

Key note address:

Survival strategies in arctic ungulates

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Abstract: Arctic ungulates usually neither freeze nor starve to death despite the rigours of winter. Physiological adaptations enable them to survive and reproduce despite long periods of intense cold and potential undernutrition. Heat conservation is achieved by excellent insulation combined with nasal heat exchange. Seasonal variation in fasting metabolic rate has been reported in several temperate and sub-arctic species of ungulates and seems to occur in muskoxen. Surprisingly, there is no evidence for this in reindeer. Both reindeer and caribou normally maintain low levels of locomotor activity in winter. Light foot loads are important for reducing energy expenditure while walking over snow. The significance and control of selective cooling of the brain during hard exercise (e.g. escape from predators) is discussed. Like other cervids, reindeer and caribou display a pronounced seasonal cycle of appetite and growth which seems to have an intrinsic basis. This has two consequences. First, the animals evidently survive perfectly well despite enduring negative energy balance for long periods. Second, loss of weight in winter is not necessarily evidence of undernutrition. The main role of fat reserves, especially in males, may be to enhance reproductive success. The principal role of fat reserves in winter appears to be to provide a supplement to, rather than a substitute for, poor quality winter forage. Fat also provides an insurance against death during periods of acute starvation.

Key words: appetite, brain cooling, caribou, energetics, fat, growth, heat balance, metabolism, muskox, *Ovibos*, *Rangifer*, reindeer.

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Introduction

The arctic is a hostile place in winter, yet the cold, dark polar 'wastes' sustain life. The environment is truly marginal and for this reason it is tempting to conclude that endothermic animals which spend the winter there must endure a truly marginal existence. Paradoxically, however, most arctic animals usually neither freeze nor starve to death. They are evidently well

adapted to the several challenges of the environment. This paper reviews some of the physiological adaptations which enable ungulates to survive and reproduce in the arctic.

Several species of monogastric mammals circumvent the problem of cold and the scarcity of food in winter by hibernating. These typically store large quantities of fat in summer and autumn and, by reducing their metabolic rate,

they may literally 'live off' their fat for weeks or even months at a time during winter. But, as a result of their reduced metabolism, they become hypothermic with body temperature falling as low as 0-4°C in some cases (Hensel, Brück and Rath, 1973).

Reindeer and caribou, however, are ruminants. Unlike monogastric species they have to remain active to feed continuously throughout winter. Moreover, they are truly homeothermic, requiring maintenance of a constant internal body temperature which is considerably above environmental temperature. For these, like other true homeotherms, the problem of survival becomes one of keeping warm. To do this they need both to reduce heat dissipation and to ensure an adequate supply of fuel, in the form of metabolites from food, for heat production. Adaptations for survival can, therefore, be divided between those which help the animals to reduce their energy expenditure (and, hence, also to reduce their food requirements), which are the subject of this paper, and those which help them to make best use of what food they find (see Orpin, *et al.* 1985; Mathiesen, *et al.* 1987; Orpin and Mathiesen, 1990).

Reduction in energy losses

In reindeer and caribou, like other arctic homeotherms which maintain a high internal body temperature, the temperature difference between the body core and the environment may be as much as 100°C. Despite this they can maintain a very low lower critical temperature. Nilssen, Sundsfjord and Blix (1984a), for example, calculated that the lower critical temperature of Svalbard reindeer was approximately -40°C in winter (Fig. 1). Reindeer and caribou have two principal defenses against cold. First, they are very well insulated by fur and second, they restrict respiratory heat loss.

The insulative properties of fur depend on the inherent thermal conductivity of the individual hairs themselves and their collective ability to trap and hold a layer of air next to the skin. This is important because the conduct-

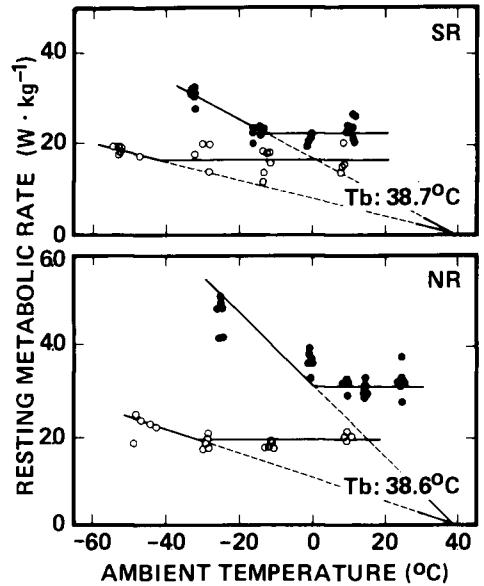


Fig. 1. Resting metabolic rate at different ambient temperatures during summer (●) and winter (○) in adult Svalbard (SR) and Norwegian (NR) reindeer fed *ad libitum*. Lines are fitted by eye to extrapolate through ambient temperature equal to deep body temperature (T_b). The animals' lower critical temperature in winter is approximately -40°C (SR) and -30°(NR). Note the pronounced reduction in the animals' resting metabolic rate in winter (from Nilssen, Sundsfjord and Blix, 1984a).

ivity of still air is less than half of that of most furs (Mount, 1979:92). Reindeer fur includes two types of fibers: long guard hairs and a fine underfur (Bohl and Nikolajewsky, 1931; Timisjärvi *et al.*, 1984). The insulative properties of the fur are enhanced both by the high density of fibres on the skin and by their special structure. Each guard hair is hollow, containing thousands of air-filled cavities separated by thin septa (Timisjärvi *et al.*, 1984).

In addition to excellent insulation by fur, reindeer and caribou defend themselves against cold by restricting heat and water loss from the respiratory tract. Respiratory heat loss can potentially account for a large proportion of total heat loss (Folkow and Mercer, 1986). In humans exposed to low ambient temperature but

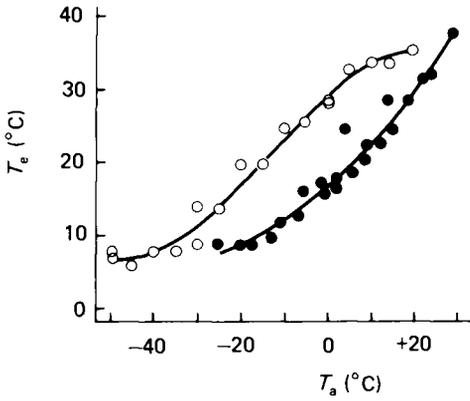


Fig. 2. Exhaled air temperature (T_e) in Norwegian reindeer over a range of ambient temperatures (T_a) in summer (●) and winter (○) (from Blix and Johnsen, 1983).

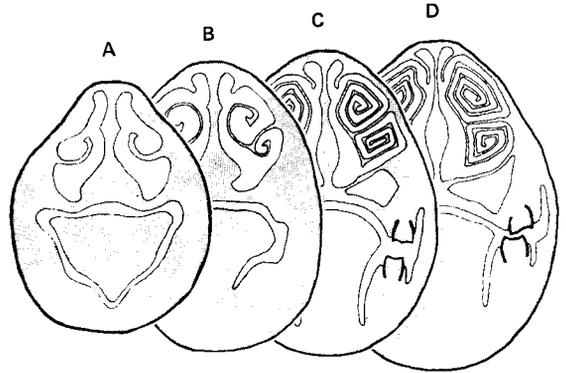
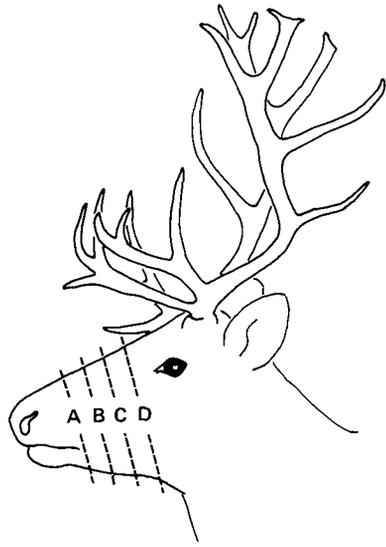


Fig. 3. Cross sections of the reindeer nose obtained at four different levels (A, B, C, and D). Sections were made at approximately 1 cm intervals and illustrate the elaborate organization of the maxilloturbinates which project into each nasal cavity from the lateral wall (from Johnsen, 1988).

warmly dressed and at rest, the lowest mean expired air temperature measured is approximately 26°C (Webb, 1951) and the heat lost in exhaled air may account for more than 20% of metabolic heat production (see Blix and Johnsen, 1983). In resting reindeer exposed to cold, by contrast, expired air temperature may be as low as 6°C, which is approximately 33°C below core temperature (Fig. 2). Hence, respiratory heat loss in these animals is much reduced. In fact, about 70% of the heat and 80% of the water added to the inspired air in the nose and lungs is regained upon expiration (Blix and Johnsen, 1983).

Such heat and water conservation in the nose is based on counter-current heat exchange in the nasal cavity (Jackson and Schmidt-Nielsen, 1964; Schmidt-Nielsen, 1981). The respiratory chamber of the nasal cavities of reindeer are filled with an elaborate system of scrolled structures (*conchae*, Fig. 3) which are coated with a richly vascularised mucosal layer (Parsons, 1971). Cold air which the animals breathe in passes over the warm mucosa and, as a result, is heated to body temperature and saturated with water vapour before it reaches the lungs. The nasal mucosa is cooled as a result

and, moreover, it stays cool while the air remains in the lungs. When the animals breathe out, the warm, humid air passes down a temperature gradient as it flows over the cold mucosa and is therefore both cooled and dried.

The *conchae* of the nasal cavity both increase the surface area over which heat exchange can occur and divide the air flow into thin layers. Consequently, the distance between the centre of the air stream and the mucosal surface is reduced to a minimum. Both factors, large surface area and short distance between adjacent

lamellae, promote rapid transfer of energy between the mucosal layer and the air stream. Nasal heat exchange is, nevertheless, not a passive process in reindeer. On the contrary, it is carefully regulated, enabling the animals to maintain thermal balance at widely varying ambient temperatures and work loads despite substantial seasonal changes in their fur insulation.

The first evidence for this is shown in Fig. 2. These data, from a study by Blix and Johnsen (1983), show that at any given ambient temperature (T_a) reindeers' expired air temperature is consistently lower in summer than in winter. The animals were evidently capable of adjusting the level of thermal exchange to conserve more heat at one and the same T_a in summer when they were relatively poorly insulated compared to in winter when their total body insulation was greatest. Johnsen, Blix *et al.* (1985) subsequently showed that nasal heat exchange is regulated by vasomotor adjustments in the nasal mucosa and that those changes are under central (hypothalamic) control (Mercer *et al.* 1985).

Reduction in energy expenditure

Metabolism

Good insulation and nasal heat exchange help reindeer and caribou to conserve energy by minimising dissipation of heat. Another potential way of reducing energy expenditure is to reduce the basal level of heat production itself. In winter, basal metabolism (BMR) accounts for between 50 and 70% of the normal daily energy expenditure of adult females (caribou: Boertje, 1985; Fancy, 1986; reindeer: Tyler, 1987a) and, consequently, even small reductions in metabolic rate would potentially contribute relatively large overall savings to the animals' energy budget.

Mammals' basal rate of metabolism is often assumed to be constant. This is not necessarily true although in many situations the approximation may be adequate. There are a variety of

circumstances in which BMR may fall below the predicted value. In several species, for example, BMR fluctuates with a pronounced diurnal cycle (Aschoff and Pohl, 1971). It may also fall in early pregnancy (Prentice and Whitehead, 1987), with increasing age (Kleiber *et al.* 1956) and during starvation (Keys *et al.*, 1950; Grande *et al.* 1958; Kleiber, 1975: 247; Markussen and Øritsland, 1986; Nordøy and Blix, 1985). Reduction in BMR during starvation, however, is fundamentally different from the reductions which occur during early pregnancy or with increasing age. The metabolic response to starvation is driven by a change in the individual's nutritional status. Reduction of BMR during pregnancy or with increasing age, by contrast, appears to occur independent of any such change.

The basal metabolic rate of several temperate and sub-arctic species of ungulates appears to fluctuate in anticipation of predictable changes in the quality and abundance of their food. Seasonal variation in animals' minimum energy expenditure has been recorded in domestic sheep (Blaxter and Boyne, 1982) and white-tailed deer *Odocoileus virginianus* (Silver *et al.*, 1969). Argo and Smith (1983) found that the interpolated metabolizable energy requirement for maintenance in Soay rams fell 25% from 6.1 W/kg $M^{0.75}$ in summer to 4.6 W/kg $M^{0.75}$ in winter (M = total body weight). A similar cycle, perhaps even more marked, might certainly be expected in arctic species such as Svalbard reindeer owing to the extreme seasonality of the food supply at high latitudes.

Rather surprisingly, however, and despite an earlier suggestion based on changes in blood levels of thyroxine which themselves appeared to indicate that the minimum metabolic rate of Svalbard reindeer might fall in winter (Ringberg, 1979), no experimental evidence has been found for such a drop, at least in captive animals (Nilssen, Sundsfjord and Blix, 1984a). The resting metabolic rate of reindeer fed *ad libitum* shows a marked reduction from summer

to winter (Fig. 1). This, however, is not in itself evidence of any seasonal change in the animals' minimum energy expenditure.

Reindeer, like many other species of ungulates (e.g. Kay, 1979), show pronounced seasonal changes in appetite (McEwan and Whitehead 1970; Fig. 4). Obviously, if an animal consumes more feed in summer than in winter, then its total heat production can be expected

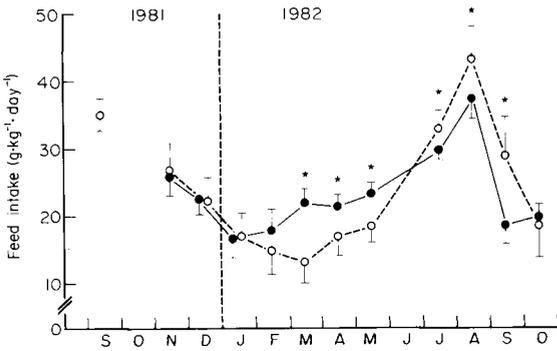


Fig. 4. Seasonal changes in voluntary food intake ($\text{g}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$) of captive Norwegian reindeer (●) and Svalbard reindeer (○) fed a concentrate ration *ad libitum*. The symbols represent mean values obtained during the middle ten days of each month and the bars represent standard deviation of the daily individual food intake. Asterisks denote significant differences (from Larsen, Nilsson and Blix, 1985).

to increase simply because there is a greater increment of heat associated with ingestion of the larger amount of feed. The significance of the seasonal changes in the metabolic rate of sheep and white-tailed deer is that they occurred independent of levels of food intake. These species, in other words, eat less in winter because their metabolic rate is reduced, not the other way around. This is the converse of the metabolic response to starvation (above): metabolism, in that case, falls as a consequence of reduced food intake. Nilssen, Sundsfjord and Blix (1984a) demonstrated a close relationship between metabolic rate and food intake in both Svalbard and Norwegian reindeer (Fig. 5).

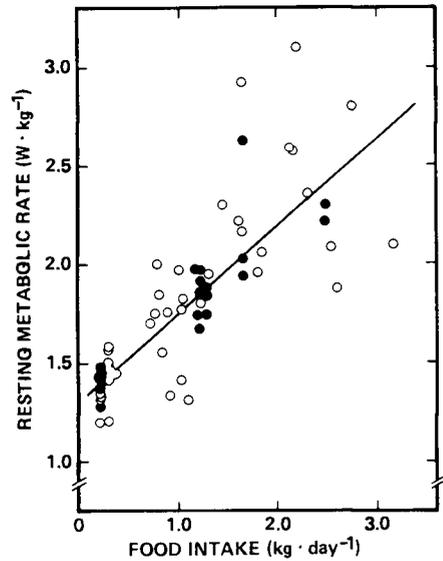


Fig. 5. Resting metabolic rate as related to daily food intake in adult Svalbard (○) and Norwegian (●) reindeer (from Nilssen, Sundsfjord and Blix, 1984a).

Furthermore, they found close agreement between the metabolic rate in reindeer based on linear extrapolation to zero food intake ($1.3 \text{ W}\cdot\text{kg}^{-1.0}$) and measured values ($1.4 \text{ W}\cdot\text{kg}^{-1.0}$). They concluded that seasonal variation in resting metabolic rate in *ad libitum* fed reindeer (Fig. 1) was due to changes in the animals' voluntary food intake and did not represent a physiological adaptation to energy conservation in winter mediated by a reduction in fasting metabolic rate (FMR).

Their conclusion was supported by observations made in a subsequent series of experiments on Norwegian and Svalbard reindeer in which Nilssen and his colleagues measured metabolism every second day for two weeks during which time the animals were given only 15% of their *ad libitum* food intake. As expected the animals' metabolism initially fell rapidly, reaching a stable minimum after 5 to 10 days. There were no differences between summer and winter minima in either sub-species (Nilssen, Sundsfjord and Blix, 1984b). Thus, it appears that there is no seasonal variation in FMR in reindeer.

Another arctic ruminant, the muskox *Ovibos moschatus*, provides an interesting contrast in this respect. These animals belong to a different taxonomic group (*Bovidae*, *Caprinae*) from deer (*Cervidae*). Muskox, unlike Svalbard reindeer, appear to have developed two metabolic adaptations to winter. First, their metabolic rate shows pronounced seasonal variation. FMR in adult female muskoxen fell approximately 20% from 3.0 W·kg M^{0.75} in summer to 2.4 W·kg M^{-0.75} in winter (Nilssen, Mathiesen and Blix, unpublished). Second, their FMR (lying) in winter appears to be almost 40% lower than the FMR (lying) of Svalbard reindeer (Table 1). The difference between these two high arctic species, as well as the difference between reindeer and sheep, is intriguing and deserves further attention.

Heart rate telemetry

All the measurements of metabolism discussed above were made by indirect calorimetry. An alternative technique involves monitoring ani-

mals' heart rate by radio telemetry. There exists a fairly linear relationship between oxygen uptake and heart rate under aerobic (steady-state) conditions, at least in tame, trained reindeer (Nilssen, Johnsen *et al.*, 1984) and it is therefore in principle possible to calculate energy expenditure in unrestrained animals from heart rate alone. Hitherto only one detailed study of the application of this technique has been carried out on *Rangifer* but the authors concluded that it is potentially useful, at least in winter (Fancy and White, 1986).

The technique has two drawbacks, however. First, as Fancy and White pointed out, the relationship between heart rate and oxygen consumption varies not only seasonally (see also Nilssen, Johnsen *et al.*, 1984) but is also individually variable in caribou, especially in summer. In reality, therefore, each animal tested must be calibrated separately. Second, and rather more fundamentally, there are circumstances in which the normal linear relationship between heart rate and oxygen consumption

Table 1. Fasting metabolic rate of different wild and domestic ungulates (all adults).

	Fasting metabolic rate (x M _b ^{0.75} kcal·day ⁻¹)			Source
Domestic sheep	48.6	W	F & C	(1)
Muskox	49.1	W	F	(2)
Cattle	76			(3)
Red deer	79	Sp	F	(4, 5)
Svalbard reindeer	80.3	W, S	F	(6)
Caribou	91	Sp	F	(7)
Roe deer	94.6	W		(8)
White-tailed deer	97.1	W	M & F	(9)
Interspecies mean	70			(10)

M_b: live body weight (kg).

M: males; C: castrates; F: females.

W: winter; Sp: spring; S: summer.

Sources: (1) Blaxter and Boyne (1982); (2) Nilssen, Mathiesen and Blix, unpublished; (3) ARC (1980); (4) Brockway and Maloiy (1968); (5) Maloiy *et al.* (1970); (6) Nilssen, Sundsfjord and Blix (1984a); (7) McEwan (1970); (8) Drozd *et al.* (1973); (9) Silver *et al.* (1969); (10) Kleiber (1975).

breaks down and during which heart rate may, in fact, considerably exceed the value predicted from the observed consumption of oxygen. This is called 'additional heart rate' (AHR) (Blix *et al.*, 1974; Strømme *et al.*, 1978). The physiological basis of this phenomenon is not known but it may be linked to some kind of psychological activation. This may explain why better results seem to be obtained with large, confident animals compared to small, nervous ones (Hudson and Christopherson, 1985). We know nothing about AHR in reindeer or caribou. Clearly, however, if AHR also occurs in these, then interpretation of data collected by telemetry from free-ranging animals would become considerably more difficult. Hudson and Christopherson concluded, somewhat pessimistically, that "there appears to be little hope of deriving suitable general regressions that could be applied to wild populations but the technique may be quite useful in studies with individually calibrated research animals" (*ibid.*).

Doubly-labelled water

One of the most interesting developments since the fourth Reindeer/Caribou Symposium has been the application in reindeer and caribou of the doubly-labelled water method for measuring energy expenditure (see Fancy, Blanchard, *et al.*, 1986). The method is based on the relative rates of decrease in the concentrations of two isotopes, $H_2^{18}O$ and either deuterated water (2H_2O) or tritiated water (3H_2O), in the total body water pool. A single dose of 'doubly-labelled water' is injected into an animal and the subsequent disappearance of each isotope is measured by taking serial blood samples normally over periods of up to ten days. ^{18}O in the body equilibrates between water and bicarbonate through the carbonic anhydrase reaction and the disappearance of the isotope therefore measures the sum of CO_2 and water fluxes. The water flux can be predicted independently from the rate of disappearance of the hydrogen isotope so that, in principle, the rate of CO_2

production can be calculated by difference. Energy expenditure is calculated from CO_2 production rates using standard calorimetric calculations (Lifson and McClintock, 1966; Nagy, 1980).

The advantage of the doubly-labelled water method over conventional techniques is that it can be used to measure the total energy expenditure of animals in their natural environments (e.g. Bryant and Westerterp, 1983; Gabrielsen, Mehlum and Nagy, 1987; Costa and Croxall, 1988) as well as to verify estimates based on additive models (e.g. Utter and Lefebvre, 1973; Weathers and Nagy, 1980; Williams and Nagy, 1984).

Application of the technique in ruminants is complicated in several ways owing to their specialised digestion. Unlike in monogastric species, for example, CO_2 produced by gut microbes can make a significant contribution to the animals' total CO_2 production. Furthermore, a relatively large proportion of total body water in ruminants is contained in the gut where it equilibrates only slowly with the rest of the body. Consequently, Fancy, Blanchard, *et al.* (1986) designed their study as a validation trial to compare apparent rates of CO_2 production (CDP) measured by the doubly-labelled water method with rates of CO_2 expiration (VCO_2) measured by open circuit respirometry.

Fancy and his colleagues circumvented problems related to slow equilibration of water between different compartments in the body by taking serial blood samples, rather than relying on the more simple 'two point' approach (Coward, Roberts and Cole, 1988). Their results showed that both CDP and VCO_2 were affected by CH_4 production. However, loss of 3H in CH_4 largely offset losses of CO_2 by reduction to CH_4 , so that the difference between methods was less than 2%. On the other hand, while the *overall* net difference between the two methods was 1.3% in one reindeer in winter, the difference in caribou in summer ranged from 5 to

20%. Part of the differences in summer were putatively attributed to net deposition of ^3H , ^{18}O and unlabelled CO_2 in growing antlers and other tissues. The authors concluded that the doubly-labelled water technique is a reasonably accurate method for measuring CO_2 production rates in reindeer and caribou, at least during periods of slow growth (i.e. winter), providing appropriate corrections are made.

Activity

Besides minimising heat loss in winter by means of increased insulation, reindeer and caribou can reduce energy expenditure by adopting appropriate behaviour; in particular, by reducing their total daily locomotor activity.

The daily energy cost of locomotion is influenced by three variables: the total distance which the animals travel per day, the overall distance which they climb and the nature of the surface over which they move. Two other variables, running speed and the angle of ascent, have less significance first, because the weight-specific net cost of climbing in ungulates appears to be independent of the angle of ascent, at least on moderate slopes (Fancy and White, 1985) and second, because in reindeer and caribou, like other terrestrial mammals, the relationship between running speed and the rate of energy expenditure is effectively linear (Taylor, Heglund and Maloiy, 1982; Parker, 1983; reindeer: Nilssen, Johnsen *et al.*, 1984). Consequently, the net cost of travelling a given distance is, for an animal of a given body weight, largely independent of the speed at which it moves.

The nature of the surface over which animals travel, on the other hand, has a very important influence on the cost of locomotion. White and Yousef (1978), for example, showed that reindeer expended 30% more energy when walking on wet tundra compared to on hard-packed roads. The costs of walking across soft or crusted snow are even higher and rise exponentially as the animals sink deeper. In one case, in

which a caribou sank to 60% of brisket height at each step, the relative net cost of locomotion increased almost six times (Fancy and White, 1985). The capacity of snow to support an animal depends on the hardness of the snow and the pressure (foot load) which the animal exerts on it. Thus, if snow hardness consistently exceeds foot loads, animals can walk on top of the snow or will sink to only a fraction of its total depth. The broad, spreading feet of reindeer and caribou, a well-known characteristic of this species, is clearly an adaptation to walking on snow, through minimising the extent to which they break through the crust and sink in. In fact, reindeer and caribou, with the exception of musk deer *Moschus moschiferus*, have the lowest foot load measured in any ungulate (Fancy and White, 1985).

The potential significance of reducing locomotion as a means of saving energy is made clear from Fancy and White's (1985) calculation that the costs of locomotion for a 90 kg caribou breaking the trail at the head of the spring migration will represent an increment to its minimal metabolism of 82%. For the animals following the packed trail in its wake, the incremental cost would be equivalent to about 33% of their minimal metabolism, a saving of more than half (Fancy and White, 1985). At the other extreme, Svalbard reindeer appear to be able to reduce their activity to a level at which the total daily energy cost of locomotion becomes almost negligible. These animals are typically sedentary, walking, on average, <0.7 km (net) per day in winter (Tyler and Øritsland, 1989) and rarely running at all unless provoked. The daily cost of locomotion amounts to only about 2% of their daily energy expenditure (DEE) (Tyler, 1987b). In barren-ground caribou which, by contrast, travel on average approximately 5 km per day in winter (Fancy *et al.*, 1988), the energy cost of locomotion is correspondingly higher: approximately 8% of DEE (Boertje, 1985; Fancy, 1986).

Selective cooling of the brain

The net energy cost for an animal of given body weight moving from one place to another is largely independent of the speed at which it travels. This begs the question: Why don't reindeer always run? The answer is that the insulation which enables them to survive under extremely cold conditions predisposes them to heat stress if they exercise hard and presumably the costs of thermoregulation outweigh any potential saving.

Heat production in reindeer increases very rapidly with increasing running speed. The rate of heat production in Svalbard reindeer trotting at 8 km/h, for example, is four times higher than the rate of heat production when standing (Nilssen, Johnsen *et al.*, 1984; Fig. 6). Hot reindeer can increase heat loss both by peripheral vasodilation (Johnsen, Rognmo *et al.*, 1985) and by respiration which, by making appropriate vascular adjustments in the nasal mucosa, may be used to conserve or to dissipate heat (Johnsen, Blix *et al.*, 1985). Nevertheless, if an animal runs hard during winter, perhaps because it is being chased by a predator, it can soon reach a stage at which it produces heat more rapidly than it can lose it, with the consequence that body temperature rises (e.g. Johnsen, Rognmo *et al.*, 1985). It would be advantageous, in terms of survival, to be able to prolong the length of time it can maintain a high degree of physical activity, but to do so requires that thermally sensitive tissues, such as the brain, are protected.

Several species in the orders *Artiodactyla*, including reindeer, *Carnivora* and *Cetacea* have developed a system which enables them selectively to cool their brain tissue independently of the rest of the body core (Johnsen *et al.*, 1987). The principle of selective brain cooling is illustrated in Fig. 7. During mild heat-stress, venous blood, cooled at the evaporative surfaces of the nose, flows via the facial vein directly to the caval veins and is used for general body cooling. If the heat stress becomes severe, however,

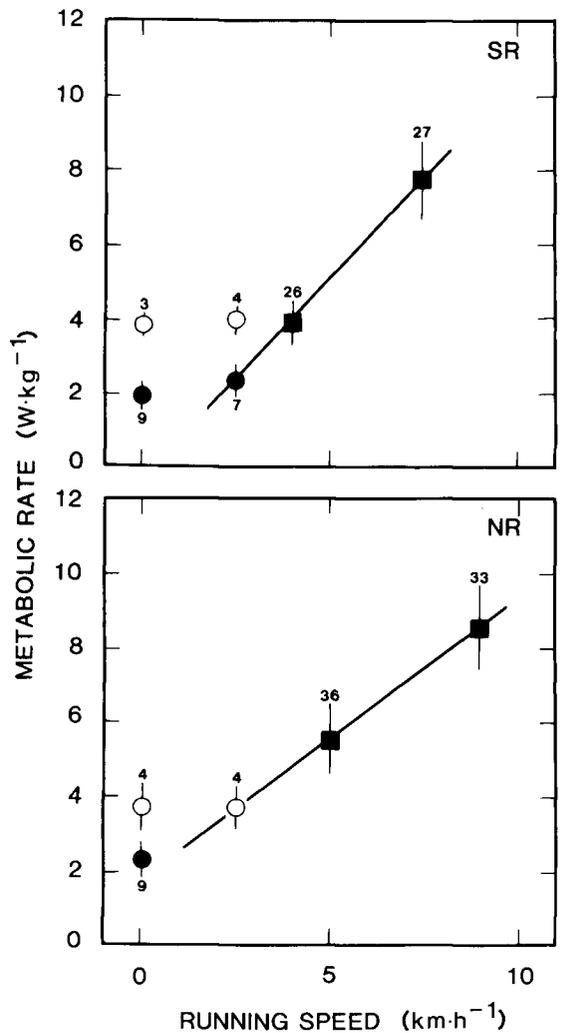


Fig. 6. Relationship between metabolic rate and running speed in Svalbard reindeer (SR) and Norwegian reindeer (NR). Symbols represent energy expenditure at different ambient temperatures: -24°C in summer (o) $+9^{\circ}\text{C}$ in summer, $+8^{\circ}\text{C}$ and -30°C in winter (■); all temperatures/seasons (■). The numbers above each symbol represent the number of measurements in two animals. Vertical bars indicate standard deviation (from Nilssen, Johnsen, Rognmo and Blix, 1984).

the facial vein is closed off and the cooled blood is directed, instead, through the *angularis oculi* veins to a venous sinus at the base of the brain (Fig. 8). Here heat is exchanged with warm blood in the carotid artery, into which a *rete* is

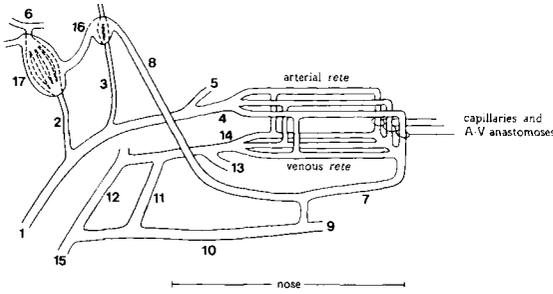


Fig. 7. Arterial and venous vasculature of reindeer nose. During heat conservation, blood may run countercurrent in the two *retia* and leave the nasal mucosa through the sphenopalatine group of veins (14), with the dorsal nasal vein (7) constricted. During heat dissipation, however, blood may run unidirectionally in both *retia* and leave the nasal mucosa by way of the dorsal nasal vein (7), and the sphenopalatine group of veins (14) would now be constricted. In this way heat dissipation by way of the respiratory tract is optimized, and cooled venous effluent may be directed, either via the facial vein (10) to the external jugular vein (15) for general body cooling or via the angular oculi veins (8) to the ophthalmic plexus (16) and the cavernous sinus (17) for selective cooling of arterial blood to the brain. 1, common carotid a.; 2, arterial supply to carotid *rete*; 3, arterial supply to orbital *rete*; 4, sphenopalatine a. with its branches; 5, infraorbital a.; 6, circle of Willis; 7, dorsal nasal v.; 8, angular oculi v.; 9, maxillary labial v.; 10, facial v.; 11, deep facial v.; 12, maxillary v.; 13, infraorbital v.; 14, sphenopalatine group of veins; 15, external jugular v.; 16, ophthalmic venous plexus with orbital *rete* (dashed lines); 17, cavernous sinus with carotid *rete* (dashed lines) (from Johnsen, Blix, *et al.*, 1985).

inserted to facilitate heat transfer (Fig. 9). The result of this is that the brain is cooled selectively while heat is stored (as an increase in temperature) in the rest of the body - to be dissipated subsequently when the stress is past.

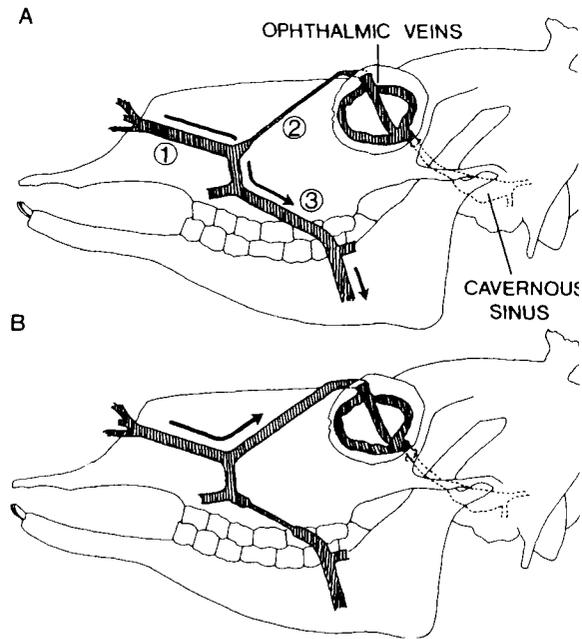


Fig. 8. Schematic diagram of superficial veins of nose and their connections with the cavernous sinus at the base of the brain in relation to the outline of the skull in reindeer. Figures illustrate the proposed mechanism for distribution of cold blood from nose of hyperthermic reindeer. A: operation of mechanism during moderate heat stress, where cold venous effluent from the mucosal lining of the nasal surfaces returns to the caval veins via the facial veins (\rightarrow), thus by-passing the cavernous sinus. It is suggested that the direction of venous return through this pathway is due to sympathetic stimulation of the angular oculi and facial veins, which results in release of pressure-induced inherent myogenic tone in the facial veins and simultaneous constriction of the angular oculi veins. In contrast, when body temperature exceeds the threshold value for onset of brain cooling, sympathetic activity to the veins in question is reduced. This will result in dilatation of the angular oculi veins and activation of inherent myogenic tone in the facial veins (B). In this situation cold blood returning from nose is directed mainly to the cavernous sinus for selective cooling of the brain (\dashrightarrow); 1, dorsal nasal vein; 2, angular oculi vein; 3, facial vein (from Johnsen and Folkow, 1988).

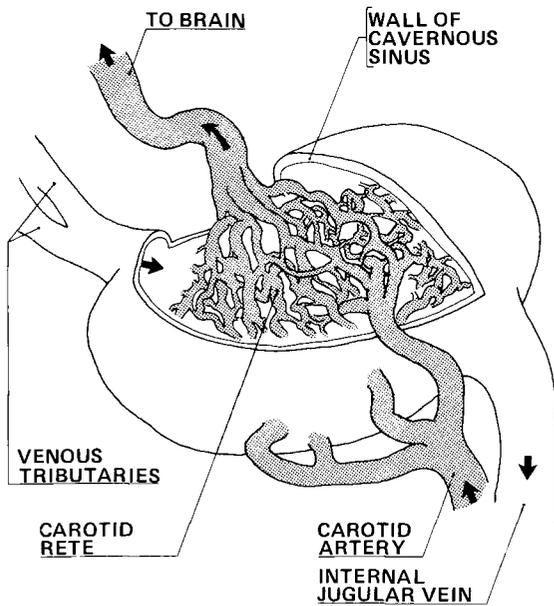


Fig. 9. Carotid *rete* of a sheep exposed in a cutaway drawing. This structure lies at the base of the brain. Cool venous blood, draining from the nose, enters an enlargement of the venous tributaries called the cavernous sinus. Here it bathes a network of small arteries called the carotid *rete*, which is inserted into the carotid artery, and leaves via veins that enter the internal jugular vein at the right. At the same time warmer arterial blood arriving from the heart enters the *rete* via branches of the external carotid artery and is subsequently cooled by the venous effluent before continuing up to the brain. Selective cooling of the brain normally occurs only when animals sustain hard exercise and therefore are in danger of overheating (redrawn from Baker, 1979).

Appetite and growth

The central concept in most models of animal energetics is animals' 'maintenance energy requirements' (e.g. Hudson and Christopherson, 1985). This, together with the concept of 'energy balance', has become so familiar that there is sometimes a tendency to consider maintenance of energy balance almost as an end in itself, if not actually synonymous with survival. How-

ever, wild reindeer and caribou, like many other arctic species, normally lose weight throughout winter (Fig. 10, Table 2). Evidently, they can survive perfectly well despite being in negative energy balance for months at a time. Clearly, therefore, maintenance of energy balance *per se* is not a prerequisite for survival. Moreover, an important point which is often ignored, is that slowed growth and even weight loss are not necessarily consequences of undernutrition.

Loss of weight during winter is still frequently regarded as diagnostic of undernutrition despite experimental evidence that this is not necessarily so (e.g. Mortensen and Blix, 1985; Mrosovsky and Sherry, 1980). Several species of cervids show a pronounced seasonal cycle of appetite and growth which appears to follow an intrinsic rhythm, entrained by photoperiod and associated with changes in levels of circulating hormones. These cycles, which have been described in detail in red deer *Cervus elaphus* (e.g. Brown *et al.*, 1979; Kay, 1985; Pollock, 1974; Suttie and Simpson, 1985), seem also to occur in reindeer and caribou. In winter their appetite falls by as much as 70% of autumn values (Larsen, Nilsson and Blix, 1985), growth slows or even stops (Ryg and Jacobsen, 1982a; McEwan, 1968) and the animals begin to mobilize their fat reserves even when good quality food is freely available (e.g. Larsen, Nilsson and Blix, 1985).

Interpretation of patterns of growth and weight loss in free-ranging animals is complicated by the difficulty of distinguishing the effects of spontaneous anorexia (a voluntary reduction in food intake) from the effects of involuntary starvation (true inanition). Nevertheless, it is interesting to note that a marked difference exists between the sexes in the phasing of the weight cycle (Dauphiné, 1976; Leader-Williams and Ricketts, 1982), an observation which strongly implicates the influence of some intrinsic control. Surprisingly, however, as Leader-Williams and Ricketts (1982) pointed out, the total weight of pregnant caribou kept

Table 2. Comparison of seasonal maximum and minimum mean total body weights (kg) and the proportional (%) loss of weight in adult female reindeer and caribou from different populations.

Locality/latitude	Stock/sub-species	Total body weight (kg)		Weight loss in winter (%)	Source
		Max.	Min.		
Svalbard 78° N	Wild reindeer ^a	63	45	29	Tyler (1987a)
Canada 62° N (Coats Island)	Barren-ground caribou	89	73	18	Adamczewski <i>et al.</i> (1987)
South Georgia (Busen) 54° S	Introduced reindeer	90	78	13	Leader-Williams (1988)
Norway 60° N (Hardangervidda)	Wild reindeer	54	48	11	Reimers (1980)
Canada 60° N (Kaminuriak)	Barren-ground caribou	90	80	11	Dauphiné (1976)
Finland 68° N	Domesticated reindeer	66	59	11	Nieminen (1980)
Alaska 65° N	Caribou	110	100	9	Boertje (1985)

^a ≥ 4 years old.

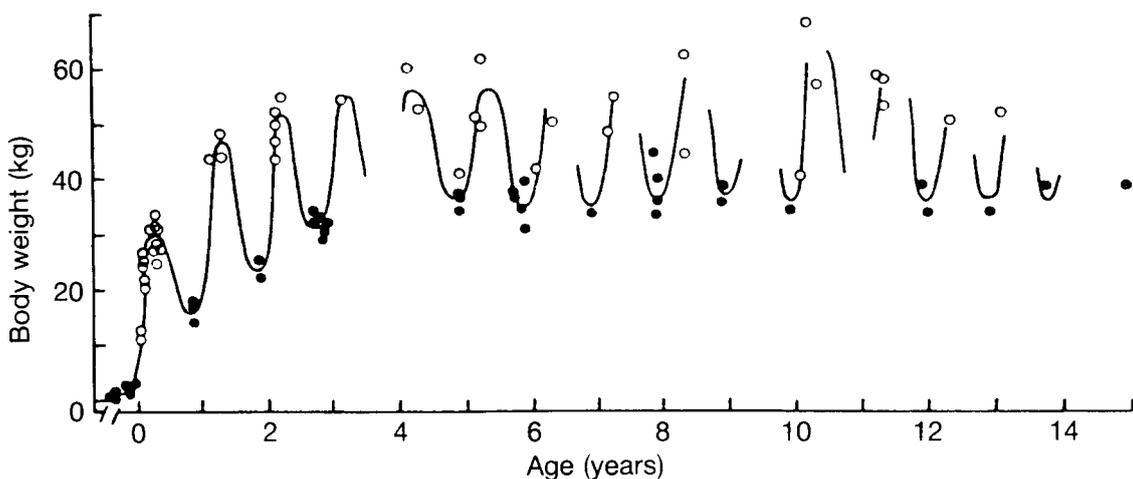


Fig. 10. Growth curve for female Svalbard reindeer. Total body weight (kg) less the weight of the reticulorumen (all specimens) and the weight of the uterus and its contents (winter specimens). Each point represents one reindeer. Summer and autumn (July to October) (o); late winter (April to May) (●), from Tyler, 1987b).

in captivity and fed *ad libitum* appeared to decrease at the beginning of winter, in phase with that of males. It is not clear why captive deer should differ so fundamentally from their free-ranging counterparts.

Intrinsic cycles of growth and fattening

appear to be adaptations for survival in seasonal environments in which animals are confronted with long, predictable periods of potential undernutrition. Slowed rate of growth and, to an even greater extent, actual loss of weight have the effect of reducing an animal's daily

Table 3. Total fat content (% live weight) of different wild ungulates^a.

Species/breed	% fat	Source
<i>Tropical (savannah)</i>		
Topi ^b	1.0 D	Ledger (1968)
Impala ^b	1.2 D	Ledger (1968)
Kob ^b	2.3 D	Ledger (1968)
Thomson's gazelle ^b	2.8 D	Ledger (1968)
Grant's gazelle ^b	3.0 D	Ledger (1968)
Wildebeest ^b	3.9 D	Ledger (1968)
<i>Temperate/sub-arctic</i>		
Norwegian reindeer ^c	3.5 E	Reimers, <i>et al.</i> (1982)
Red deer ^d	4.5 D, E	Blaxter <i>et al.</i> (1974)
Red deer ^e	5.2 D	Wallace & Davies (1985)
Red deer ^f	5.7 E	Kay <i>et al.</i> (1981)
Mule deer ^g	6.5 E	Field <i>et al.</i> (1979)
Chinese water deer ^h	6.9 D	Pond & Mattacks (1985)
Fallow deer ⁱ	7.1 E	Gregson & Purchas (1985)
North American elk ^j	7.8 E	Field <i>et al.</i> (1980)
Roe deer ^k	8.3 E	Weiner (1973)
White-tailed deer ^l	9.5 E	Robbins <i>et al.</i> (1974)
<i>Arctic</i>		
Barren-ground caribou ^m	13.5 D	Adamczweski <i>et al.</i> (1987)
Svalbard reindeer ⁿ	16.8 D	Tyler (1987b)
Svalbard reindeer ^o	28.7 D	Reimers <i>et al.</i> (1982)

^aMostly females. Values for males are mostly post-rut; the purpose of the Table is to compare the relative size of the energy reserves prior to winter, not the maximum fatness which different species can attain *per se*.

^b Adult females (all species), wild.

^c Yearling males, domesticated but free-ranging, August.

^d One 2-year-old stag, captive, post-rut.

^e Males, captive, post-rut (% carcass weight).

^f Yearling females, captive, autumn (% dressed weight).

^g Females \geq 2.5 years old.

^h Two males & two females; mean of the fattest and thinnest, captive.

ⁱ Males aged 26 months, captive, pre-rut.

^j Females \geq 2.5 years old.

^k Adult females, wild, February.

^l Adult females, captive, autumn (% ingesta-free body weight).

^m Females aged \geq 4 years (n=4), November (island population).

ⁿ Females aged \geq 4 years (n=13), September and October.

^o One 2-year-old female, August.

D Dissectible fat.

E Chemically extractable fat.

energy requirements (see Tyler, 1987b). This may be literally vitally important in winter when food is not only scarce and of poor quality but is also energetically expensive to acquire. The

endocrine control of appetite and body weight cycles in ungulates is not fully understood (e.g. Nilssen, Bye, *et al.*, 1985; Ryg and Jacobsen, 1982a,b). Nevertheless, it is clearly misleading

to regard the body weight of reindeer and caribou simply as the product of some precarious balance between food intake and energy expenditure (see also King and Murphy, 1985). Seasonal changes in body weight should be thought of, instead, primarily in terms of intrinsic cycles of growth and fattening mediated by appropriate changes in appetite (Kay, 1985; Ryg, 1983; see also Mrosovsky and Powley, 1977) rather than in terms of passive responses to seasonal changes in the quality, abundance and availability of food.

Fat

Knowledge of seasonal changes in body composition of reindeer and caribou has increased considerably during the last 20 years. One of the earliest, and still one of the best descriptive studies was made on the barren-ground caribou of the Kaminuriak herd by Dauphiné (1976) in the late 1960s. Subsequently, Cameron and Luck (1972) and Ringberg *et al.* (1981) worked on reindeer in Alaska and Krog *et al.* (1976) and Reimers *et al.* (1982) studied Svalbard reindeer. Reimers *et al.* (1982) showed, in particular, that fat accounted for almost 30% of live weight in a sub-adult female in late summer; the mean total fat content of *adult* females is rather less, however, accounting for approximately 17% of live weight (Table 3). Interestingly, Coats Island caribou fatten almost to the same extent; the mean total fat content of adult females in autumn is approximately 13.5% of their live weight (Table 3).

These studies have greatly increased our knowledge of the anatomy of adipose tissue in reindeer and caribou but the actual function of fat reserves, curiously, is still far from clear.

Many animals which live in highly seasonal environments store large amounts of energy as lipid droplets in adipose tissue during summer and autumn in anticipation of food shortage during winter. In hibernating species fat deposits may constitute up to 35% of the animals' total body weight (e.g. Linsdale, 1946; Pond and

Mattacks, 1985; Wienland, 1925). Ungulates, by contrast, usually store relatively little fat. The fat deposits of temperate and sub-arctic cervids, for example, represent usually only between 4-10% of total body weight in autumn (Table 3).

Such low values cast doubt over the widely held view that fat is a major source of energy for deer and other ungulates in winter. Even using the most conservative models of energy expenditure it seems unlikely that the fat reserves of female Svalbard reindeer, for example, could contribute more than 10-25% of the animals' energy demands during winter (Mathiesen *et al.*, 1984; Tyler, 1987b). In practice, the contribution from fat is likely to be lower than these models predict because reindeer which survive winter do not normally use up all their fat (Tyler, 1987a,b). Moreover, there is increasing evidence that the principal role of fat reserves in ungulates is to enhance reproductive success, rather than to provide a substitute for poor quality winter forage (although the very presence of fat will necessarily also provide insurance against death during periods of acute starvation).

Substantial pre-rut fat reserves, for example, enable male deer to gather, defend and serve their harems without being distracted by the need to feed and, in several species, males hardly eat at all for two or three weeks during the rut (Clutton-Brock, Guinness and Albon, 1982; Rapley, 1985; Thomson, 1977; Skogland, 1974). Consequently, in many species, mature bulls use up much of their fat before the start of winter (caribou: Dauphiné, 1976; white-tailed deer: Johns, *et al.*, 1982; reindeer: Leader-Williams and Ricketts, 1982; red deer Mitchell, McCowan and Nicholson, 1976; Wallace and Davies, 1985). None of these species, however, usually store large amounts of fat (Table 3). Svalbard reindeer bulls are very fat in autumn. As expected, they lose weight during the rut but, unlike bulls of mainland sub-

species, they still have substantial reserves when it is over (mean rump fat depth at the end of November = 42 mm, n = 3; Tyler, unpublished data). Nevertheless, the pattern of the fat cycle in Svalbard reindeer is similar to that of other sub-species of *Rangifer* and after the rut females are about 30% fatter than males.

It is more difficult to distinguish between alternative roles (reproduction and food supplement) for fat reserves in female ungulates because, in many species, these are pregnant throughout winter. Nevertheless, pregnant females may delay mobilisation of their fat reserves until the end of gestation, or early lactation, which normally occurs in spring or early summer, sometime after the period of maximum food shortage (Caughley, 1970; Dunham and Murray, 1982). Kay (1985) suggested that the principal role of fat reserves in females may be to supplement (but not to substitute for) their food intake during late pregnancy.

Recently, Tyler (1987b) found evidence of a marked difference in the pattern of mobilisation of fat between pregnant and non-pregnant female Svalbard reindeer. Pregnant animals appeared to become increasingly less dependent on their reserves as winter advanced, not only losing weight more slowly during the last two months of winter, when food availability was lowest, compared to the preceding six months but, also, losing it more slowly than non-pregnant females despite presumably having substantially increased energy requirements at that time. Thus, it appears that at the end of winter pregnant Svalbard reindeer, like certain temperate and tropical species of ungulates, spare their remaining fat reserves in anticipation of the energy demands of lactation. How they achieve this and how such a mechanism might be controlled is unknown (see Tyler, 1987b). Nevertheless, in the high arctic, where the spring melt can be delayed by several

weeks, a large store of fat with which to support lactation is likely to be very important both for ensuring the survival of newborn calves and for promoting their growth.

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