Are arctic ungulates physiologically unique?

James M. Suttie & James R. Webster

AgResearch, Invermay Agricultural Centre, Private Bag 50034, Mosgiel, New Zealand (suttiej@agresearch.cri.nz).

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.

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 Confetence in Nuuk, compared morphological, ecological and behavioural adapta-

tions 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 (mm²)			
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/cm²)			
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 slowet 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
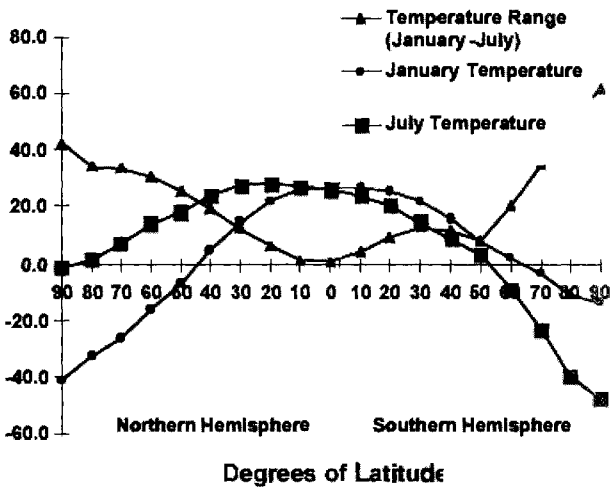
Effect of Latitude on Temperature

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. Kirkpattick *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 longet 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	[Octobet]	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 ttansduced from environmental to physiological. How this information is actually used by the animal is not known but in temperate species it is believed that eithet 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 sectetion 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 ofi 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 ot constant dark. What effect does this have on melatonin secretion? Eloranta *et al.* (1992) and Stokkan *et al.* (1994) have studied melatonin in teindeer 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
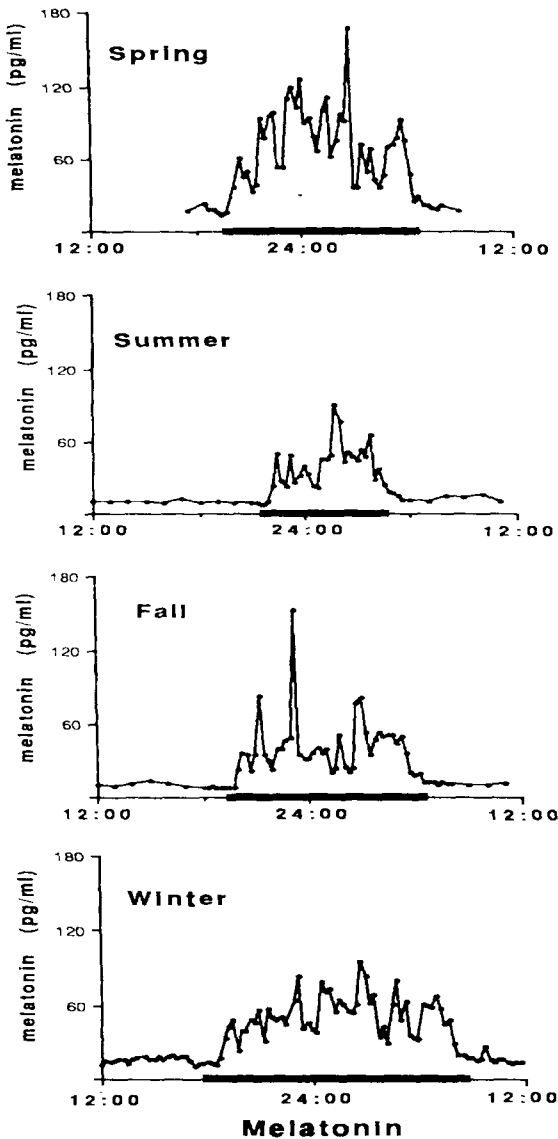
Fig. 2. Melatonin secretion during four seasons of the year in muskoxen (after Tedesco *et al.*, 1992).

muskoxen at high latitudes - respond to the lack of photoperiodic information particularly in summer to accutately 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 pottions of the year (Woodfill *et al.*, 1994). This three month period of photoperiodic information each year was sufficient to synchronise the circan-

nual 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 ftom 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 bteeding season. The lack of photoperiod information in summet 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 othet deer, as a male secondary sexual characteristics. It is assumed from the abundant behavioutal/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 (Espmatk, 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 Espmatk (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 tespect 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 antlet tissue grown during early puberty - and also the controller ofantler 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 antlet cleaning. This means
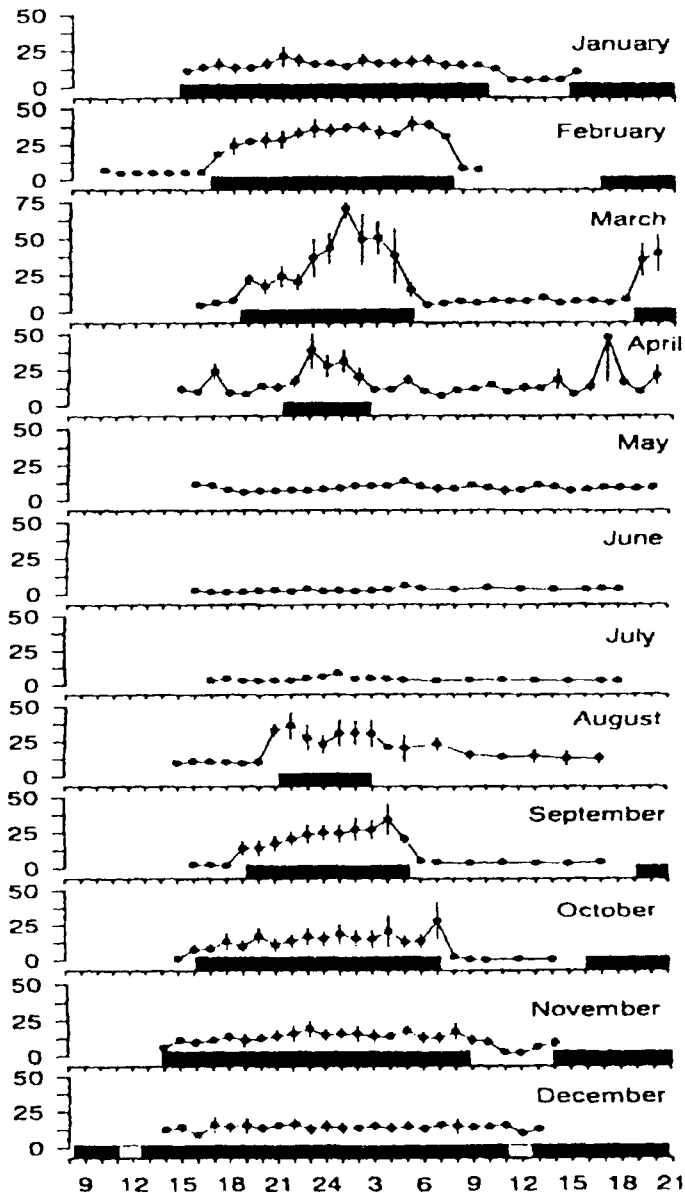
Fig. 3. Plasma melatonin in reindeer (*Rangifer tarandus*) (Stokkan *et al.*, 1994).

It is hypothesised that after initial evolution, different species have evolved sepatate antlet control mechanisms. Presence of antlers in female reindeer/caribou gave a selective advantage in the Arctic but their evolution depended on mechanisms that wete 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 srrategy. 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 tate 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 tates 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 wintet (Nilssen *et al.,* 1994). In terms of an adaptation to the Arctic, muskoxen appear to

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 casttate. In the roe deer (*Capreolus capreolus*), androgens appear to be requited 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 rhe least sensitive.

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 tequired	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	Withdtawal causes casting	6	Grows small antlers which nevet clean or cast	7
Roe deer (*Capreolus capreolus*)	Required	8	High levels required	8	Withdtawal 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 & Lactoix (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 teduction 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 mote in depth comparisons.

Comparisons between reindeer/caribou and other deer species reveal that RMR and FMR are similat (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. Dtawing the data together and relying heavily on Adamczewski *et al.* (1994a), it is clear that muskoxen have high apparent dry mattet 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 gtazer. Information on digestibility and retention time should be interpreted in relation to dry mattet 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 mote, 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

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Table 6. Comparison of metabolic rates in Bovidae.

Species	Number and sex	Time of year	Resting metabolic rate W kg⁻¹	Fasting metabolic rate W 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	Wintet 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 ate 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 fotward 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 teindeer 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	2	NS[2]	Lichens and hay	NM[3]	51	1
(*Rangifer*	4	NS	Lichens and hay	NM	44	1
tarandus)	1M,1F	NS	Grass and pelleted concentrate	NM	19.1/26.0	2
Reindeer	F	Summer	Forbs Leaves	70	NM	3
(*Rangifer*			Flowers	81	NM	3
tarandus)			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	8M	Winter	Lucerne hay *ad lib*	62	NM	4
(*Cervus elaphus*)	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	1F	Winter	Lucerne hay	51.9	NM	6
(*Alces alces*)	1F	Winter	Timothy brome hay	55	NM	6
	1F	Wintet	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	2M	Winter	Lucerne hay	51.5	NM	6
(*Cervus elaphus*)	2M	Wintet	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. Fteudenberger *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 sttessed, thus there is high pressure to grow rapidly at the cotrect time. To determine if the growth of arrcic ungulares is unique, growth data from the litetature and unpublished sources were compared. Weight gain over the four months of shortest daylength (W) and weight gain fot 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.

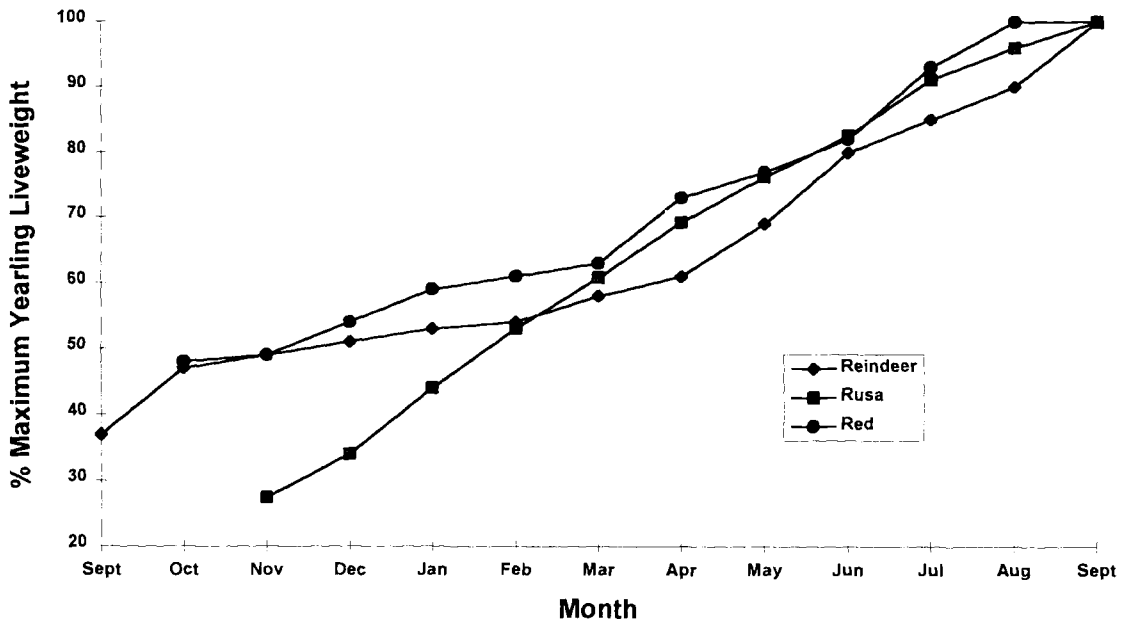Fig. 5 is a representative set of data. Unfor-

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 & Woodfotd, 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 summet 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 transpotted to another for study appeat 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 cotrection of 60 days is necessary to account fot 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 ensute the most rapid growth possible during summer. Interestingly IGF 1 is also seasonal in muskoxen but Adamczewski *et al.*
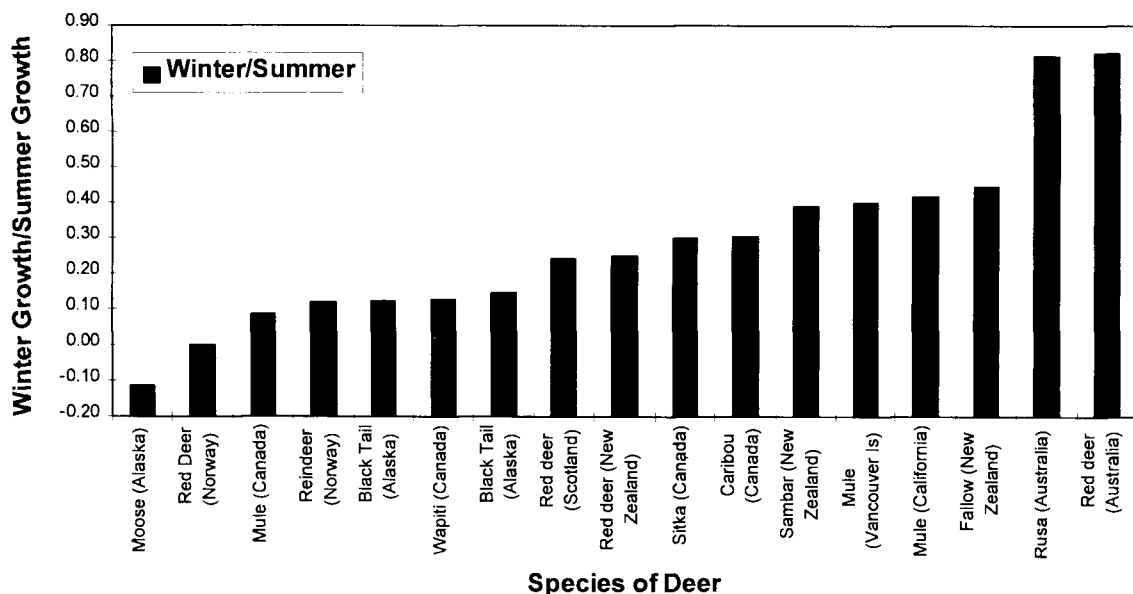
Fig. 5. Winter growth/summer growth ratios in deer species.

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 deet (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 & Woodfotd, unpubl.
Red deer (Australia) (*C. elaphus*)	Suttie & Woodford, unpubl.

(1992) have shown that the peak IGF 1 is later in the summer, and corresponds bettet 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 cattying a pregnancy in sub-optimal conditions ate high and possibly life-thteatening. 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 rhe 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 othet species, for example wildebeest, which conceive and give birth during seasonal
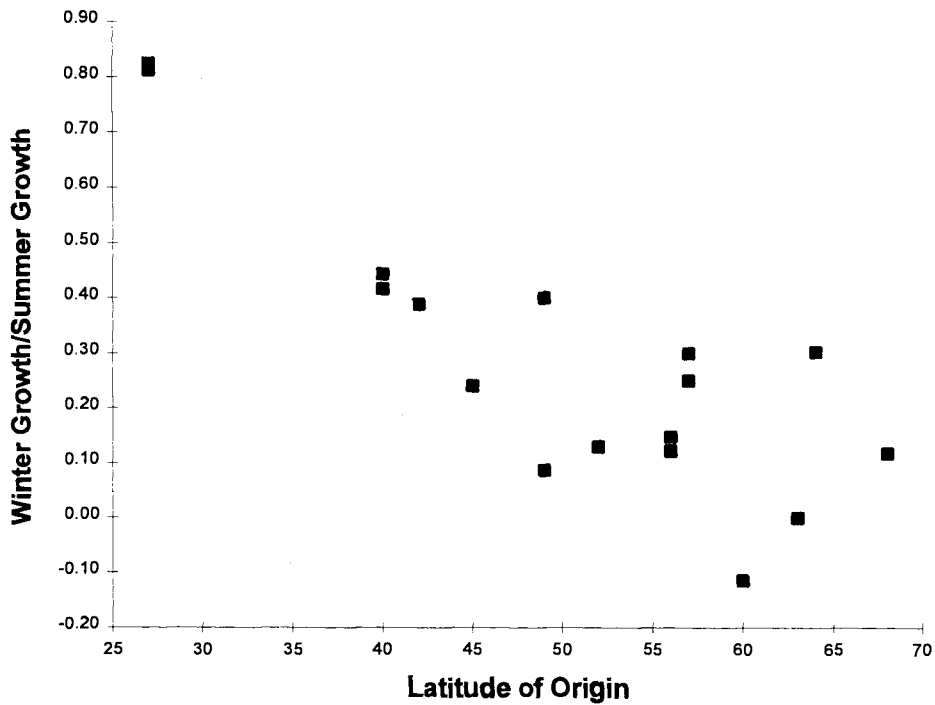
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Fig. 6. The effect of latitude of origin of the study animals on the tatio of the amount of growth taking place in wintet with the amount of summer growth. Each datum point is from fig. 5, and represents the ratio of growth (winter/summer) for male deer of various species and locations of origin during their first winter and second summer of life.
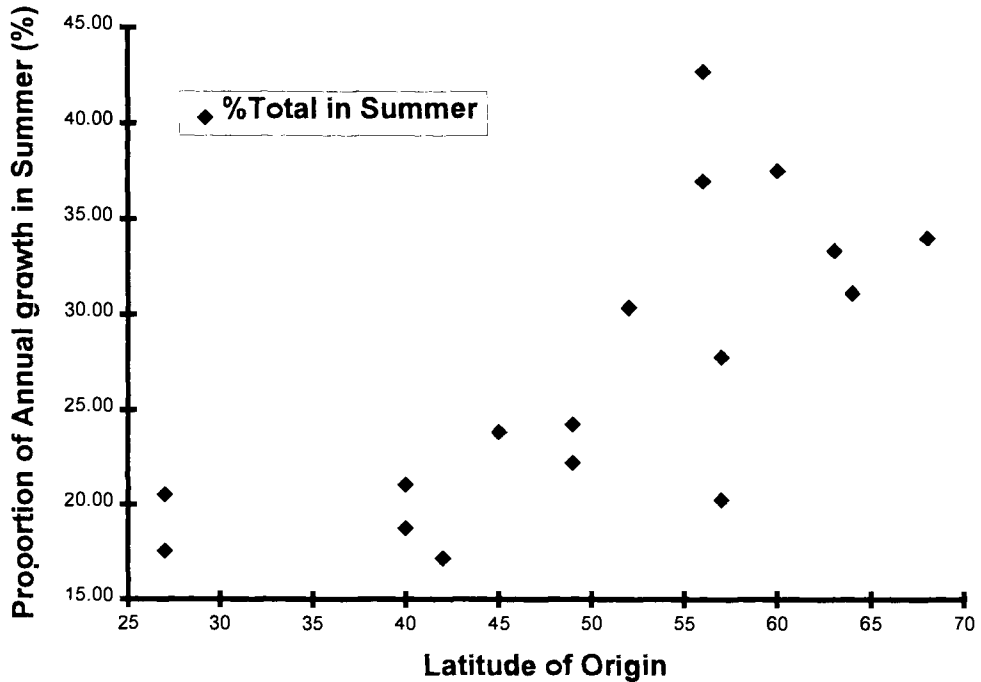

Fig. 7. The effect of latitude of origin on the ptoportion of annual growth which took place in summer. Each datum point is ftom fig. 5, and represents the ratio of growth (wintet/summer) for male deer of various species and locarions of origin during rheir first winter and second summer of life.

Table 10. Are arctic ungulates unique?

	Reproduction	Photopetiod information ttansduction	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 tempetature?	Yes - very good digestion ofi low quality fotage	No - follows seasonal variation
Reindeer/ Caribou (*Rangifer tarandus*)	Yes? - short gestation petiod - 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 ofi 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 duting periods ofi 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 ofi the seasonal cycle ofi food intake with metabolism may have a mote 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 ofi a complex of adaptive sttategies which is more important in its entirety than either part separately. In the context ofi 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 sttategies which may be called unique to the arctic, but the reindeer/caribou appear to be following the typical cervid model.

In terms ofi digestion the muskoxen is a very good grazer within the Bovidae, but the reindeer/caribou, as a concentrate selector is similar to many othet species ofi deer. It is possible that the ability to digest lichens is unique and the lichen digestibility in reindeer seem to be much highet 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 feedets 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 ofi food abundance and quality by timing periods ofi growth to coincide with these events. We do not consider this in itselfi unique but rather an extreme example of the situa-

tion 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 wintet but is very fast duting 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 imptessive 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 wintet, they are also supremely adapted to making the best use of summer. To enable this, arctic ungulates tequire 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 ate unique in the way they integrate this tange 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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