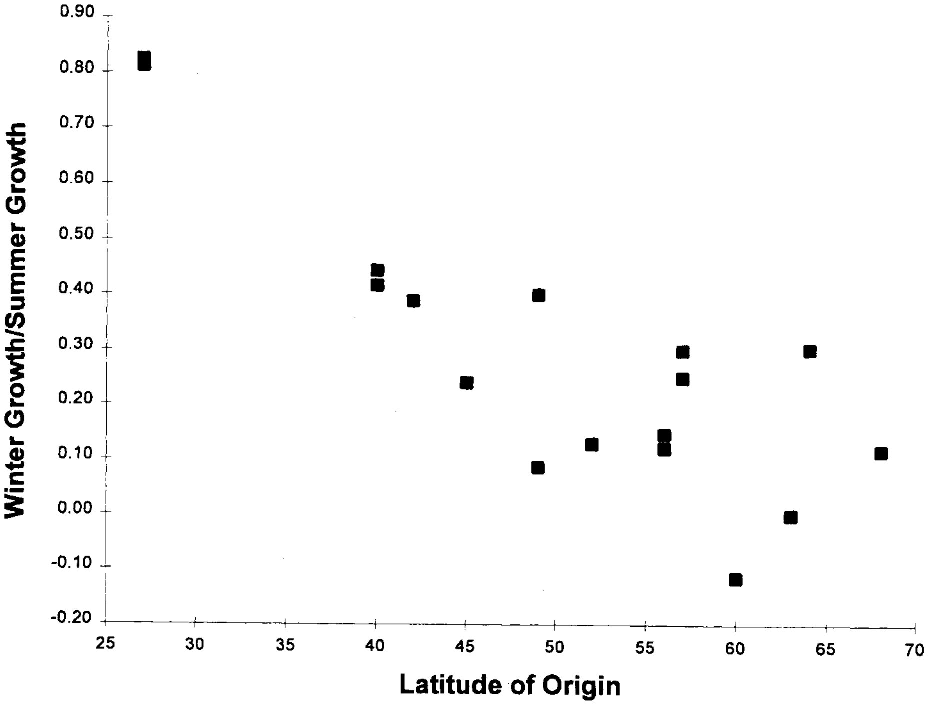

Fig. 6. The effect of latitude of origin of the study animals on the ratio of the amount of growth taking place in winter with the amount of summer growth. Each datum point is from fig. 5, and represents the ratio of growth (winter/summer) for male deer of various species and locations of origin during their first winter and second summer of life.

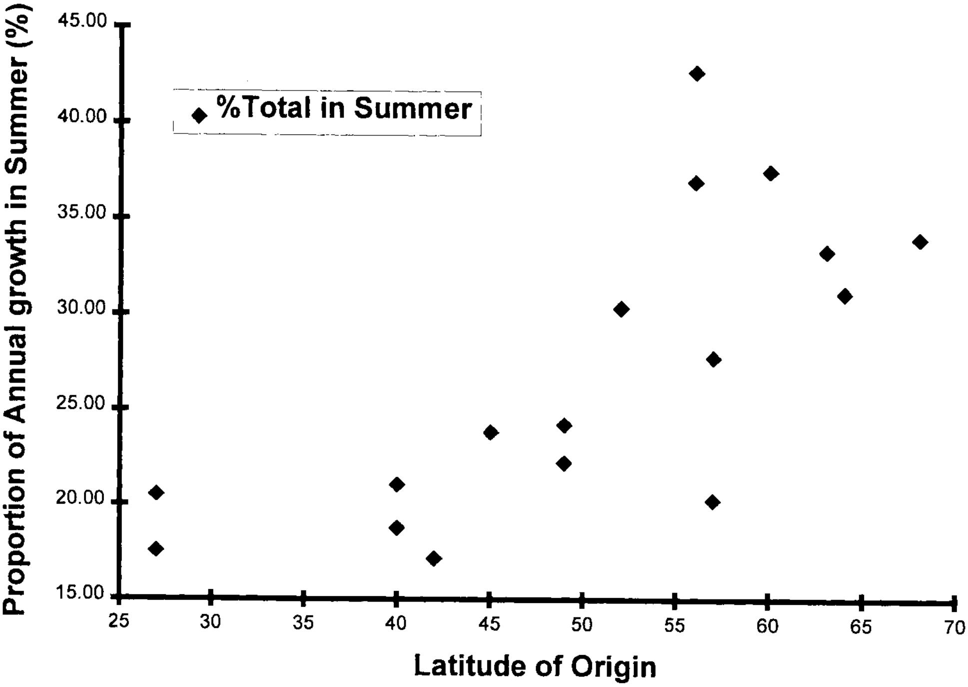

Fig. 7. The effect of latitude of origin on the proportion of annual growth which took place in summer. Each datum point is from fig. 5, and represents the ratio of growth (winter/summer) for male deer of various species and locations of origin during their first winter and second summer of life.

Table 10. Are arctic ungulates unique?

	Reproduction	Photoperiod information transduction	Antlers	Metabolism	Digestion	Growth
Muskoxen (*Ovibos moschatus*)	Yes - luteal regression - pregnancy progesterone	No? - interesting test of rhythms hypothesis	None	Yes - seasonal difference - effect of low temperature?	Yes - very good digestion of low quality forage	No - follows seasonal variation
Reindeer/ Caribou (*Rangifer tarandus*)	Yes? - short gestation period - long oestrus cycle	No? - interesting test of rhythms hypothesis	Yes - females - androgen mechanisms	No - similar to other deer	No? - lichen digestion	No - follows seasonal variation

migration. The way in which arctic ungulates perceive photoperiodic information is likely to be an extreme case of our current understanding of the control of seasonal rhythms. Reindeer and muskoxen, however, behave in the way they would be predicted to do. That is, they appear to secrete melatonin during periods of darkness only. To test hypothesis relating to the relevance of the precise pattern of melatonin secretion, standard endocrine withdrawal/administration studies should take place. Pinealectomy in muskoxen could prove a challenge due to the skull thickness. It would be useful to attempt to advance seasonal breeding in reindeer/caribou with melatonin treatment, and also attempt to delay it by exposure to extended long daylength. On balance we do not consider that photoperiod information transduction is a unique adaptation to the arctic, per se, but rather appears to be an extreme example of normal seasonality mechanisms observed in temperate ungulate species.

Muskoxen but 'not' reindeer/caribou alter metabolic rates seasonally, which may reflect an overall Bovidae/Cervidae difference (see paragraph on Energy Metabolism). However more comparative data, especially for Bovidae, is required. The integration of the seasonal cycle of food intake with metabolism may have a more meaningful physiological significance than either nutritional aspect taken separately in Bovidae/Cervidae. What this means is that food intake, metabolic and possibly growth cycles, *per se,* form part of a complex of adaptive strategies which is more important in its entirety than either part separately. In the context of uniqueness to the arctic, each ungulate species has several possible options to respond to the constraints of the environment. The answer may be unique, but the sum of the parts is most important. Muskoxen may have an obligate food intake reduction strategy coupled with a reduction in RMR in winter. In contrast the more mobile reindeer/caribou could have a more variable strategy of reduced food intake with constant RMR in winter. Both species appear to be able to increase food intake in summer. Hence we postulate that muskoxen may have the most extreme strategies which may be called unique to the arctic, but the reindeer/caribou appear to be following the typical cervid model.

In terms of digestion the muskoxen is a very good grazer within the Bovidae, but the reindeer/caribou, as a concentrate selector is similar to many other species of deer. It is possible that the ability to digest lichens is unique and the lichen digestibility in reindeer seem to be much higher than in sheep and pig (Nordfeldt *et al.*, 1961). However musk deer (*Moschus moschiferus*) also consume lichens (Green, 1987). (Musk deer are forest dwelling animals the range of which extends north through China and deep into Siberia. They are apparently highly selective feeders though they feed on a large variety of different plant species and, like reindeer/caribou, they eat a substantial amount of lichen in winter.) Seasonal differences in digestion appear restricted to muskoxen among the Bovidae.

Lastly, arctic ungulates are supremely adapted to a highly seasonal pattern of food abundance and quality by timing periods of growth to coincide with these events. We do not consider this in itself unique but rather an extreme example of the situation in temperate deer species. The seasonality of growth appears as a continuation across latitudes, certainly in cervids. Hence no unique arctic adaptations are evident. The paucity of comparative growth data for Bovids makes the parallel comparisons impossible. This is regrettable.

The link between the degree of seasonality of growth and latitude is strong. This means that at high latitudes growth is not only slow during winter but is very fast during summer. That is the deer have adjusted their physiological mechanisms to best suit the environmental constraints.

After reviewing a vast and diverse literature database, it is impressive that although survival in the cold winter was very important, successful life at high latitudes also depended on the ability to make the best use of a short summer.

Thus arctic ungulates are not only supremely adapted to winter, they are also supremely adapted to making the best use of summer. To enable this, arctic ungulates require a wide range of adaptations and a fine balance and control between seasons. This concept is not strictly new, as mentioned by previous reviews from Norway and Alaska. However arctic ungulates are unique in the way they integrate this range of adaptations. The different combinations of adaptations to seasonality between muskoxen and reindeer/caribou as their ecological strategies differ are more relevant than any one adaptation on its own.

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Contaminants in food chains of arctic ungulates: what have we learned from the Chernobyl accident?

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Abstract: The Chernobyl accident of 1986 caused radioactive contamination of widespread areas of reindeer pasture in Scandinavia. Reindeer (*Rangifer tarandus*) are especially exposed to radioactive fallout due to their winter diet, of which lichens are an important part. Much knowledge about the transfer of radiocaesium to reindeer, and via reindeer meat to man, was accumulated by intense scientific investigations, undertaken during the 1960's and 1970's, following nuclear weapons testing. Various ways to reduce the transfer of radiocaesium to animals and humans were also developed during this time. Much of the older knowledge proved to be of great value in the attempts to determine potential consequences of the Chernobyl accident and to suggest possible ways to ameliorate the effects of contamination. After Chernobyl, not only did reindeer prove to be a problem; many other food products originating from natural and semi-natural ecosystems were found to accumulate significant amounts of radiocaesium. Intense scientific work has produced new knowledge about the role of ungulates in the transfer of nutrients and contaminants within these systems. Different measures, like providing uncontaminated feed, use of caesium binders, altering the time of slaughter have been used with good results to minimize the transfer of radiocaesium to animals grazing natural pastures. The high cost of countermeasures has enforced consideration of cost against risk, which may also be of general interest with respect to other forms of pollution. Information, introduction of countermeasures and so forth would be more efficient in case a similar accident were to happen again. The Chernobyl accident is an obvious example of how human failures when dealing with a modern technical system can have global consequences and also be a potential threat to what we like to think of as the unspoiled wilderness of the Arctic.

Key words: radioactive contamination, fallout, radiocaesium, reindeer, *Rangifer tarandus*.

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Introduction

In the morning of April 28, 1986, an alarm caused the immediate evacuation of one of the Swedish nuclear power plants, Forsmark, north of Stockholm. Local contamination detectors had registered greatly increased levels of radioactive material in the air. At this time, no reports of radioactive release had been received from elsewhere.

In the evening of the same day, news of a serious accident at the Chernobyl nuclear power plant in the Ukraine, about 2000 km distant from Forsmark, was released on Moscow television. As a result of a technical experiment, on 26 April, two explosions in quick succession had blown the roof off one of the reactors at the power plant. The explosion and fire had caused the release of considerable amounts of radioactive material, consisting of both transuranic elements and fission products (IAEA, 1991). Smoke and fumes had risen almost 2000 m into the atmosphere.

Much of the radioactive material was precipitated close to the reactor site, especially the heavier particles, but a substantial part was also carried away by the wind and deposited over other parts of Europe. Clouds carrying radioactive material reached the Nordic countries, causing major radioactive fallout on two occasions, April 27-30 and May 8 (Persson *et al.,* 1987). The maximum deposition of ^{137}Cs recorded in Sweden was about 200 kBq m^{-2} (Edvarson, 1991). High deposition densities were recorded also in Norway (Henriksen & Saxebøl, 1988), southern Finland (Saxén *et al.,* 1990) and at many locations in eastern and southern Europe (Graziani *et al.,* 1991).

The fallout from Chernobyl created serious problems in many countries, as it was necessary to predict the potential human exposure to radiation and to decide what actions to take, to minimize the radiation doses to humans. The widespread, uneven distribution of the fallout and the consequent transfer of radiocaesium to food products, required a regional approach to the problem (UNSCEAR, 1988). It was obvious early on that problems were especially serious in areas where food was obtained from natural or semi-natural systems (Bennet & Bouville, 1988). This is the case in regions where natural pasture is used for animal production (as in reindeer husbandry) or where hunting and fishing provide much of the food for the local population.

The efforts to contain the problem that arose as an effect of the radioactive fallout, have generated important experience and knowledge. In this paper I shall highlight a few examples of new knowledge that has been acquired regarding radioactive contaminants in arctic and subarctic environments.

Before Chernobyl

The Chernobyl accident was not the first event to cause widespread radioactive fallout. Atmospheric testing of nuclear weapons, made by several nations from 1945 until 1962, caused a global fallout of radioactive material. Occasional tests carried out later, the most recent in 1980 (UNSCEAR, 1993), produced additional fallout. The largest amounts of radioactive material were deposited in a belt between latitudes 30° and 60°N (UNSCEAR, 1982). Variations between different areas at the same latitude were mainly attributable to differing amounts of precipitation (Langham, 1961).

The fallout from the nuclear bomb tests initiated scientific work in radioecology in many countries. Much interest focused on radiocaesium and radiostrontium in the food chain: lichen - reindeer/caribou (*Rangifer tarandus*) - man (or predator) (e.g. Hvinden & Lillegraven, 1961; Salo & Miettinen, 1964; Svensson & Lidén, 1965; Hanson, 1967). The reason why reindeer are especially susceptible to fallout is their diet, where lichens play an important part, particularly during the winter. Lichens absorb nutrients and contaminants directly from both air and precipitation (Tuominen &

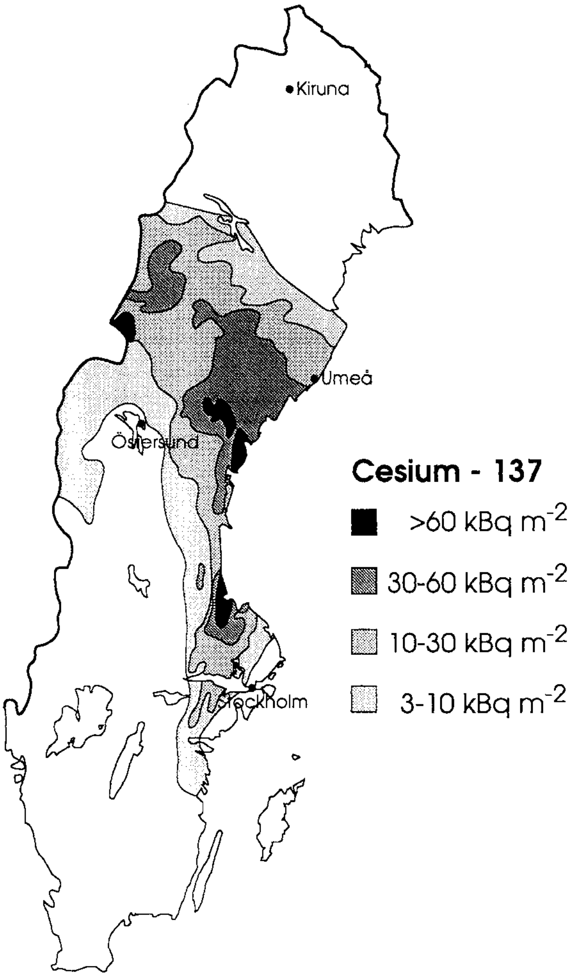

Fig. 1. Ground deposition of ^{137}Cs over Sweden according to aerial measurements May - October 1986 (redrawn from map by Swedish Geological Co. 1986).

Jaakkola, 1973), resulting in an effective uptake of radionuclides from fallout. Activity concentrations of ^{137}Cs in reindeer after the nuclear bomb tests were at their maximum, at around 3000 Bq kg^{-1} in 1966 (Westerlund *et al.,* 1987). Thereafter the levels declined with an effective half-life of 5 to 7 years (Westerlund *et al.,* 1987; Rissanen & Rahola, 1990).

Most work in radioecology, apart from that dealing with reindeer, was concentrated on agricultural systems (Coughtrey & Thorne, 1983). Levels of radiocaesium and factors affecting its uptake were, however, studied in some wild species of Cervidae (*e.g.* Whicker *et al.,* 1965; Longhurst *et al.,* 1967; Plummer *et al.,* 1969). Johnson & Nayfield (1970) also reported the role of fungi for the intake of radiocaesium by white-tailed deer.

Contamination of pasture and animals after the Chernobyl accident

As a result of the Chernobyl fallout, most of the central and southern parts of the Swedish reindeer pasture land became contaminated with radiocaesium (Fig. 1), as were the Norwegian reindeer pastures (Henriksen & Saxebøl, 1988). Finland sustained fallout mainly in areas outside reindeer pasture land (Saxén *et al.,* 1990). Most of the deposition from Chernobyl was washed out from radioactive clouds with precipitation in the form of rain or snow showers, resulting in a scattered fallout pattern.

The radionuclides considered to be of primary interest for human health and for the environment, were two caesium isotopes (^{134}Cs and ^{137}Cs), iodine (^{131}I) and strontium (^{90}Sr). The iodine is short-lived (8 days' physical half-life) and consequently there was only an initial interest in this nuclide. The ratio of ^{90}Sr to ^{137}Cs in the Chernobyl fallout was low (1 to 100, as measured over central Europe, UNSCEAR, 1988). Interest was therefore concentrated mainly on radiocaesium. It was anticipated, from the fallout pattern and previous knowledge (e.g. Hvinden & Lillegraven, 1961; Svensson & Lidén, 1965; Hanson, 1967), that reindeer and reindeer husbandry would be severely affected in the areas that had been contaminated.

The Chernobyl fallout contaminated the reindeer ranges at the start of the growing season when vascular plants (grass, herbs and leaves) gradually become more important in the diet. It was just before calving and reindeer calves may have received significant amounts of radioactive iodine via the milk. Monitoring of radiocaesium in Swedish reindeer in June 1986 showed that some animals had up to 7000 Bq ^{137}Cs per kg in the muscles (Åhman, 1986). Even higher levels were found in wild reindeer in Norway (Skogland, 1986). It was predicted that the levels would rise considerably in the autumn when the reindeer started to feed on lichens (Skogland, 1986; Åhman, 1986). This was confirmed the following winter, when the highest activity concentrations of ^{137}Cs in Swedish reindeer reached almost 100 000 Bq kg^{-1} (Åhman & Åhman, 1994). Maximum levels of up to 150 000 Bq kg^{-1} were recorded in Norway (Strand *et al.,* 1990).

The contamination of reindeer was not the only problem after the Chernobyl accident. Meat from wild herbivores, mainly moose and roedeer, was also found to be important in the transfer of radiocaesium to humans (Johanson & Bergström, 1994). Activity concentrations of ^{137}Cs around 1000–2000 Bq kg^{-1} in moose meat were found in highly contaminated areas of Sweden (Johanson, 1994). Roedeer from the same areas had somewhat higher activity concentrations, with peak values around 5000 Bq kg^{-1} in August and September, when edible fungi are an important dietary component. Meat from game animals is an important part of the diet of many people in all Nordic countries. The total consumption of all game meat in Sweden amounts to around 20 million kg y^{-1}, compared with about 2 million kg y^{-1} of reindeer meat (SCB, 1996).

Dealing with the contamination problem

The deposition of radiocaesium raised several problems for the authorities in many European countries. How should humans be protected from potentially dangerous radiation via contaminated food and how should people involved in food production be protected from economical loss? Furthermore, could radiation from the Chernobyl fallout be harmful to ecosystems or to certain species?

The problem of protecting the public was generally tackled by introducing control procedures for food produced in contaminated areas and by setting upper limits of radiocaesium contamination for food that was sold on the market (Salo & Daglish, 1988). In Sweden, the threshold for intervention was first set for ^{137}Cs at 300 Bq kg^{-1} for all food products (Bruce & Slorach, 1987). A year later, in May 1987, the Swedish National Food Administration agreed to raise this limit for wild berries, freshwater fish, game and reindeer meat to 1500 Bq kg^{-1}. The products mentioned had been found to retain far more radiocaesium than others, but were considered to form only a small part of the diet of the general Swedish population. People eating these foods regularly were, however, recommended to apply the lower limit of 300 Bq kg^{-1} for themselves. The general aim was that the radiation dose due to food (excluding radiation from naturally occurring radioisotopes like ^{40}K) should not exceed 1 mSv y^{-1}. According to dose conversion factors (ICRP, 1990) this corresponds to an intake of 77 kBq of ^{137}Cs or 53 kBq of ^{134}Cs. Other countries made somewhat different judgments than Sweden when setting threshold levels for food products. In Norway, the threshold for radiocaesium (^{134}Cs + ^{137}Cs) in all types of food except milk and baby food was first set at 600 Bq kg^{-1} (Strand *et al.,* 1990). This threshold was raised to 6000 Bq kg^{-1} for reindeer meat in November 1986, but again changed to a lower level, 3000 Bq kg^{-1}, in August 1994.

Refunding systems were established in Sweden (Lantbruksstyrelsen, 1986) as well as in other countries, e.g. Norway (Strand *et al.,* 1990), to reduce the economic loss sustained by food producers, and to compensate for costs or loss of income caused by radioactive contamination. An early interest was raised after the Chernobyl accident in different ways of avoiding contamination or to decontaminate animals and food products (Howard *et al.,* 1991; Gaare & Staaland, 1994).

The biological half-life of caesium in the body of mammals seems to vary from 7 to 100 days, with a generally longer half-life in larger animals (Stara *et al.,* 1971). Since the excretion of caesium by reindeer is relatively rapid, with a biological half-life of 2-4 weeks in winter (Holleman *et al.,* 1971; Åhman, 1996), contaminated reindeer could be decontaminated in a relatively short period of time if they are prevented from eating contaminated food. One possible measure is thus to move the animals away from contaminated areas. Reindeer were moved on two occasions after the Chernobyl accident in one area of Sweden (Jones *et al.,* 1990). However, the method is restricted by the limited access to uncontaminated pasture land. Moving semi-domestic reindeer also involves moving the reindeer herders, which is also a serious drawback. Another effective method that is frequently used, also for other animals than reindeer, is to keep the animals in enclosures and provide non-contaminated feed for a sufficient period of time (Howard *et al.,* 1991). From 1993 to 1997, around 16% of the slaughtered reindeer in Sweden were fed before slaughter to reduce the levels of radiocaesium. The costs for feeding are relatively high but in many cases this is the most practical method available.

If uncontaminated food cannot be provided, it may be possible to give the animals various compounds that can bind the contaminant and prevent it from being absorbed from the gut. Some techniques in this field were devised already after nuclear weapon testing (e.g. Mraz & Patrick, 1957; Giese, 1971; van den Hoek, 1976). Two types of compound are available for binding caesium: clay minerals (bentonite or certain zeolites) and hexacyanoferrates (Prussian blue, Giese-salt). Bentonite and hexacyanoferrates have been fed to reindeer with good results (Gaare & Staaland, 1994; Åhman, 1996). Clay minerals are needed in relatively large amounts and are added to the feed, whilst hexacyanoferrates, which are effective in very small amounts, can be added to salt licks or be incorporated in slow-releasing boli placed in the rumen of the animal. Boli used for reindeer (Hove *et al.,* 1990) last for about two month and reduced the activity concentrations of radiocaesium in the muscles of the reindeer with 60%. The method requires that the animals are gathered and handled at some occasion, up to two month before the planned slaughter, and that the same individuals are regained again at slaughter. This limits the application of the method on freely grazing species as reindeer and game animals. Salt licks containing hexacyanoferrates have been used to wild ungulates, mainly moose, and have been shown to reduce the activity concentrations of radiocaesium in muscle with 20-25% (Johanson, 1994).

One practice that has been widely used for e.g. reindeer and roedeer is to shift the slaughter (or hunting) season according to the seasonal variations in radiocaesium levels (Fig. 2). This is often an effective and relatively simple method (Åhman & Åhman, 1990; Johanson, 1994).

The problem of the potential harm of ionizing radiation to wild animals or ecosystems has been the subject of many earlier investigations (IAEA, 1992) but has received less attention after the Chernobyl accident. However, there is some evidence of genetic disorders in small rodents inhabiting the highly contaminated area close to Chernobyl (Shevchenko *et al.,* 1992). Studies in Norway (Røed *et al.,* 1991) suggest a possible genetic effect of radiation on reindeer calves from one highly contaminated area. These calves had received total doses ranging from

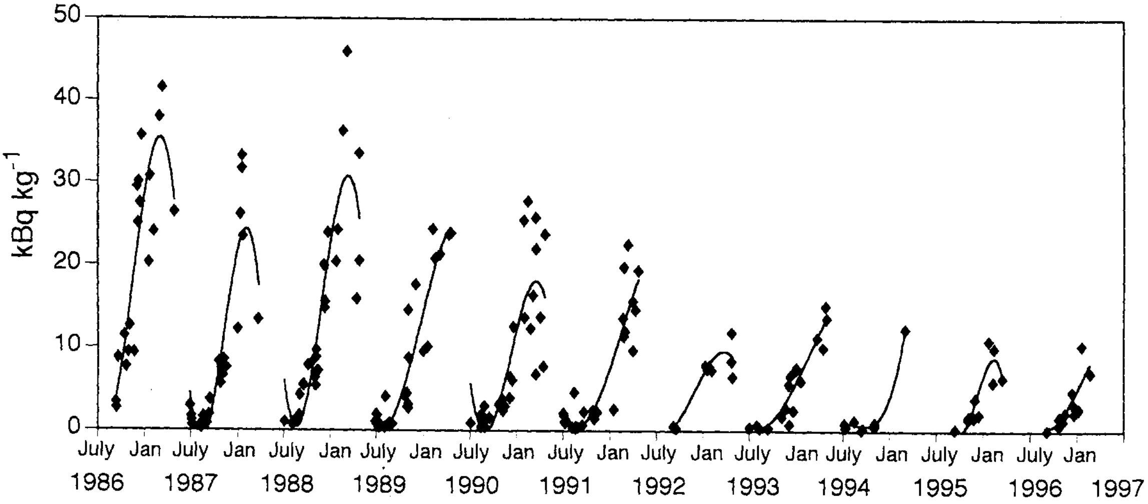

Fig. 2. Seasonal variations of ^{137}Cs in reindeer (Bq kg^{-1} in muscle) in the district of «Vilhelmina Norra» from July 1986 to February 1997 (mean values from reindeer slaughter and live reindeer monitoring).

40 to 80 mSv. However, the International Atomic Energy Agency (IAEA, 1992) states that higher doses, over 1 mSv day^{-1} for a longer period of time (years), are needed to cause observable effects at the population level in terrestrial animals. It has therefore not been considered necessary to apply any countermeasures, as a result of the Chernobyl accident, to protect animal populations from radiation.

Protecting humans from the effects of Chernobyl fallout has been expensive. The total cost for the Swedish state during the first year after the accident was over 300 million SEK (40 million USD). This sum includes cost for administration, information and radiocaesium control, as well as compensation to producers for loss of income and expenses for countermeasures. During the first year, much of the money (63% of the total cost) was spent in connection with agricultural production and fishery. Later, most of the cost was related to reindeer meat production - a total sum, from 1986 to 1996, of nearly 500 million SEK (65 million USD).

Justification for these costs can be assessed by comparing the reduction in risk to the human population with the cost of countermeasures. In a rich developed country it might be worth about 100 000 USD to save the population from a collective radiation dose of 1 manSv (ICRP, 1991). Bengtsson & Moberg (1993) argues that a justified cost for radiation protection should be between 0.4 and 2 million SEK (50 000-260 000 USD) manSv^{-1}.

The countermeasures used in Sweden during the period July 1995 to June 1996 have been estimated to have reduced the collective radiation dose via reindeer meat to humans by 11 manSv (from 18 manSv to 7 manSv) at a total cost of 17 million SEK (B. Åhman, unpubl.), that is 1.54 million SEK (200 000 USD) manSv^{-1}. One feasible way to reduce the costs is to make cost-benefit comparisons of the individual countermeasures to select the most cost-effective. A tempting way to reduce costs for the state would be to raise the limit for ^{137}Cs in food products (1500 Bq kg^{-1} for reindeer meat in Sweden). However, this would cause problems for the reindeer meat market, which has only recently recovered from customer resistance due to public fear of radiation after the Chernobyl accident. Another obvious risk with raising the threshold, unless not absolutely justified, is that it might diminish public trust in the authorities concerning these matters.

The future

The rate of decline of radiocaesium in reindeer after the Chernobyl accident has been relatively rapid, corresponding to 3–4 years' effective half-life for reindeer grazing on natural pasture (Åhman & Åhman, 1994). This is faster than the approximately 7 years observed for weapons test fallout (Westerlund *et al.*, 1987; Rissanen & Rahola, 1990). The highest activity concentration recorded in

Swedish reindeer during 1996 was 24 000 Bq kg^{-1}. However, even though the effective half-life is relatively short, problems with radiocaesium in reindeer are expected to persist for at least 15 more years in Sweden.

It would seem that the rapid decline reported above applies only to reindeer, suggesting that the decline is mainly an effect of the disappearance of radiocaesium from lichens. In the forest ecosystems in general, most of the radiocaesium remains and is available for plant uptake. According to Swedish investigations (Johanson, 1994; Palo & Wallin, 1996) the decline in radiocaesium in moose and roedeer has not been significantly faster than the radioactive decay (30 years physical half-life for ^{137}Cs), which also seem to agree with the decline in radiocaesium in moose after the weapons test fallout (Johanson & Bergström, 1994). The decline in radiocaesium in sheep also seems to be considerably slower than in reindeer (Hove *et al.,* 1994).

The apparent slow decline in radiocaesium in vascular plants (which comprise the diet of moose, roedeer and sheep) is of importance for predictions of radiocaesium levels in reindeer. As the lichen content of radiocaesium declines, vascular plants will contribute relatively more to the radiocaesium intake of reindeer, thus effectively prolonging its ecological half-life. A tendency in this direction has already been observed (Åhman & Åhman, 1994).

Concluding remarks

At the time of the Chernobyl accident, much of the previous knowledge proved to be essential for those trying to cope with the effects of the radioactive fall-out. One conclusion from this is that, as long as hazardous materials are produced and handled, there has to be adequate and practical knowledge of how to protect people and other living organisms if such materials are released into the environment, whether accidentally or intentionally.

The major route of transfer of radiocaesium to man following the Chernobyl accident has been in the form of meat from reindeer, game animals, sheep on natural pastures and freshwater fish. This demonstrates the crucial role of natural and semi-natural systems in the transfer of contaminants to man.

As a result of the Chernobyl accident, scientists and public authorities have gained more experience in dealing with contamination affecting large human populations. The production and release of information, adjusting food production, introduction of countermeasures and so forth would be more efficient in case a similar accident were to happen again.

The Chernobyl accident is a glaring example of how single human failures made in modern, highly technical systems can have large global consequences and also be of potential harm to what we like to think of as the unspoiled wildernesses of the arctic regions.

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Wild reindeer *Rangifer tarandus* (L.) in Chukotka[1]

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Abstract: We reviewed historical records of the abundance and distribution of wild reindeer (*Rangifer tarandus* L.) in Chukotka and studied reindeer numbers, distribution and behavior from 1983 to 1993. There were large numbers of wild reindeer in Chukotka until the end of the eighteenth century, but during the nineteenth century the population declined probably from intensive harvest after the introduction of firearms by the Cossacks. During the nineteenth century herding of domestic reindeer also increased, and reindeer herders continued to hunt wild reindeer intensively. During the 1950s there were only about 8500 wild reindeer in two separate herds in Chukotka. By the late 1970s the wild reindeer population had increased to about 11 000. Ten years later we estimated 16 534 reindeer, and found only one contiguous population. Presently, the population calves and spends the summer in the Anadyr Uplands and migrates west and southwest to spend the winter in forest tundra and northern taiga regions. Predators, primarily wolves and brown bears, kill a significant number of calves. Today, the wild reindeer in Chukotka coexist with 300 000 domestic reindeer. However, current costs of gasoline and helicopters make it prohibitive to herd reindeer in much of central Chukotka, so that wild reindeer have room for expansion. Poaching is a major conservation problem. Poachers shoot wild reindeer from helicopters to obtain velvet antlers. Leaders of domestic reindeer cooperatives encourage poaching by telling people that wild reindeer are in fact just stray domestic reindeer and there is no enforcement of game laws.

Key words: caribou, population size, Russia.

Rangifer, 18 (3–4): 127–132

Introduction

Written information about the existence of a large population of wild reindeer *Rangifer tarandus* (L.) in Chukotka comes from reports by Russian travelers in the first part of the nineteenth century (Sarychev, 1802; Wrangell, 1841). However, pictographs of kayakers hunting wild reindeer were found on the Pegtymel River and these have been dated to the second century B.C. (Dikov, 1989). Research on the Neolithic camps along the Anadyr River also show us that reindeer hunting was an important activity.

Large numbers of wild reindeer inhabited the Chukotka region until the end of the eighteenth century. During the nineteenth century they were subjected to intensive harvest with firearms brought by the Cossacks (Wrangell, 1841; Argentinov,

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[1] This paper has been revised by Patrick Valkenburg.

Table 1. Numbers of domestic reindeer in Chukotka (from Dikov, 1989).

Year	Total number of reindeer
1933	395 000
1940	437 000
1946	414 000
1951	442 000
1955	408 000
1959	571 000
1970	553 000
1978	565 000
1980	540 000
1983	519 000
1985	464 000

1860; Maidel, 1894; Iochelson, 1898). Numbers of wild reindeer then decreased slowly (Sokol'nikov, 1927; Druri, 1949).

At the same time, the population of the domestic reindeer increased in this area. Reindeer herders shot wild reindeer and harvested them at river crossings. Until the 1930s, overhunting was an important reason for decline of the wild reindeer population (Table 1).

Until the 1960s, the existence of wild reindeer in Chukotka was a subject of scientific discussion. Some authors (Tavrovskyi *et al.*, 1971; Kichinskii & Flint, 1973) said nothing about wild reindeer. Others including Druri (1949) and Zaitzev (1966) wrote about the wild reindeer herd that inhabited the Main-Anadyr's valley. Zaitzev estimated their numbers at 1500 individuals.

Obukhov (1967), Egorova (1973), and Chernyavskii (1974) wrote about the small herds of wild reindeer on the upper reaches of the Anyi River. In addition wild reindeer were noted in the upper of the Rauchua, Yarakvaam, Ugatkyn and Enmyvaam Rivers (Chernyavskii, 1974).

These reports were the basis for Zhelesnov's (1980) belief that three isolated herds of wild reindeer were found in northeastern Siberia. In our opinion, these areas were inhabited by the formerly large herd of wild reindeer and were never isolated from each other.

During the time domestic reindeer decreased in Chukotka the number of wild reindeer increased (Table 1). The first reports of the growth of wild reindeer came in 1983 (Chernyavskii *et al.*, 1990).

Study area

The Anadyr Upland is the source of the Anadyr, Enmyvaam, Yurumkuvem and Ugatkyn Rivers. In the northern part, average height of the mountains is around 700 m, in the southern, around 1200-1300 m. The plateaux and the tops of the hills in the area are rocky, mountain tundra with lichens and *Dryas* spp. The gentle slopes and the parts of the river valleys are covered with tussock tundra, and taller willows and poplar (*Salix* spp. and *Chosenia* spp.) occur along the rivers. Permafrost polygons are found on the low-lying areas and meadows occur where annual snowfields form.

Tall willow and alder (*Alnus* spp.) are found on the Anadyr-Main Lowland. The floodplain is large and covers about 40% of the area. Horsetail (*Equisetum* spp.) meadows and sedge (*Carex* spp.) and grass meadows are developed here too.

The forest tundra of the Anadyr Lowland is the wet, tussock tundra, with Siberian Dwarf Pine (*Pinus pumila*) bushes and alder. The hills of the northern and southern parts of the Anadyr valley are covered with Siberian Dwarf Pine.

The northern taiga zone where the wild reindeer spend part of their winter is mostly a sparse mountain larch (*Larix sibirica*) taiga with lichens and Siberian Dwarf Pine on the lower elevations.

Materials and methods

We collected data and made ground observations on the numbers and distribution of wild reindeer during the following periods: April to October 1983, Anadyr-Main Lowland; April to October 1984, Anadyr-Main Lowland; July to August 1985, Anadyr Upland; September 1985, Anadyr-Main Lowland; June and July 1986, Anadyr Upland; July to October 1986, Anadyr Lowland; July to September 1987, Anadyr Upland; May to September 1988, Anadyr Upland; June to September 1989, Amguema River Drainage and Chukotkan Upland; June to October 1990, Oloi River Drainage; July and August 1993, Anadyr Upland.

An Antonov (AN-2) aircraft equipped with an aerial camera and four observers was used for aerial observations and counting reindeer. The aircraft was flown at 200 m above ground level at a speed of 150-160 kph. Reindeer were counted in a 1000 m strip on each side of the aircraft. Reindeer outside the strip were also counted. Reindeer groups were either photographed or counted visually. All counts

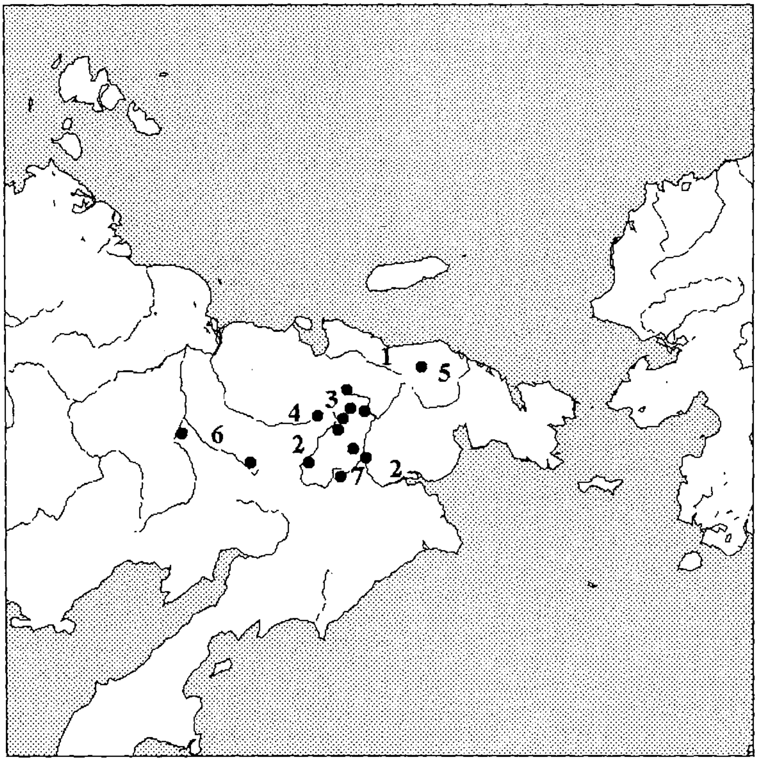

Fig. 1. Study area in eastern Siberia. 1. Pegtymel river. 2. Anadyr river. 3. Anadyr Upland. 4. Malyi Anui river. 5. Amguema river. 6. Oloi river. 7. Anadyr lowland.

were done in winter. In December 1985 we flew 3855 km in April 1986, 6560 km; in April 1987, 7276 km; in October 1987, 9990 km.

Population estimates were made using two methods of extrapolation. In the first, the mean density of reindeer was extrapolated to the entire area over which transects were flown. In the second, the mean density was extrapolated to only the part of the area in which reindeer occurred.

We estimated the age and sex structure of the population from the ground with binoculars, and from analysis of scats of predators (30 wolf scats, 14 wolverine scats, and 148 bear scats).

We reconstructed historical migration routes by mapping old reindeer trails which were very distinctive in summer and fall.

Results and discussion

Population size

During the late nineteenth and early twentieth century, the formerly large population of wild reindeer in Chukotka declined probably as a result of overhunting by reindeer herders and conflict with increased herding of domestic reindeer. By the 1950s the population of wild reindeer was very low and was divided into two parts-about 7000 in central Chukotka and 1500 in the Anadyr-Main Lowland. The population has recently increased and coalesced into one herd with a single calving area in the central part of the Anadyr Uplands.

The number of wild reindeer in Chukotka has recently been subject to much discussion and some controversy. Novikov *et al.* (1980) first estimated 11 000 wild reindeer in 1977. Subsequently, the Regional Hunting Office in 1982-1983 estimated their numbers at 7000-9000 (Reports of the density estimation work of Anadyr State Hunting Office, 1982). At the same time, Zhelesnov (pers. comm.) estimated their number at 6000-7000 individuals. However, six years later Kolpaschikov (1990) estimated their number at 32 000.

The large difference between the estimates of Kolpaschikov (1990) and other authors may be due to differences in census techniques. For mountain country with few reindeer the best method of estimation is to extrapolate only to areas in which reindeer are known to be distributed. This method was used on the Taimyr Peninsula by Pavlov *et al.* (1975), Pavlov & Borjgonov (1981), and Egorov & Popov (1970) in northern Yakutia.

In the present study we estimated 16 534 reindeer with the partial extrapolation methods of Pavlov et al. (1975) compared with about 30 000-32 000 with the complete extrapolation methods similar to those of Kuzmin *et al.* (1984) and Kolpashchikov (1990). We believe the latter method resulted in an overestimate.

Behavior

Wild reindeer in Chukotka have a main calving area in the central part of the Anadyr Upland. In summer they use the mountain tundra in this territory, and fall and winter, like most wild members of the genus *Rangifer* they move to the forest-tundra and northern taiga regions.

In April wild reindeer prefer the melted southwest slopes with developed tussock tundra. During late winter mean group size averaged 25.3 (n = 18).

The main calving area of the wild reindeer is located in the central part of the Anadyr Upland, in the mountain tundra around the Elgygytgyn Lake and in the upper drainages of the Malyi Anui, Ugatkyn, Enmyvaam and Yurumkuvem Rivers. In this territory, the herds of the wild reindeer begin to concentrate in April and May. Here groups of reindeer prefer low hills with newly thawed snowless patches and calving begins at the time of active snow melting. Usually, approximately 50% of the tundra is free of snow by the time the first calves are born. In 1986 and 1988 the first newborn calf was observed on 31 May and the last on 13 June. The weight of the newborn calves ranged from 3.6 to 6.5 kg.

Wild reindeer begin to gather in big herds in early July. This period coincides with the emergence of mosquitoes, blackflies and the two bot fly species. The insects are probably one of the stimuli that cause reindeer to concentrate (Egorov, 1965; Yakushkin *et al.,* 1975; Syroechkovskii, 1986).

Big gatherings of wild reindeer usually travel fast, around 30 km in 24 hours. We noted two types of movement. The first, called «the rush» type of the movement, was typical of relatively small groups (300-1000 individuals). With this type of movement, the reindeer usually traveled about 4-5 km. During these movements they stopped little, only for 0.5 to 2 min in some places with green grass and water. After these movements, the reindeer often stopped for a long rest.

Another type of movement we called the «slow shift». It was typical for the largest gatherings, but occurred when aggregations were not dense. These movements were slower and reindeer moved in separated loose groups so that the direction of movement came from the local movements of various parts of the main group.

During summer movements, groups traveled in two major formations-the «columns» and «fronts» (Kretchmar & Aksenov, 1993). When in columns, reindeer traveled 6-10 abreast with large adult males in the lead and in the middle of the column and females with calves and young animals in the rear. «Fronts» were characterized by groups about 3-6 times wider than they were long. Males were often in the lead in these movements as well with females and younger animals behind.

Wind direction determines the direction of reindeer movement. Reindeer generally moved into the wind, except for larger groups (> 70) which often moved with the wind. When reindeer occupy a restricted territory, as in Chukotka, this phenomenon can be one of the most important influences on the seasonal migration of the animals (Chernyavskii, 1974).

During the last two weeks of July aggregations of wild reindeer began to divide into smaller groups. The number of insects declines during this period. We observed the last large gathering on 28 July (more than 4000 individuals) (Kretchmar & Aksenov, 1993).

In August we observed only single reindeer or groups of just two or three animals in the central part of the Anadyr Uplands. From 10 August to 20 August they preferred to graze in wet parts of the valleys where fresh green grass was growing. Later most wild reindeer used dry lichen tundra on top of plateaux and on hills. During all of August reindeer showed no tendency to form groups and wind direction did not appear to influence the direction of travel.

At the beginning of September, the tendency of wild reindeer to form herds increased. Herds observed before the breeding season contained low numbers of large males (4%, n = 881). In two cases we observed only two large males in a herd of 200 and a herd of 250 individuals (Kretchmar & Aksenov, 1993). At that time many small herds (usually 8-12 in number) consisted of only large males.

The most important factor influencing wild reindeer migrations and distribution in a winter appeared to be snow cover. In November and December wild reindeer preferred snow-free tops of plateaux and hills. Group sizes ranged between 200 and 500. In March and April the wild reindeer preferred northern and northeastern slopes of the hills and mountains that had shallow snow. They seemed to prefer grazing not on the snow-free areas, but where the snow cover was 15-45 cm thick.

In September wild reindeer formed groups of 300-500 individuals. Cleaning of the antlers occurred in the second week of September. The males at this time become very active, and the most numerous contacts between wild and domesticated reindeer occur then.

The peak of rut occurred in mid October. At this time single males and small groups of adult males move from one band of females to another. During October there is a western and southwestern movement toward the boundary of forest-tundra zone.

Mortality

Mortality of the calves is high during the first month but the mortality rate varies from year to year and depends on weather and other factors. On 19 July 1985 the percentage of the calves in a group of 460 reindeer was 18.5%. Two years later, on 27 July 1987 a group of 1336 (12.3%) animals consisted of only calves. The subsequent year, at the end of July 1988, there were 26.5% calves in a group of 1339 reindeer.

Predators kill a significant number of calves. Seventy-nine percent of the wolves' scats gathered in the spring (n = 30) contained hair and bones of reindeer calves. Remains of reindeer were also found in bear and arctic fox scats that were gathered in spring. However, it is possible that these predators also eat carcasses of reindeer that die for other reasons.

Interactions with man and domestic reindeer

Twenty thousand wild reindeer in Chukotka must coexist with around 300 000 domestic reindeer. However, now that the costs of gasoline and helicopters have increased to the point that herders can no longer use the central parts of Chukotka, wild reindeer have more room for expansion. A major problem is the lack of law enforcement in Chukotka. Poachers take wild reindeer for velvet antlers from helicopters. The authors found headless wild reindeer lying on the tundra on 26 July while doing fieldwork. The leaders of reindeer herder's cooperative encourage poaching by claiming that wild reindeer are really just domesticated deer that have strayed.

Today we have no independent information about the numbers of wild reindeer in Chukotka. All estimation of numbers of Chukotka wild reindeer is under the control of the local government and local governments are interested in protecting the interests of the heads of reindeer herding cooperatives.

When domesticated reindeer join wild herds they tend to move separately at a distance of about 30-50 m from the main herd. The same behavior has been in other regions where wild and domesticated reindeer exist together (Zakharov, 1975). Thus, when domestic and wild reindeer are together, the number of wild reindeer can still be counted. At the present time wild reindeer appear to be trying to reestablish their old migration patterns but are impeded by man and domestic reindeer. In fall reindeer herders deliberately shoot all male wild reindeer they encounter to prevent them from breeding with domestic reindeer (Chernyavskii *et al.*, 1993).

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Alaska's indigenous muskoxen: a history

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Abstract: Muskoxen (*Ovibos moschatus*) were widespread in northern and interior Alaska in the late Pleistocene but were never a dominant component of large mammal faunas. After the end of the Pleistocene they were even less common. Most skeletal finds have come from the Arctic Coastal Plain and the foothills of the Brooks Range. Archaeological evidence, mainly from the Point Barrow area, suggests that humans sporadically hunted small numbers of muskoxen over about 1500 years from early Birnirk culture to nineteenth century Thule culture. Skeletal remains found near Kivalina represent the most southerly Holocene record for muskoxen in Alaska. Claims that muskoxen survived into the early nineteenth century farther south in the Selawik - Buckland River region are not substantiated. Remains of muskox found by Beechey's party in Eschscholtz Bay in 1826 were almost certainly of Pleistocene age, not recent. Neither the introduction of firearms nor overwintering whalers played a significant role in the extinction of Alaska's muskoxen. Inuit hunters apparently killed the last muskoxen in northwestern Alaska in the late 1850s. Several accounts suggest that remnant herds survived in the eastern Brooks Range into the 1890s. However, there is no physical evidence or independent confirmation of these reports. Oral traditions regarding muskoxen survived among the Nunamiut and the Chandalar Kutchin. With human help, muskoxen have successfully recolonized their former range from the Seward Peninsula north, across the Arctic Slope and east into the northern Yukon Territory.

Key words: archaeology, cryptozoology, Eskimo, extinction, hunting, Pleistocene.

Rangifer, 18 (3–4): 133–144

Introduction

My purpose is to bring together information from several unpublished sources as well as published material regarding the indigenous muskoxen of Alaska and adjacent Yukon Territory with emphasis on the nineteenth century. Before turning to muskoxen of the Holocene I will treat briefly Alaska-Yukon muskoxen of the Pleistocene. Localities mentioned in the text are shown in Fig. 1.

Pleistocene history

The first dispersal eastward out of Asia into the area of Alaska and the Yukon Territory occurred during the Illinoian glaciation, 150 000 to 250 000 years before present (BP). A portion of a skull found in a gravel outwash of Illinoian age near Nome, Alaska, provides the best evidence for this early invasion (Harington, 1970, 1977). The habitat in the area around Nome was apparently a dry steppe or steppe-tundra. Other skeletal remains from muskoxen thought to have lived during this period have been found in the Fairbanks area. During the late Pleistocene *Ovibos* lived amidst a rich array of large herbivore species across the vast belt of cold, arid grasslands which stretched during glacial periods all the way from eastern Europe to just east of the Mackenzie River in northern Canada. The wool-

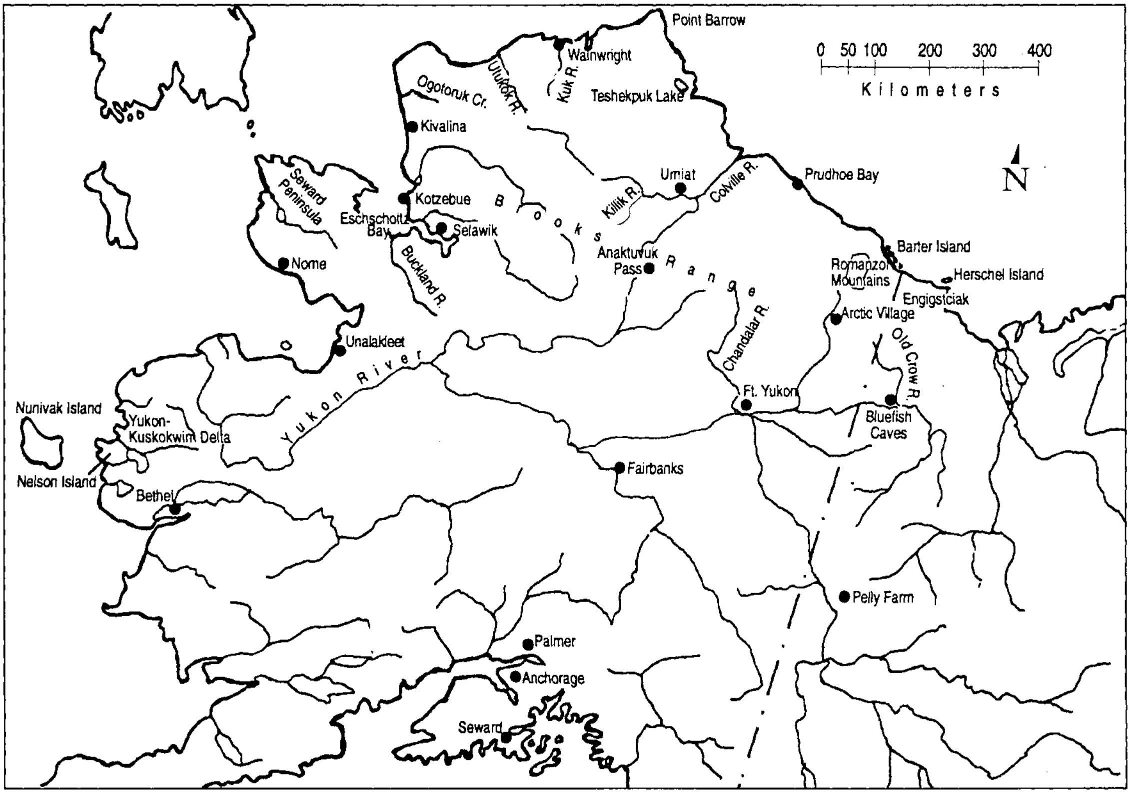

Fig. 1. Map of northern Alaska and adjacent Yukon Territory.

ly mammoth (*Mammuthus primigenius*) was a widespread and dominant species of this steppe environment. Its relatively common fossil remains serve as indicators of the past presence of these Pleistocene steppe communities, the «mammoth steppe» as Guthrie (1982, 1990) has called it.

Although this Pleistocene steppe environment was generally an arid one with rather sparse plant cover, the primary productivity was apparently much higher than in modern tundra communities. Grazers predominated in the mammoth steppe, based on what we know from the comparatively well studied Late Pleistocene sites of Interior Alaska. Among the thousands of fossil remains from four sites near Fairbanks analyzed by Guthrie (1968), bones of the extinct steppe bison (*Bison priscus*) were most frequent. Two other grazers, the horse (*Equus* spp.) and the woolly mammoth, were next in abundance at all sites. The caribou (*Rangifer tarandus*) and muskox ranked a distant fourth and fifth in overall abundance, comprising only a small proportion of fossil elements at any site. Ovibos accounted for a little over 6% of the estimated remains at one of the sites but occurred in much lower frequency at the other three. The extinct helmeted muskox (*Bootherium bombifrons*) occurred in «trace» numbers. Moose (*Alces alces*) made up nearly 5% of individuals at one site but <1% at the other three. Guthrie estimated that overall grazers comprised 94 to 98% of the biomass of large mammals in these assemblages.

The fossils uncovered at another late Pleistocene site in east central Alaska, estimated to be approximately 30 000 years old, represented at least 11 Dall sheep (*Ovis dalli*), three steppe bison, two caribou, one small «Yukon horse» (*Equus lambei*) and one moose (Porter, 1986). Neither *Ovibos* nor *Bootherium* occurred at this site. Porter (1988) also analyzed finds from Lost Chicken Creek where *Bootherium* was present in small numbers but the occurrence of *Ovibos* was questionable. Harington (1997) found tundra muskoxen to be relatively abundant along with Dall sheep at one site in the Sixtymile area of the Yukon, just across the border from Alaska. Animals in this assemblage lived around the peak of the last glaciation (21 000 BP).

Overall, however, low rates of occurrence of muskoxen are the rule, consistent with the evidence from Eurasia.

The mummified remains of Pleistocene mammals provide another source of information about these faunas. The frozen, desiccated remains of ice age mammals have attracted immense attention and scientific interest for at least two centuries. About 50 examples of soft tissue from Pleistocene mammals have been found in Siberia alone (Dubrovo, 1990). Of these, mammoths have been most commonly reported; 12 to 15 good specimens are documented, including two calves. Over the years northerners have also found four or five woolly rhinoceros (*Dicerorhino* sp.), three steppe bison, at least two horses, two helmeted muskoxen, wolverine (*Gulo* sp.) and several smaller mammals, and limbs and other body parts of several stag elk (*Alces latifrons*) and caribou (Guthrie, 1990). One report makes mention of a whole muskox body discovered on Laikhof Island, one of the New Siberian Islands (Allen, 1913). Another apparent example of a preserved muskox (*Ovibos*) was found on Eschscholtz Bay, Alaska in 1828. I will say more about this specimen later.

Of course, many factors besides the relative abundance of living representatives contribute to the likelihood of a mammal being preserved and subsequently discovered and reported. For example, caribou seem to be poorly represented; perhaps some finds of this species are never reported because the Pleistocene forms are not noticeably different from the living species. Nevertheless, the finds of ice age mummies are consistent with my contention that *Ovibos* was not particularly common in the Pleistocene.

In the Pleistocene steppes numerically dominant migratory species exploited the expanses of grasslands and mixed seasonally with smaller numbers of more sedentary, residential species. Presumably, *Ovibos* persisted by occupying niches that these more abundant grazers were not able to exploit as successfully. *Ovibos* in Beringia apparently used a broad range of habitat types, ranging from wet lowland patches to river valleys and broken uplands. In that sense, their pattern of habitat use resembled that of the mammoths. However, muskoxen probably specialized in using relatively small patches of plant communities, such as those with mixed grasses, sedges and low shrubs in mesic locations. They would have sought out productive wet sedge communities, but these covered perhaps only 10% of the steppe landscape (Guthrie 1968, Bliss & Richards, 1982). Although these communities were among the most important to muskoxen, they were also used by caribou and mammoths and to a lesser extent by other large herbivores. Muskoxen also would have used smaller patches of windblown habitat in winter, perhaps those in hilly topography, as they do today. Although critical for survival these would have been relatively unproductive.

Despite the fact that no assemblage of paleontological or archaeological material from any Pleistocene or early Holocene site has revealed a high abundance of muskoxen there is a perception in the popular literature and even among some paleontologists (Anderson, 1984a) that the muskox must have been highly successful and considerably more abundant during the ice age. Bliss & Richards (1982) attempted to estimate the numbers of large herbivores that might have once roamed over the rangelands of Beringia, based largely on densities of large herbivore species in present day arctic and subarctic ecosystems. They concluded that a typical 1000 km^2 of this hypothetical Beringian landscape would have contained 840-1605 muskoxen (0.8-1.6 individuals km^{-2}), as well as many horses, a few hundred each of bison and moose, 1320-2700 caribou, and 43-61 mammoths. According to these estimates the biomass of muskoxen exceeded that of any other large herbivore species and only caribou were more numerous.

Such figures are untenable. They promote the false image of the muskox as ubiquitous and abundant, dominating ice age ecosystems. Even accepting the greater diversity of plant communities and the generally higher primary productivity in the mammoth steppe compared to existing tundra rangelands, the matter of competition must be given greater attention. The Holocene tundra biome and boreal forest, with their impoverished large mammal faunas, are not valid models for their intended purpose. Calculations based solely on present day ecosystems also ignore the presence of several extinct large herbivore species, including Bootherium, which occurred as far north as Point Barrow during interglacials. In addition, in communities where permafrost was absent the density and variety of small and medium sized mammalian herbivores, many of them burrowing forms, greatly exceeded that of tundra communities.

Overall, the competition for forage and the limited extent of suitable habitats held muskox densities in Pleistocene environments to a fraction of that estimated by Bliss & Richards, probably less than 0.25/ km^2 overall. This density is comparable to that presently occurring on Low Arctic ranges of mainland Canada. My rough estimate is based on suppositions that muskoxen were numerically abundant on only a small portion of the mammoth-steppe landscape, probably less than 20% of the area and that their relative proportions among Pleistocene remains is in rough relationship to their relative abundance in these communities.

The above findings suggest that, contrary to popular belief, the tundra muskox was a relatively uncommon large herbivore in Pleistocene ecosystems. Obviously, in limited areas where favorable conditions existed muskox densities would have reached or perhaps slightly exceeded values seen in the most productive tundra ecosystems. Even before the arrival of humans in North America the muskox was not an abundant species in interior or northern Alaska. Finds of fossil *Ovibos* are most frequent from the middle and upper Yukon River drainage, along the northern coast of the Yukon and Alaska as far south as Norton Sound. and along rivers draining the central portion of the Alaskan Arctic Slope such as the Itkillik, Colville and Meade (Harington, 1961; Geist, 1962). Presumably there were opportunities for interchange between muskox populations in the Alaska-Yukon region and those farther east at least prior to the establishment of human hunters in the region of the lower Mackenzie River. In a brief comparative study Harington (1970) found no significant differences between fossil specimens found in the Yukon Territory and Alaska and skulls of recent muskoxen of mainland Canada.

Holocene history

We have no direct evidence for the contraction in the range of *Ovibos* and its shift to occupancy of the newly developing tundra ecosystems as the Pleistocene passed. We can only guess at these events based on our rather uncertain understanding of the changes in landscapes and vegetation at this time. Evidence for utilization of muskoxen by hunters prior to about 2000 years ago is extremely limited and comes largely from the area of the present Yukon Territory. At the Pelly Farm site, skeletal material representing three muskoxen may be approximately 5000 years old (MacNeish, 1964). Another very old muskox hunting site occurs at Engigstciak, where hunters apparently often waited for caribou and other game on a hilltop near the mouth of the Firth River. Reintroduced muskoxen now roam this same area within Ivvavik National Park. MacNeish, (1956) claimed the site was occupied as early as 8000 years BP, but evidence of muskox hunting seems to be more recent, put at about 3250 years BP by Harington (1977).

Later, people of the Birnirk culture occupied coastal areas in northwestern Alaska from 600 to 900 AD. The Birnirk people on the Alaskan mainland had not yet developed technology for whaling to the point of the later Thule culture Inuit; nevertheless they subsisted in large part on marine mammals. In addition to focusing on marine resources, they continued to use caribou and, sporadically, muskoxen as well.

At archaeological sites near Point Barrow and Wainwright, Ford (1959) found scattered items demonstrating use of muskoxen by Birnirk Period inhabitants. Birnirk people possessed muskox robes; some were apparently buried in them. They also used ladles and spoons of muskox horn. Evidence of muskox exploitation ranged from early Birnirk, about 1500 years ago, into the era of Thule culture as recent as 200 to 300 years BP. Thus, hunting of muskoxen and use of muskox implements continued through the transition from Birnirk to Inuit (Thule) culture. However, the digs revealed only intermittent and minor use, never large scale exploitation. At the Walakpa site near Barrow Stanford (1976) also found only rare (less than 1% of bone fragments) occurrence of muskoxen. Here also, however, evidence of muskoxen exploitation occurred at all three principal levels: Birnirk, early Thule and late Thule.

About 480 km southwest of Barrow, Inuit living at a coastal site on Ogotoruk Creek also used muskox horn implements; one dates to roughly 200 years ago. The people of this remote settlement engaged in taking guillemots (*Uria* spp.) and other birds and bird eggs at the nearby sea cliffs and in hunting caribou. Apparently, they rarely encountered muskoxen, for the excavators identified only one muskox bone out of more than 2000 skeletal parts of vertebrates (Hadleigh-West, 1966). Geist (1961) also found a few muskox bones in the Ogotoruk area and Pruitt (1966) reported an unfossilized muskox horn core found along the beach near Cape Thompson. With one exception, the finds in the vicinity of Ogotoruk Creek represent the most southerly records for «recent» remains of muskoxen along the Alaskan coast. A muskox skull apparently of recent age was found at Heart Cave inland from the village of Kivalina (approximately 80 km southeast of Ogotoruk). According to Giddings, who examined this cave in 1959, «[the] skull of a young musk ox looked fresh where it lay on the cave floor» (Giddings & Anderson, 1986). The following year his assistants dug a broad trench in the entrance to the cave. Caribou and muskox bones were plentiful in the upper centimeters, the remainder of the trench was sterile. The published notes are inadequate to determine whether the bones represented one or possible more individuals, but it is reasonably certain that only one skull was evident. Unfortunately the archaeologists visiting this site gave this unique specimen little attention. Subsequently, the skull was removed from the cave by a school teacher and lost on the tundra near Kivalina (E. Burch Jr., pers. comm). Thus the mystery regarding this skull remains.

Were Inuit farther south along the western coast of Alaska ever hunters of muskoxen? Neither archaeological studies nor oral history provide clear evidence of such utilization. However, at Elephant Point, on Eschscholtz Bay, the Beechey party found the remains of a muskox in 1826. Earlier explorers had visited this site, about 50 km southeast of the present town of Kotzebue, and reported well-preserved remains of mammoths and other species of mammals in the frozen silts of the sea cliffs. When the site was visited by the Beechey party other skeletal material and portions of carcasses lay in the waters of the quiet bay in proximity to the eroding cliffs (Beechey, 1831). These finds included a muskox and caribou as well.

Buckland (in Beechey, 1831) who examined the specimen brought back to England by Beechey, considered that the muskox was contemporaneous with the caribou and that these were remains of recently dead animals that had washed into the bay, mixing with those of fossil species coming down into the waters from the eroding cliffs. Regarding the muskox find, he concluded that, «..the condition of the skull and horns ... differs so essentially from the condition of all the bones of elephants from this place, that it is impossible it can have been buried in the same matrix with them ...» The head was said to be so lightly decayed that it «had not long since been stranded by the waves» (Buckland, Appendix to Beechey, 1831, p. 336). Incredibly, Buckland chose not to provide an engraving of the muskox head in his contribution because it was not a fossil! My efforts to locate this specimen in the U.K. have been unsuccessful. Captain Beechey (1831) interviewed (without a good interpreter) natives who came from up the Buckland River, which flows into Eschscholtz Bay from the base of the Seward Peninsula. He concluded that they were familiar with the species, recognizing the specimen and an illustration of a muskox.

Buckland's argument for the distinctive freshness of the muskox specimen is less than convincing in light of his comments on one other find. He refers to the horn of an «ox» (not a muskox) that was said to have been found in a state equally fresh with the head of the muskox and also recently cast up on the shore. However, it is even less likely that this horn sheath was derived from an animal then living in western Alaska. According to Lydekker (1898), the «ox» in question was a Pleistocene bison, *Bison priscus.* Reverend Buckland's comments and analysis were certainly influenced in part by a continued hesitancy on the part of the scientific community to accept that «elephants» (mammoths) and arctic species such as caribou and muskoxen could have once lived together under the same climatic conditions. Buckland, for example, also declared that the bones of Pleistocene animals found in a cave in Wales had been swept in through the entrance during the biblical flood, and he was convinced that the skeleton of a young man of Paleolithic antiquity uncovered in the same cave was that of a woman buried there by the Romans (Stern, 1969).

Quakenbush (1909) carried out a more detailed investigation of the Elephant Point site and a reconnaissance for fossils along the Buckland River. He located fossil material from muskoxen in both areas and found mammoth bones and mammoth hair in the bluffs. He concluded that the material considered by earlier visitors to have washed into Eschscholtz Bay was in fact derived from the eroding bluffs or, in the case of caribou, had been left by hunters. The brief comments by Beechey and conclusions of Buckland have been used as evidence that muskoxen inhabited the Kotzebue Sound - Seward Peninsula region in the early nineteenth century (Smith, 1987). However, in light of later findings, such as those of Quakenbush, and in the absence of any corroborating evidence from archaeological or ethnographic sources, I consider it most likely that the Elephant Point muskox represented a particularly well preserved «mummy». It seems improbable that muskoxen were still living in this area in the nineteenth century. The people from the Buckland River could well have been familiar with muskoxen from travels farther north or through trade.

In the northern part of Alaska the Thule whaling culture was well developed by around 900 AD. These people lived in larger communities than the earlier Birnirk culture, aided by technology that allowed increased specialization for whaling. An increasingly complex and affluent society developed (Sheehan, 1985). Even if exploitation of the low numbers of muskoxen was only occasional these larger, more stable populations could have had great impact.

Especially after 1200 AD, the numbers of Inuit living in interior portions of northwestern Alaska increased. These were caribou hunters who lived a largely nomadic existence. As late as the late nineteenth century these people, known broadly as the Nunamiut, lived in small bands in the Brooks Range and tundra region of northwestern Alaska. Substantial contact between Inuit of northern Alaska and westerners did not occur until the 1840s and 1850s, although trade goods from Siberia had been known in northern Alaska since about the end of the 17th century. Near the end of the 19th century the Nunamiut were decimated by influenza. Dispersal and mixing of the survivors with people of coastal settlements followed (Spencer, 1959).

Some of the remaining Nunamiut eventually regrouped in Anaktuvuk Pass at a site strategically located for intercepting the annual migrations of caribou through the Brooks Range. Despite the devastating changes resulting from contact with westerners the Nunamiut Eskimos of Anaktuvuk Pass retained a rich folklore based on hunting experience and information passed down from generation to generation. When first interviewed by anthropologists and biologists at this settlement in the 1950s, only one living Nunamiut had ever seen a live muskoxen. This aged hunter had traveled as a youth beyond the Coppermine River in Canada, 1000 km to the east. Nevertheless, the surviving oral traditions included specific knowledge about muskoxen (Rausch, 1951; Gubser, 1965).

The traditional muskox hunting areas known to the Nunamiut lay in the northern foothills region along the Colville River above Umiat and near where the Colville is joined by the Killik River, as well as on the lower Anaktuvuk River. In the early decades of the nineteenth century Nunamiut people lived in scattered, mobile bands in these areas, particularly in the Colville River drainage (Hall, 1978; Burch, 1977).

A legend regarding muskoxen and the people of the Killik River region was still being told in the 1950s. Two versions both involve a menstruating girl. The young woman violated taboos by not remaining hidden while menstruating. In one version she looks upon a hunter driving muskoxen toward the camp, and thus both the hunter and the muskoxen are turned to stone. The Nunamiut storytellers still knew the location of these rocks in the 1950s. Such associations of stories and places helped to keep these folk tales alive, reflecting ties with the land going back many generations (Ingstad, 1954).

The Nunamiut had available a wider variety of resources and raw materials than did some of the Inuit of the Canadian High Arctic. Driftwood was abundant and Nunamiut hunters frequently penetrated the northern fringes of the boreal forest. They had access to products from a variety of marine mammals and even to trade goods from Siberia. Thus, horn and bone from muskoxen must have been of less critical importance here compared to the High Arctic. But the coastal Eskimos certainly valued Dall sheep horn (Spencer, 1959). Surely, muskoxen horn would have been equally prized and perhaps at one time easier to obtain than sheep horn? Nunamiut informants also stated that muskox skins were valued (Gubser, 1965). Perhaps the greatest importance of muskoxen was as a food source when the migrating caribou failed to come as expected. At times of such crises hunters could seek out the more sedentary muskox herds at locations known by tradition. The muskoxen would thus be a «critical resource» in the sense of Wilkinson (1975), aiding survival during relatively short period when other resources, such as caribou, failed. At least one Nunamiut informant actually suggested that heavy hunting had been responsible for the disappearance of muskoxen from northwestern Alaska. The muskoxen were said to have disappeared or gone eastward (Ingstad, 1954), a statement made also with regard to caribou when they were scarce.

Dall sheep have continued to play a role as a critical food resource when caribou were unexpectedly absent. They are prized in spring time because, like the muskox, individuals often still possessed substantial body fat at a time when caribou had depleted their subcutaneous reserves. After the decline in caribou and the extirpation of the muskox overharvesting led to a marked decline in Dall sheep numbers in the late nineteenth century (Campbell, 1978).

Because of the lack of corroborating archaeological evidence, Wilkinson (1975) believed that the Nunamiut informants interviewed in the 1950s had exaggerated the importance of muskoxen to their ancestors. The archaeological evidence for exploitation of muskoxen in the mountains and foothills of northern Alaska continues to be basically non-existent. Twentieth century Nunamiut stated that they have often found unfossilized horns or skulls of muskoxen in their travels in the Brooks Range and northern foothills, but only a skull collected on Tulugak Creek has been specifically documented (Rausch, 1951).

Most muskox skulls of recent origin have been found on the tundra or associated with old habitations closer to the coast, including on Herschel Island, in the Colville River Delta, near Teshekpuk Lake, along the lower Meade and Kuk rivers and in the vicinity of Wainwright (Allen, 1913; Bee & Hall, 1956; Chesemore, 1980). Early traders and explorers found ample evidence that muskoxen had been recently hunted and used by Inuit along the northern coast of Alaska. Charles Brower, the first trader at Point Barrow, reported finding both bones and pieces of skin in association with old dwelling sites. Similarly, Stefansson collected hides, skulls and bones from house sites (Allen, 1913).

Hunters from a coastal Inuit settlement killed the last known muskoxen in northwestern Alaska just prior to the upheaval that struck Inuit society starting in the 1860's. This last muskox hunt probably occurred in 1858. Both Brower and Stefansson provide similar versions of this event, told by an Inuk named Mangi (Mangilanna) who died in the winter of 1899-1900. Stefansson's version is as follows:

"About 1858 there was a scarcity of food in winter at Cape Smythe {Point Barrow}. Mangi's father and other hunters went inland looking for caribou «...and some distance up the Kuuk {Kuk} River which flows into Wainwright Inlet, they fell in with a band of 13 muskoxen and killed them all. Since then no one near Point Barrow is known to have killed muskoxen or seen them" (Allen, 1912, 1913).

The mouth of the Kuk River lies near the present village of Wainwright. A tributary of the Kuk River that enters it a few miles inland is known as Omikmak Creek, a name derived from the Inupiat word for muskox (Hornaday & Brower, 1911; Allen, 1912, 1913). These reports and the specimens found by the first explorers and traders confirm that Inuit in northern Alaska were still occasionally taking muskoxen in the first half of the nineteenth century. Taken together with the archaeological finds of Ford, Hadleigh-West, and Stanford, described earlier, they provide evidence of continued, if erratic, use of muskoxen by people living along the coast of northwestern Alaska for at least 13 centuries (500 to 1850 AD). Hunters killed this last band in northwestern Alaska before the introduction of effective firearms (Sonnenfeld, 1960).

Farther east in the Alaskan Arctic marine mammal resources were more limited and the human population correspondingly lower. One small coastal village (Kaktovik) and a few sites of seasonal or short-term occupancy existed at the time of first European contact. Nunamiut may have been living inland in the eastern Brooks Range during certain periods, but the evidence for this is both sketchy and controversial (Anderson, 1984b). Athapaskan (Kutchin) Indians who lived south in the northern edges of the taiga on the south side of the Brooks Range were principally hunters of caribou. The Chandalar Kutchin, also encountered muskoxen on the northern fringes of their hunting grounds according to information they related to McKennan (1965). Kutchin hunters sought caribou and Dall sheep in the rugged terrain of the Brooks Range, where wind-swept hilltops rose above sparsely timbered slopes. According to the Kutchin, they also found small numbers of muskoxen in this high country. We know little about these muskoxen, other than what the Chandalar Kutchin learned from their ancestors: that a few muskoxen frequented the south side of the eastern Brooks Range in the nineteenth century. Oral traditions relating to hunting of muskoxen are sketchy, but informants believed that they were sometimes driven over cliffs. A small mountain near Smoke Creek, a tributary of the East Fork of the Chandalar River, southwest of the Kutchin settlement of Arctic Village, is called «Muskox Shirt Mountain» in the Kutchin tongue.

All told, however, the density of hunters in the eastern Brooks Range was lower than to the west (Anderson, 1984a). It is not surprising that the last few remnants of native muskoxen in Alaska apparently survived in this region. In the rugged, incised terrain with sheltered, productive valleys groups of muskoxen might have gone undetected for some time.

In the last decades of the century east-west movements of both Indians and Inuit intensified in northern Alaska. «Alaskan» Eskimos had been involved in hunting muskoxen as far east as the Coppermine River and maintained ties with Inuit of the Mackenzie Delta area (Hone, 1934; Smith, 1984). Conversely, Athapaskan Indians from far to the east had on occasion moved into northeastern Alaska and hunted and mixed with the Kutchin people of Alaska. Alaskan Inuit often accompanied the whaling vessels. Further, the decline in caribou numbers in western Alaska, disease, starvation and social disruption caused migrations, primarily west to east.

With regard to the decline in caribou in northern Alaska there is still some question as to whether it started before the arrival of Europeans or was a result of the introduction of firearms and the demand for food by American whalers overwintering in the Arctic. In any case, the slaughter in western Alaska was immense in the 1880s and later to the east in the 1890s, as whalers progressed farther into the Arctic in search of new stocks. In the western Arctic of Canada, there is no doubt that taking of muskox occurred into the twentieth century. Whalers wintering at the Baillie Islands and Langton Bay, about 320 kilometers east of the Alaska border, received muskox meat and hides in trade, hunted some themselves and also obtained a few live muskox calves (Anderson in Allen, 1913; Bockstoce, 1986).

The demand for game meat led to increased exploitation of caribou in Alaska, but there is no unequivocal proof of procurement of muskoxen for or by whalers or traders. Only a few tantalizing bits of evidence suggest that some muskoxen might have survived into the era of commercial whaling in Alaska or in Canada west of the Mackenzie River. Turner (1886) reported that both the Inuit and Indians of northeastern Alaska were familiar with the muskox and that a few muskoxen might remain in or north of the «Rumiantzof» [Romanzof] Mountains. His remarks were apparently accurate, but unfortunately he gives no clue of what led him to mention the Romanzof Mountains specifically.

The naturalist, Andrew Stone, also referred to the Romanzof Mountains «...from which specimens of musk-ox are reported to have recently been brought, by way of Camden Bay» (Whitney, 1904:89). However, after visiting northeastern Alaska in 1898-99 and interviewing many Inuit, missionaries and traders, Stone concluded emphatically that no muskoxen lived in the region nor had any been seen or killed in recent years. Allen (1912) also concluded that the muskox hides to which Stone referred had actually come from east of the Mackenzie River. Campbell (1978) suggested that Chandalar Indians might have provided muskoxen hides to the Hudson's Bay Company via the early Fort Yukon trading post but provided no evidence for this. Stone, who made specific inquiries in the area, obtained no hint of any such trade.

However, some accounts exist that suggest Alaska's last native muskoxen survived in the eastern Brook Range. We are indebted to Irving McKinley Reed, a life-long resident of Alaska, for collecting these accounts. An engineer and early member of the Alaska Game Commission, he maintained an intense interest in muskoxen and their reintroduction into Alaska. Reed grew up in Nome, the most important port of call on the west coast of Alaska. As a youth in that town he talked to many men about their experiences in the Arctic.

One story related by Reed (1946) hints that muskoxen might have been taken in Northeastern Alaska by or for whalers wintering at Herschel Island, 60 miles east of the Alaska-Yukon border and only a little over 100 miles from the Romanzov Mountains. In 1906, while engaged as a blacksmith's assistant on Ophir Creek not far from Nome, he worked with a man who claimed to have hunted muskoxen from Herschel Island in the 1890s. It is quite possible that misunderstanding may have garbled this account and that the hunting may have actually taken place farther east. However, another bit of evidence also suggests that muskoxen might have been available to these whalers from some source. In a letter dated October 10, 1890, Marion (Mrs. Horace P.) Smith, wife of an arctic whaling captain, mentions to her mother that she had recently received a muskox skin robe. This letter is significant because it provides a more precise date, one that was prior to the time that whalers were penetrating past the Mackenzie River Delta and thus it seems unlikely (although not impossible) that the muskox skins had come from so far east (John Bockstoce, pers. comm).

According to other information collected by Reed, a band of Chandalar Kutchin killed a herd of muskoxen in mountainous terrain between Christian and the Sheenjek River in the eastern Brooks Range, in 1892 or 1893. An effort to locate the skulls of these last muskoxen was not successful (D. Klein, pers. comm.). If such a kill had occurred, neither meat nor hides would be likely to have gone north to Herschel Island and the whalers but rather south to the Kutchin settlements and trading posts.

Reed (1946) also related a story told to him by Henry Rapelle, a man who subsequently lived in Fairbanks for many years. In January 1895, Rapelle had been traveling by dog team along the Yukon River between the settlements of Circle and Eagle. He stayed overnight with an Indian family at the mouth of Charlie Creek. The old Indian man of this household possessed a head and hide of a young male muskox. He told Rapelle that he had shot it late the previous year up the Kandik River, having thought it was «a bear with horns». The Kandik flows southwest into Alaska from the Yukon Territory, joining the Yukon River about 80 km west of the international border. According to Reed, Rapelle was able to make an accurate identification of the muskox because he had previously spent time in the Canadian Arctic.

Reed suggested that the young male had been a lone survivor from the band killed in 1892 or 1893 and had wandered about 150 miles south down from the mountains into the edges of the taiga before meeting his end. This tale would seem implausible except that the events are remarkably similar to an occurrence documented in 1970, after the re-introduction of muskoxen into northeastern Alaska. A group released on the coast near Kaktovik on Barter Island scattered widely. One young male wandered alone about 250 km south over the Brooks Range and was shot by an Indian hunter from Arctic Village. The man had never seen a muskox before and later stated that he shot it from the rear thinking it was a bear (Lent, 1971). Certainly at a quick glance, perhaps of an animal fleeing through heavy brush, a muskox, with its long hair, coloration and loping «rocking-horse» gait might be confused with a grizzly bear. The muskox killed in the 1890s could plausibly have been a survivor from one of the last groups in the Brooks Range.

Based on conversations with informants in Nome, Reed related one final event in the history of Alaska's native muskoxen. In 1897 or 1898 two French Canadian trappers allegedly killed an entire herd, 18 head in all, east of Chandalar Lake on the North Fork of the Chandalar River, between Lake and Tobin creeks. This account, like the others cited above, has not been confirmed from other sources. Nevertheless, the details are consistent among the stories and with Turner's general statement. There was no apparent reason or incentive for informants to fabricate these accounts. Although not confirmed by the apparently thorough inquiries of Andrew Stone, the accounts are consistent: small numbers of muskoxen probably survived in the eastern Brooks Range until nearly the end of the nineteenth century.

All writers of the late nineteenth and early twentieth century and all archaeological and ethnographic sources are in agreement that the muskoxen of northern Alaska were extremely rare and nearly extinct prior to the arrival of Europeans and the availability of firearms. Were Alaska's muskoxen exterminated by aboriginal overhunting or were these last herds simply remnants in marginal habitat, unable to sustain themselves in the face of a warming climate?

But other technological innovations perhaps did play an important role leading to the final extinction of Alaska's muskoxen. The built-up sled pulled by dogs seems to have come relatively recently as a significant element in northern Alaskan Inuit life. Hall (1978) has compiled evidence suggesting that this technology and all its accoutrements (including pegged runner shoes, etc) did not become commonplace until about 1600. Even a relatively small team of three to five dogs allowed the hauling of heavy loads of meat and hides cross country for the first time. The expansion of the Nunamiut into the areas north of the Brooks Range in recent centuries was facilitated by improved dog traction. The desire to maintain greater numbers of dogs probably put further pressure on the caribou population, and on inland and anadromous fisheries, and increased both access to and demand for furbearers (Hall, 1978). Muskoxen would have been particularly in demand in times of caribou scarcity or as emergency food during long sled journeys. In addition, coastal villagers had increased opportunities to hunt far inland with the aid of larger dog teams. New patterns of exploitation arose. Prior to these developments isolated groups of muskoxen were more likely to have survived far from the small centers of human habitation, and colonizing animals would have on occasion moved out from these groups. Human dispersal and the increased mobility of hunting bands might well have contributed to the final demise of Alaskan muskoxen.

Coastal Inuit also suffered periods of crisis with winter food shortages resulting from failure of whaling. Such crises occurred every 6 to 10 years, according to Spencer (1959). Minc & Smith (1989) characterized the period from 1780 to the early 1900s as cool and wet with high amplitude climatic fluctuations of longer duration - a time of great year-to-year variability. This was a period of intensive, specialized focus on whaling, but the coastal inhabitants turned to trade and increased use of terrestrial resources when whaling failed. Such shifts to other prey might also have contributed to the extirpation of the last bands of muskox.

Some climatic change occurred in the late nineteenth and early twentieth century. For example, the Chandalar Indians report that moose were rare, almost unknown, in the Brooks Range and elsewhere in northeastern Alaska up until early in this century. Much of the area north of the Yukon River where spruce predominates today was said to be principally willow-covered shrublands in the mid-nineteenth century (McKennan, 1965). On the other hand, the Nunamiut told Rausch (1951) that their ancestors had long hunted moose in the Colville River drainage. Historical evidence suggests, however, that resident moose population have substantially increased in northern Alaska in this century.

Inuit themselves provided two opinions regarding the disappearance of muskoxen. «Mangi» told Charles Brower in 1888 that muskoxen had been abundant on the coastal plain until large numbers of caribou became evident (Brower, 1952). In contrast, a Nunamiut informant attributed the disappearance of muskoxen to hunting pressure by Inuit (Ingstad, 1954).

Conclusions

There is no clear evidence of climate change in the last centuries of sufficient magnitude to explain the extinction of Alaskan muskoxen. Climate fluctuations of greater degree had occurred prior to this reset Holocene period (Haworth, 1989). The most likely scenario is that muskoxen were restricted by competition and climatic factors to relatively limited areas in northern Alaska. Although the species had persisted for millennia in northern Alaska it was not abundant, probably surviving in small isolated populations. These were vulnerable to hunting by an increasing human population. Technological advances allowed greater stability in human numbers and greater mobility by Inuit hunters. The presence of a large Inuit population in the Mackenzie Delta area would have precluded recolonization of northern Yukon and Alaska by muskoxen from the population centers to the east of the Delta. Thus, my scenario differs from that of Wilkinson (1975) in that I believe hunting by Inuit and Indians could have led to the extirpation of Alaska's indigenous muskoxen even through the species did not serve as a staple resource for these people. One fact is certain: The success of the reintroduced muskoxen in northern Alaska demonstrates that extensive suitable habitat has continued to exist there.

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Population structure and dynamics in captive muskoxen at the Large Animal Research Station, 1988-1994

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Abstract: The muskox colony at the Large Animal Research Station, started in 1979, totaled 22 individuals before calving in 1988. Between 1988 -1994 cows of breeding age have been maintained on either a high plane (HP) or low plane (LP) of nutrition, and as far as possible, female offspring are kept with their mother's group. During this time the population has increased from 22 to 43 animals (25 females and 18 males). Fifty-four calves were born with an overall sex ratio of 52:48 (male:female). When partitioned between the 2 nutritional planes the sex ratio was HP 45:55 and LP 62:38. The calf/cow ratio was 0.83 in 1988 and 0.86 in 1994. The LP group accounted for most of the variability in pregnancy rate, primarily through delayed puberty and breeding pauses. Calf mortality was due mainly to abortions, stillbirths and neonatal death (*n*=12), 7 deaths occurred between 2 weeks and 1 year of age. All stillbirths and abortions (*n*=4) and 6 of 8 neonatal deaths affected calves of HP cows. Thirteen adults died, 4 males were loaned to other facilities and 2 new calves were added.

Key words: herd composition, rate of increase, calf production, yearling recruitment, sex ratio, mortality.

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Introduction

Analysis of captive populations of wild animals are rarely published. Because so many more variables can be measured in captivity, the experience of rearing captive wild animals can add useful insights for studies on natural populations. Inherent controls on growth of captive populations could convey both advantages and disadvantages to analyzing population structure. In captivity, we can collect detailed information on behavior, activity budgets and physiology. We know the age of our animals, the exact number and sex of animals that are born and, in most cases, specific causes of death. We also can control a wide range of variables including group size and composition, diet, breeding season, predation, immigration and emigration. Conversely, captivity constrains population analysis through small sample size, replacement of natural foraging with an artificial diet and feeding regimen, and restricted animal mobility and dispersal. Close contact with humans and/or other species can enhance the potential for injury and disease transmission.

This paper is the demographic analysis of a captive population of a species that responds well to confinement, the muskox (*Ovibos moschatus*). Periodic epidemiologic surveys are part of a management protocol used to evaluate the relative health of our captive muskox population at the

Large Animal Research Station (LARS), University of Alaska Fairbanks. Because epidemiology employs essentially the same tools used in population analysis, we present data in a form for comparison with free-ranging populations. This provides a framework for interpretation of captive information. While it is always imperative to keep in mind the physical differences between captive and wild populations, the similarities and differences among population parameters can provide insights into mechanisms controlling free-ranging populations (*sensu* Hamilton & Blaxter, 1980; Albon *et al.*, 1986; Parker *et al.*, 1990; White *et al.*, 1997).

Animals and methods

We extracted data from the herd management records at LARS and from the pathology records at Veterinary Services, Institute of Arctic Biology. For the purposes of this paper, the total of all captive muskoxen at LARS are referred to as the captive population. Within this population, animals maintained in different pens (social units) are referred to as groups. In 1987, 6 female muskoxen of breeding age (2-7 yr.) were placed on either a high (n=3) or low (n=3) nutritional plane. High-plane (HP) animals were allowed to graze pasture (brome grass). They had year-round access to brome-grass hay and were supplemented throughout the year with a pelleted ration. Low-plane (LP) cows were provided similar pastures to HP cows, were allowed year-round access to brome-grass hay but did not receive the pellet supplement. In winter, LP cows had access to hay only. Between mid-August to mid-October a breeding bull was placed with each group. The adult bulls and cows remained separate in the non-breeding season. Healthy calves born to cows within a dietary treatment remained with their dams and were raised on her nutritional treatment until natural weaning occurred. At weaning, males were removed and females remained within the treatment group. Exceptions to this protocol were made if the calf required medical attention. In some cases this necessitated artificially weaning the calf and removing it from the nutritional experiment. A more detailed account of the nutritional experiment can be found in White *et al.* (1997) and Rowell *et al.* (1997). All research protocols were approved by an independent animal welfare committee.

The total LARS population was 22 individuals before the 1988 calving season and it increased to 43 by the end of 1994. Within any pen we controlled the group or harem size and age/sex composition in a manner that ensured all healthy cows ≥ 2.5 years old were provided the opportunity to mate with a mature bull. Emigration (4 males were loaned to other facilities) and immigration (2 zoo-born calves were donated in 1994) were limited. Annual population size and yearling recruitment were based on counts made prior to calving. Data were log transformed and regressed against year. Calf production was calculated as % of population size and as % of cows of breeding age (≥ 3 years). To examine the effect of diet on calf production, the data between 1988-1994 were pooled by nutritional group (HP or LP).

Results and discussion

Population composition and annual rate of increase

Changes in age and sex ratio of the captive population over 7 years are depicted in (Figs. 1a, b). This includes emigration (4 bulls loaned to another facility) and immigration (2 calves donated to LARS). These graphs show a marked increase in the younger cohorts and a disproportionately higher death rate among males.

The slope of the regression for population size over time gave an average exponential rate of 8% (y= 2.99+ {0.0798x}, s.e. slope = 0.0174, r^2 = 0.777, P=0.0038). Estimates of annual rate of increase from the wild range from a low of 2% in south eastern Greenland (Ferns, 1977) to 16-17% for newly introduced populations in Alaska (Spencer & Lensink, 1970; Jingfors & Klein, 1982) to a high of 20-25% for expanding populations in the Canadian Arctic (Vincent & Gunn, 1981; Gunn *et al.*, 1984; McLaren & Green, 1985) and highly productive areas in Alaska (Jingfors & Klein, 1982). The relatively low rate of increase identified in our captive population has been attributed to the nutritional treatment and high calf mortality and will be discussed in more detail in the following sections.

Calf production

In 1988 calf production was 23% of the population or a calf/cow ratio of 0.83. In 1994 calf production was 36% for the population with a calf/cow ratio 0.86 (Fig. 2).

Dietary treatment had an effect on calving rate (Fig. 2). Over the 7 year period, calf production per HP cow was 0.94. This was similar to estimates from expanding and reintroduced populations in

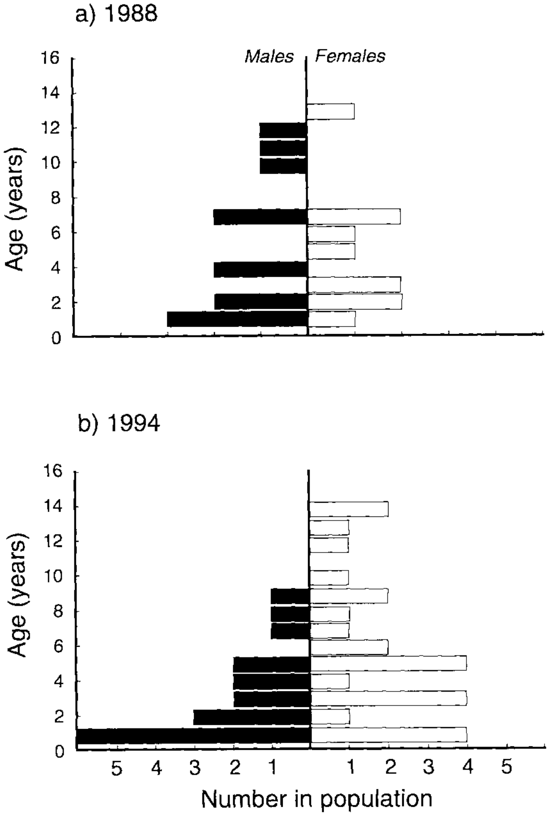


Fig. 1. Age and sex composition in 1988 (a) and 1994 (b) for a captive population of muskoxen (≥ 1 year-old) at the Large Animal Research Station, Fairbanks. The population was allowed to increase from 22 individuals in 1988 to 43 individuals in 1994.

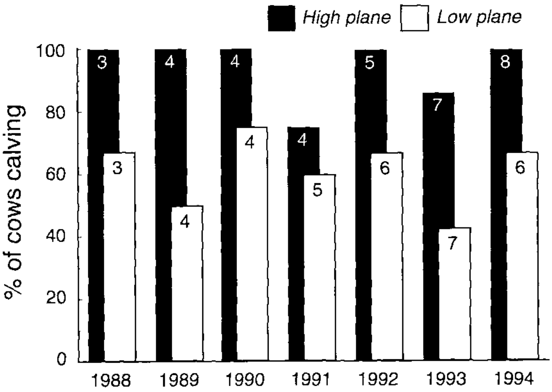


Fig. 2. Annual muskox calf production for muskox cows on a high (HP) and a low (LP) nutritional plane. Data are presented as a % of cows ≥ 3 years-old calving. Numbers on the bars indicate the number of cows of breeding age for each group.

the wild; Banks Island, 0.83 (Latour, 1987), West Greenland, 0.90-1.0 (Olesen, 1993), Nunivak Island, 0.80 (Smith, 1984) Northern Quebec, 0.86-0.97 (Le Henaff & Crête, 1989) and Northeast Alaska, 0.89 (Jingfors & Klein, 1982). Calf production among the LP cows was 0.60, consistent with estimates from less productive populations; NE Greenland, 0.39-0.57 (Thing *et al.*, 1987) and 0.58-0.63 (Lassen, 1984). Among the LP cows, lowered calf production was a function of delayed onset of first breeding and breeding pauses in parous cows (Rowell *et al*, 1997). A more detailed discussion of the effect of dietary treatment on breeding success can be found in White *et al.* (1997).

Also of interest is the association of diet and calving date (Fig. 3). While the sample size was too low to detect significant differences, the majority of HP cows calved earlier than LP cows. Mating behavior was consistently observed earlier among HP cows (Rowell, unpubl. observ.). Early born calves have the potential to gain more weight before the first winter, thus enhancing survival. In Fairbanks, early born calves usually avoid high ambient temperatures during the vulnerable neonatal period. Yet, in the captive population, the majority of neonatal mortalities occurred among HP cows, obscuring any positive effect of early birth. Neonatal mortality is discussed in a separate section.

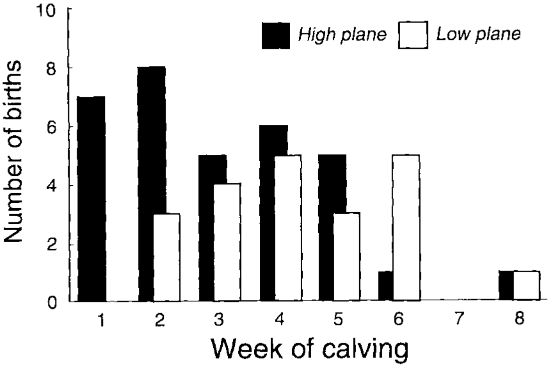


Fig. 3. Maternal plane of nutrition and timing of calving among captive muskoxen, 1988-1994. Week 1 begins on April 23 and week 8 ends on June 19.

Sex ratio

The sex ratio for 54 calves born between 1988-1994 was 52:48 (M:F) and did not differ significantly from 1:1 (Fig. 4), consistent with sex ratios identified in the field (Spencer & Lensink, 1970; Latour,

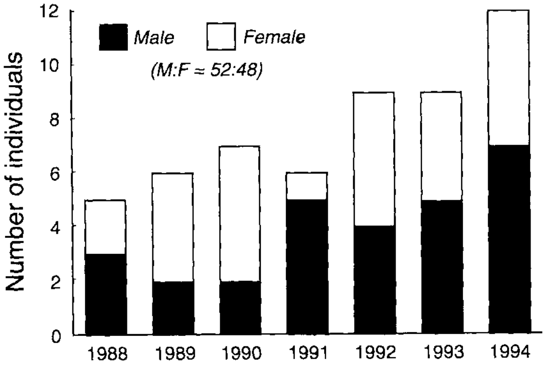


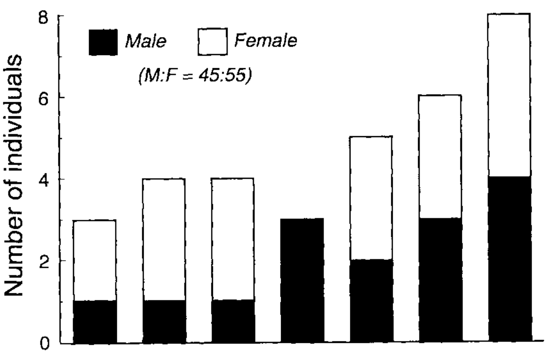
Fig. 4 Sex ratio of 54 muskox calves born at the Large Animal Research Station between 1988-1994. The ratio of males to females did not differ significantly from 1:1.

1987). Sex ratios within the two treatment groups were 45:55 for the HP and 62:38 in the LP group (Figs. 5a, b) but these ratios were not significantly different (P=0.348), possibly due to small sample size. While these data are interesting, the small sample size and lack of experimental design to specifically evaluate the effect of diet on sex ratio make it premature to draw conclusions.

Yearling recruitment

Yearling recruitment in 1994 was 12% with a yearling/cow ratio of 0.25, a reflection of high calf losses. Between 1988-1994 death during the first year of life in the captive population averaged 30%. In wild populations yearling recruitment is a reflection of both calf production and calf survival. Estimates of proportion of yearlings vary from lows of 6.8-8.7% in parts of the Canadian Arctic (Gunn *et al.*, 1989) to 10-16% for more productive populations of the Canadian arctic (Gunn *et al.*, 1989), Greenland (Thing *et al.*, 1987) and Nunivak Island (Spencer & Lensink, 1970) to highs of 24% or 0.62 yearlings/cow on Banks Island (Latour, 1987).

a) High plane



b) Low plane

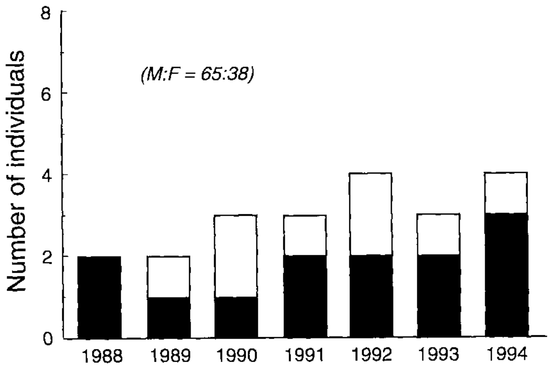


Fig. 5. Maternal nutritional plane and calf sex ratio. (a) sex ratio of calves born to muskox cows maintained on a high (HP) plane and (b) a low (LP) plane of nutrition.

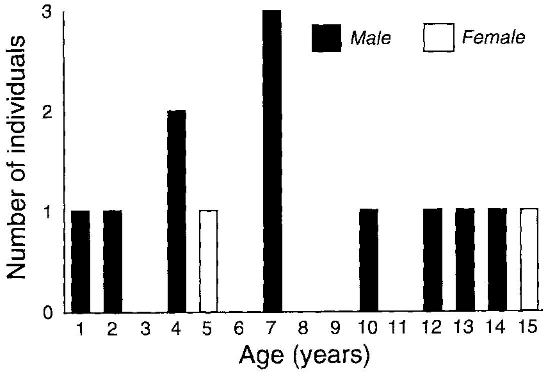


Fig. 6. Age specific mortality among male and female captive muskoxen ≥ 1 year-old, 1988-1994. Causes of mortality are listed in Table 1.

Adult mortality (> *1 year*)

Over the 7 years, 11 males and 2 adult females died (Fig. 6; Table 1). Almost half (n=5) of the male deaths were attributable to a nutritional problem that occurred during the winter and spring of 1990-1991. All 5 males were housed with 15 other animals in a pasture suspected to be of poorer quality compared to other areas of LARS and they did not receive a pelleted supplement. Only 2 of the 5 were available for necropsy. Three males died during heavy snows mid-winter and the carcasses, found in the spring, were too autolysed to examine. However, all three had abundant body fat suggesting a problem similar to the fatty liver, copper deficiency seen in the other two. There is very little information on muskox trace mineral status or trace

Table 1. Description of adult muskox mortality (≥1 year old) at the Large Animal Research Station, 1988–1994.

Category	Diagnosis	Individuals involved
Intraspecific Conflict	1) Skull fracture / cerebral hematoma 2) Broken ribs / lung bruising / renal failure	1 male 1 male
Foreign Body Ingestion	1) Chronic peritonitis 2) Brain abscess secondary to thoracic abscess	1 male castrate 1 male castrate
Metabolic Disorder	Fatty Liver Syndrome / copper deficiency. Spring 1991	2 male castrates
Immobilization Problem	1) Hyperthermia under etorphine / xylazine 2) Aspiration pneumonia following etorphine / xylazine	1 male 1 female
Calving Problem	Emphysematous fetus / metritis and septicemia	1 female
Miscellaneous	Meningitis secondary to tooth abscess	1 male
Unknown	Lost in woods during heavy snow winter of '90-91; found in spring Severe autolysis but all had abundant body fat Suspect Fatty Liver Syndrome / copper deficiency	3 males

mineral requirements, although instances of muskoxen using natural mineral licks have been documented (Thing *et al.*, 1987). The importance of copper, molybdomen, zinc and cobalt in captive muskox diets has been underestimated and the role of these minerals in wild muskox diets is unknown.

In captivity, death from starvation or predation did not occur. Trauma resulting from intraspecific conflict and meningitis from a tooth abscess are both conditions encountered in the wild. The ingestion of foreign objects is a ubiquitous problem, and a higher risk for animals that frequent areas disturbed by humans. It is a recognized source of accidental death in captivity but almost impossible to measure in the wild.

Due to the primary focus of our research programs, females are handled more often, therefore, inconspicuous clinical problems are recognized early and appropriately treated. Both female deaths are considered incidental. One died due to systemic infection following the death *in utero* and maceration of her term fetus. Sporadic losses due to calving problems such as this also occur in free-ranging muskoxen (Norment, 1980; Blake, pers. comm.). The other female died following aspiration of rumen contents during immobilization with etorphine/xylazine.

Regardless of the cause of death, mortalities were much higher among males than females. This also is a finding among many free-ranging populations (Parker *et al.*, 1975; Smith, 1984; Thing *et al.*, 1987; Gunn *et al.*, 1989). Disease investigations of free-ranging muskoxen on Banks Island identified a summer mortality caused by yersiniosis that produced a significantly higher mortality rate in mature, well conditioned males than in any other age or sex class (Blake *et al.*, 1991). It has been hypothesized that stressors imposed upon the males during and after the rut may predispose them to a higher prevalence of disease (Blake *et al.*, 1991) and/or nutritional problems (Gunn *et al.*, 1989). Male behavior in general (intraspecific competition, solitary movements) places them at greater risk for accidents, injury and predation.

Calf mortality

Calf mortality was high, despite medical intervention. We divided calf mortality into age categories: (a) abortion and stillbirth (b) neonatal (1-14 days of life) (c) 2 weeks-1 month (d) 1-3 months (e) 3-6 months and (f) 6-12 months (Fig. 7b). The greatest number of deaths (12) occurred from abortion/stillbirth and during the neonatal period. Of these, 10 of 12 were from calves of HP cows (Fig. 7a). Causes of abortion/stillbirth remain undetermined although extensive diagnostic work has ruled out common infectious causes. With few exceptions the neonatal deaths were caused by acute infections with *Escherischia coli.* Factors contributing to disease susceptibility in muskoxen of this age are poorly understood and warrant further investigation (Holst, 1990). A total of 7 deaths occurred for all

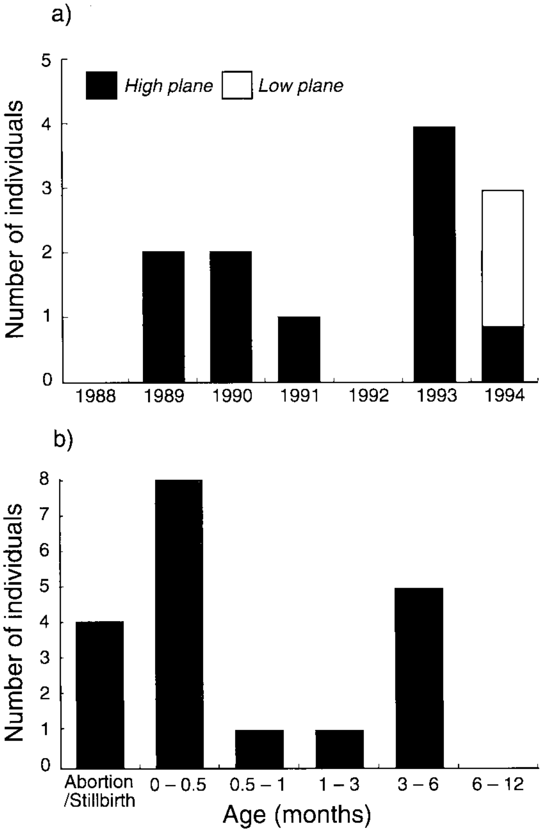


Fig. 7. Calf mortality. (a) late term abortions, stillbirths and neonatal (birth to 14 days) deaths among captive muskoxen, 1988-1994. HP and LP refer to the nutritional plane of the dam. (b) muskox calf mortality up to 1 year of age. These data combine both nutritional groups and include stillbirths and abortion.

other age groups with 5 of these occurring in the 3-6 month category (Fig. 7b). Four of the 5 deaths at 3-6 months were from an enteritis/malabsorption syndrome of viral and bacterial etiology with a possible nutritional component. This has affected all calves every fall since 1992 and only aggressive medical intervention has prevented higher losses. Again, factors contributing to susceptibility are currently being investigated. The remaining 3 losses were considered incidental (2 died from accidents and 1 from an oral abscess).

The high number of neonatal mortalities among HP cows was unexpected and we are unable to explain these results as a product of the nutritional treatment. High plane cows had more calves (33) than LP cows (21) hence, a greater probability for calf health problems. Four of the deaths were from primiparous cows (3 HP and 1 LP) and may reflect difficult births and/or poor mothering. High plane cows calved consistently as 3-years-olds, while LP cows were more likely to delay first calving for a year. Two HP cows accounted for 50% (5) of the HP calf deaths.

With the exception of a single report of a breech birth (Norment, 1980), there are no estimates of perinatal and neonatal mortality among wild muskoxen. Thus, although low calf production is often considered the primary cause of low yearling recruitment among wild populations, neonatal mortality is an extremely difficult phenomenon to measure in free-ranging animals. The fact that high neonatal mortality has not been reported in wild populations should not be replaced with a complacent attitude that it doesn't occur.

Conclusions

While acknowledging the constraints captivity places on a population of muskoxen, the tools for analyzing population structure have provided useful insights on the captive population. The nutritional model corroborates field observations of depressed calving in moderate to poor habitats. In addition, finding a trend towards skewed calf sex ratio and later calving among the LP group is intriguing and worthy of further investigation.

Mortality investigations highlight our lack of information on trace mineral status in general. High calf mortality remains a persistent problem among captive muskox herds worldwide (Holst, 1990). Captive calves are extremely susceptible to a host of infectious and dietary disorders, many of which are common, relatively benign conditions in domestic livestock. Abortions and stillbirths remain a baffling and perseverant problem. Understanding the conditions that contribute to this lack of robustness during pregnancy and in early neonatal life will help us understand the limits to the species adaptability.

Acknowledgments

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With this issue of Rangifer the proceedings of the Fairbanks meeting are finally accomplished. Papers submitted to Rangifer are gathered in the following issues of the journal: 1996, 16 (2): 49–92; 1997, 17 (1): 3–50; 1997, 17 (3): 10–138; 1998, 18 (3–4): 99–154.

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Proceedings Issue No. 4 – Rangifer Vol. 18, No. 3–4, 1998

Migration – utopia or myopia[1]?

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Peter Osborne spent a sabbatical in northern America and was surprised that so many scientists and students stated that caribou migration was largely the result of mosquito pressure. He failed however to find any documented evidence of this claim although he was constantly confronted by the well known «facts» that mosquitoes had been observed to drive caribou crazy and even kill juveniles. The issue Osborne wishes to focus is that an experimentally unsubstantiated anthropomorphism appears to have become critical evidence in support of a theory. A recent article in Nature (393, 511-513, 1998) devoted to the uses of 'science in fiction' to stimulate thought and discussion about aspects of academia encouraged him to write the following comment in the form of a parody of ancient Greek dialogues.

Rangifer, 18 (3–4): 155–156

Skepticus: What makes Alaskan and Canadian caribou migrate?

Status Quovicus:If you mean what factors contribute to the seasonal movement of caribou from highland calving grounds to Arctic coastal tundra then the answer is considered to be the interaction of availability of forage and insect pressure.

S: Intuitively I can accept the importance of the availability and quality of forage but, insect pressure?

SQ: Yes, mosquito harassment of caribou is considered by biologists and some members of the general community to be a most important factor contributing to the migration of caribou.

S: How can that be possible?

SQ: As you know on the tundra, during the summer calving period the biomass of mosquitoes is tremendous, some estimates say equal to the weight of the caribou herds themselves. As such the mosquitoes can be considered as a predatory burden upon the caribou.

S: You mean the mosquito's predation upon the caribou results in anemia of the caribou?

SQ: No. Russian studies have shown that the daily blood loss from the caribou, as a consequence of mosquitoes predation, is unlikely to be more than a healthy caribou can replace. It is considered that the cumulative predation pressures of the *Aedes* mosquitoes results in relentless harassment of the caribou which then adopt the strategy of continual movement in order to escape. Anecdotal reports from hunters and researchers suggest that in some instances mosquitoes have been observed to drive caribou crazy and under extreme circumstances be associated with the death of calves.

S: This axiom would appear to hang heavily on the researchers and hunters ability to assess the mental condition and motives of caribou - an extremely challenging task, even of animals that are capable of speech. Your evidence is at best a tenuous relationship and certainly doesn't indicate cause. I have two disagreements with your line of logic which I will

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[1] Myopia means short-sightedness.

attempt to expose to you. Firstly, this particular predator- prey relationship is long standing with both participants interacting for thousands of years. As such I would suppose that the influence of the mosquito upon the caribou would be, in general, innocuous as neither of these two participants display anatomical peculiarities indicative of an evolutionary battle between skin thickness and ever increasing proboscis length. Secondly and more importantly, if movement away from an area of extreme mosquito density was used as a strategy by the caribou it is unclear to me how this would result in migration. What you are implying is that caribou move continually down gradients of mosquito harassment. Within a given area of tundra surely mosquito numbers would vary according to microclimatic features such as temperature, wind velocity and height. Topographically, this is unlikely to result in corridors of low mosquito density leading from spring calving grounds to the sea or summer feeding grounds. It is more likely to result in what would effectively be described as the brownian motion of caribou between the mosaic of pockets of low mosquito density randomly scattered across the tundra. However even if we should invoke the use of chaos theory to illuminate order from these patterns of movement, I am even then unwilling to accede that this would result in the movement of herds of caribou in determined but unobvious trails from mountain to sea.

SQ: No. I think your flippancy disguises that you miss the point. I agree with your doubt regarding the existence of corridors of low mosquito density but I dispute your denial that mosquito pressures are reduced between the calving grounds and the summer pasture.

S: Oh, sir, you are mistaken. I do not dispute your observation, merely your statement that this observation is related to the cause of migratory behavior in caribou. Given this observation, I would suggest that this migratory behavior is not a learned avoidance of mosquito harassment since with learned behaviors the greater the time interval between the task or stimulus and the reward, the quicker the learned behavioral response becomes extinct. In the scenario you proffer, the behavior of moving on to avoid the mosquito harassment would be reinforced only upon arrival at an area of low mosquito density. If this time interval between departure and arrival was long, in the order of a few minutes, the behavior you attempt to explain would not be reinforced. In addition unless the wind is horrendously strong and the caribou herd is well spaced I must also doubt that the migrating caribou would move at a pace that would out distance the predatory mosquito.

– thoughtful pause –

However, after uttering this last doubt I am now forced to reassess my entire argument. It would seem reasonable to conclude from the available evidence that the pursuing mosquito is driving the caribou in a manner analogous to sheep dogs driving cattle. What say you Status Quovius?

SQ: I think that both unlike and like the caribou, I will grow a thicker skin and walk away from this argument before I am driven crazed to my death.

Dissertations

Tove Hilde Aagnes Utsi successfully defended her Doctor Scient. thesis ***"Digestive strategies in reindeer in winter"*** at the University of Tromsø, Norway 16th May 1998.

Tove Hilde Aagnes Utsi is from Gildeskål municipality in Nordland county, Norway and was educated at the Department of Arctic Biology, Institute of Medical Biology, University of Tromsø. She was Cand. Scient. in 1990 with a thesis entitled *"Bacterial fermentation of lichen and ruminal responses to starvation in Norwegian reindeer"*. Aagnes Utsi continued with a scholarship for the period 1991-1994 studying ruminal responses to a natural winter pasture in reindeer and grass silage as emergency food for reindeer. The study has been in close collaboration with the Norwegian Crop Research Institute, Holt Research Centre, Tromsø and Norwegian College of Veterinary Medicine, Department of Arctic Veterinary Medicine, Tromsø. She has from 1995 had a position at the Norwegian Reindeer Husbandry Administration in Alta.

Her thesis is based on the following five papers:

I. **Aagnes, T. H. & Mathiesen, S. D.** 1994. Food and snow intake, body mass and rumen function in reindeer fed lichen and subsequently starved for 4 days. – *Rangifer* 14: 33–37.

II. **Aagnes, T. H, Sørmo, W. & Mathiesen, S. D.** 1995. Ruminal microbial digestion in free-living, in captive lichen-fed and in starved reindeer (*Rangifer tarandus tarandus*) in winter. – *Appl. Environ. Microbiol.* 61: 583–591.

III. **Aagnes, T. H., Blix, A. S. & Mathiesen, S. D.** 1996. Food intake, digestibility and rumen fermentation in reindeer fed baled timothy silage in summer and winter. – *J. Agric. Sci., Camb.* 127: 517–523.

IV. **Olsen, M. A., Aagnes, T. H. & Mathiesen, S. D.** 1997. The effect of timothy silage on the rumen bacterial population in rumen fluid of reindeer (*Rangifer tarandus tarandus*) from natural summer and winter pasture. – *FEMS Microbiol. Ecol.* 24: 127–136.

V. **Aagnes, T. H. & Mathiesen S. D.** 1996. Gross anatomy of the gastrointestinal tract in reindeer, free-living and fed baled timothy silage in summer and winter. – *Rangifer* 16: 31–39.

Summary: Deep snow and overicing in the sub-Arctic areas in winter can result in restricted pasture availability or acute starvation for the reindeer. In such situations provision of emergency food may be necessary to prevent loss of animals. Emergency food for free-living reindeer needs to have high acceptability and should not cause any digestive disorders, even in animals starved for some days. In addition, it should preferentially meet the animals maintenance energy requirements. To find such food, basic knowledge of the digestive processes in reindeer were needed and made basis for this study.

To investigate if reindeer had special adaptation to maintain the rumen function when exposed to acute starvation, rumen fluid volume and fluid turnover time were measured in reindeer fed pure lichen and after four days of starvation, by using a liquid-phase chromium-EDTA marker (paper I). In lichen fed reindeer rumen fluid volume and turnover time varied considerably between animals (volume range 3.8-10.8 l; turnover range 22.5-69.0 h), but were fairly constant in individual animals. These values did not change significantly in response to starvation, mainly due to a conspicuously increased snow intake. This fact naturally reduced reticulo-rumen dry matter and microbial population, which in turn will reduce the ability of the animal to digest plant material after starvation.

In free-living reindeer from northern Norway, eating a mixed winter diet dominated by lichens, the rumen fermentation, bacterial population density and composition were studied, and compared with reindeer fed pure lichen and subsequently starved for four days (paper II). Bacterial population densities in the rumen fluid and associated to the plant particles were recorded, using the dilution method and habitat stimulating growth medium, both in lichen fed and free-living reindeer ranging between 15.0-500.0 x 10^8 bacteria per ml rumen fluid and per gram rumen solids. The bacterial population density associated to the plant particles was significantly higher in the free-living reindeer than in the lichen fed. The bacterial composition in the free-living reindeer seems to be adapted to a fibre digestion, which could not be found in the lichen fed animals. Total ruminal volatile fatty acid concentrations ranged between 57.4-72.1 mM in the lichen fed reindeer compared to 70.4-82.6 mM in the free-living reindeer. Starvation for 4 days reduced the rumen bacterial population densities both in the rumen fluid and associated to the plant particles more than 90%, the bacterial composition changed, ruminal pH increased and ruminal volatile fatty acid concentration decreased considerably. The study indicates that intake of a natural mixed winter diet improve the growth condition of the

rumen bacteria and microbial digestion in reindeer compared with a pure lichen diet. When the reindeer are exposed to acute starvation, the ruminal microbial environment changes considerably.

To understand the ability of reindeer to adapt to a grass diet in winter, food intake, digestion, ruminal fermentation and bacterial population, gastrointestinal anatomy and body condition have been investigated in reindeer taken from a natural winter pasture and fed different round baled grass silage qualities. (paper III, IV, & V).

Well preserved qualities of grass silage, independent of maturity of the plants have been shown to be highly acceptable to reindeer. The silage structure and chemical composition however, seem to influence the gastrointestinal tract anatomy substantially and hence, the utilisation of the silages. Reindeer easily adapted to high-quality timothy silage with 89% leaves, 38.7% dry matter cel wall content and 30.0% dry matter water soluble carbohydrates content. Both summer and winter the digestibl energy intake was high (range 13.9-17.2 MJ/d), reticulo rumen digesta load small (range 9.6-18.3% of bod mass) and carcass weight high (range 45.8-52.6% o body mass). In reindeer fed fibrous timothy silage wit 27% leaves, 57.8% dry matter cell wall content an 6.2% dry matter water soluble carbohydrates conten the digestible energy intake was low (range 8.3-9. MJ/d), reticulo-rumen digesta load was great (rang 25.1-33.3% of body mass) and carcass weight was lo (range 34.3-42.2% of body mass). This indicate tha reindeer have limitations in utilising roughage with hig fibre content.

Thus, high-quality leaf rich timothy silage seems to b a diet suitable as emergency food for reindeer.

Wenche Sørmo defended her thesis ***"Interactions between the function of the digestive system and pasture plants in reindeer"*** for the degree of *Doctor scientiarum* at the University of Tromsø 13th June 1998.

Wenche Sørmo was born in Mo i Rana, North Norway in 1966 and was educated at the University of Tromsø where she joined the Department of Arctic Biology in 1988. Here she started research on the bacteria of the small intestinal mucosa of reindeer. Since 1994, her focus has been on the functional anatomy of the digestive system of Svalbard reindeer and the impacts different pastures have on the function of the digestive system.

The thesis is formed by the following five papers:

1. **Sørmo, W., Haga, Ø. E., Gaare, E., Langvatn, R. & Mathiesen, S. D.** The effect of plant species in the rumen and chemical and structural fibre composition on the fill of the fermentation chambers in Svalbard reindeer. Submitted *J. Zool.*
2. **Sørmo, W. & Mathiesen, S. D.** 1993. Bacteria in the small intestine of lichen-fed Norwegian reindeer (*Rangifer tarandus tarandus*). – *Letters in Applied Microbiology* 16: 170–171.
3. **Sørmo, W., Aagnes, T. H., Olsen, M. A. & Mathiesen, S. D.** 1994. The bacteriology of the small intestinal mucosa of free living reindeer. – *Rangifer* 14: 65–78.
4. **Sørmo, W., Haga, Ø. E., White, R. G. & Mathiesen, S. D.** 1997. Comparative aspects of volatile fatty acid production in the rumen and distal fermentation chamber in Svalbard reindeer. – *Rangifer* 17: 81–95.
5. **Sørmo, W., Haga, Ø. E. & Mathiesen, S. D.** 1998. Cellulolysis in the rumen and distal fermentation chamber in Svalbard reindeer (*Rangifer tarandus platyrhyncus*). – *Rangifer* 18: 47–50.

Abstract: The plant quality did not affect the size of the rumen in Svalbard reindeer but the distal fermentation chamber (DFC) seemed to increase in size with increasing amounts of hemicellulose in the diet (Paper 1). Size of particles in the rumen contents was not dependent on plant quality and differences in gastro-intestinal (GI) tract fill were mostly a result of changes in body mass. However, in autumn the GI tract of lactating females was larger than of non-lactating females with the same body mass .

The next two papers describe how a diet of pure lichen and a normal winter pasture respectively affects upon the adherent small intestinal bacterial populations. The mucosal bacteria are thougt to create a protective, physical and chemical barrier between the small intestinal epithelium and the ingesta. Reindeer in pens fed pure lichens had high population densities of lactic acid producing bacteria associated with the small intestinal mucosa compared to the very low densities in free living animals on a normal winter pasture. This difference could either be explained by the release of antibacterial substances in the diet of the free living animals after the food had been exposed to the acidic environment in the abomasum, or by a higher contamination pressure of micro-organisms when the animals were kept in pens. The role of the micro-organisms in the small intestinal mucosa of reindeer is still unknown.

Paper 4 describes how differences in plant quality influenced on the production rate of volatile fatty acids (VFA) in the rumen and in the DFC of Svalbard reindeer. Ruminal and DFC concentration of VFA were not correlated to production rates of VFA, probably owing to differences in pH, and therefore differences in rates of absorption over the intestinal wall. Ruminal and DFC production of VFA were low in winter when food was of low quality but high in summer and autumn. High production rates of VFA in DFG were not related to the size of the organ but to high plant quality.

The fifth paper illustrates how energy and nitrogen levels in the food affect rumen and DFC micro-organisms' ability to digest cellulose *in vitro.* If water soluble carbohydrates and protein were of relatively high concentrations in the rumen contents, rumen fermentation of cellulose *in vitro* was high, and DFC fermentation was low, and *vice versa.* In the DFC, fermentation of cellulose *in vitro,* seems to be inversely related to content of cellulose.

The student network CAES – Grants

Circumpolar PhD Network in Arctic Environmental Studies (CAES) is a research education program addressed to PhD students and post-doctoral scientists involved in Arctic and Subarctic environmental studies. Master students are also asked to attend the network. CAES includes the network started for students in reindeer husbandry The Network aims to foster interdisciplinary research and partnership between natural and social scientists, and to supplement other Arctic study programs. The CAES Network organises workshops and annual courses with field seminars and excursions in different regions of the North, arranges mobility grants for students and maintains an electronic network and website. The CAES Network is funded for 1999-2001 by the Nordic Academy for Advanced Study (NorFA).

The first course of the CAES program will focus on the actual research questions in reindeer husbandry and related environmental issues, and it is due to be held as combined seminars and field excursions in several places in Fennoscandia and north-western Russia in August 2000. The course will take several approaches to the study of reindeer husbandry and environment in the North.

Prior to the course, an initial interdisciplinary workshop "Reindeer 2000" and gathering of students around this theme will be arranged in Tromsø, Norway (August 1999) in conjunction with the 10th Arctic Ungulate Conference. The CAES Network encourages students on higher level to participate in the workshop via a limited number of travel grants. Applicants should submit a brief CV (1 page), an abstract (max. 200 words) describing their current research and research interests, a cover letter that describes how the applicant will benefit from and contribute to the workshop, and an estimate of travel costs. **The deadline is March 1, 1999.** Please send the application (preferably by e-mail) to:

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The 2nd announcement for the 10th Arctic Ungulate Conference, Tromsø 9-12 August, 1999, is found on the conference's homepage
http://www.fm.uit.no/info/imb/arktisk/ungulate/ungulate.html
If you wish to pre-register and have not already done so, please contact Ms. Elin Giæver at **eling@fagmed.uit.no**
We look forward to seeing you in Tromsø.

The Organising Committee

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