Thermoregulation in reindeer

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Abstract: Thermoregulation was studied in Finnish reindeer (*Rangifer tarandus* L) on captive and herded individuals during 1977-85. Newborn calves maintained a high rectal temperature (Tre) (+39-41°C) even at —23°C by increasing heat production 5- to 6-fold through non-shivering thermogenesis, stimulated by cold-induced noradrenaline (NA). Plasma NA and thyroxine (T4) were high (18 ng/ml and 459 nmol/l) in neonatal reindeer. Sensitivity to exogenous NA was lost during the first 3-4 weeks of life. At +20°C and above, calves increased Tre (ca 1°C), oxygen consumption and heart rate, thereby showing poor heat tolerance. Thermal conductance was low in a cold environment, but rose sharply as ambient temperature (Ta) increased above +10°C. The Tre of adults (+38-39°C) was independent of Ta (—28 to +15°C). Coarse (hollow) hair density and length in adults averaged 2000/cm^2 and 12 mm on the legs, 1000/cm^2 and 30 mm on the abdomen and 1700/cm^2 and 30 mm on the back (calves 3200/cm^2, 10 mm), respectively. The dependence of skin temperature on the Ta was linear in excised fur samples, but complex in living animals being strongest in the legs. Serum adrenaline correlated with the weight, age and total lipids. Serum NA and dopamine-ß-hydroxylase were highest in spring and decreased by autumn. Serum T4 was highest in summer and lowest in spring.

Key words: thermoregulation, insulation, catecholamines, reindeer.

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Introduction

The semi-domestic Finnish reindeer *(Rangifer tarandus tarandus* L.) is well adapted to wide seasonal changes in climate, nutrition and photoperiod in the subarctic. Seasonal thermoregulation involves changes in insulation and metabolism. Energy expenditure is lower in winter than in summer and metabolic requirements of thermoregulation are minimal. Heat is saved by effective fur insulation and peripheral heterothermia of the extremities (Irving and Krog, 1955). Consequently, the reindeer endures cold as severe as —62°C without evident difficulty (Gultsjak, 1954).

Calving begins in late April, when pastures are still snow covered. Survival of the calves in the harsh postnatal environment demands the maintenance of a high body temperature. Primary protection against cold is provided by a birth fur. Further, heat production by metabolism of brown adipose tissue, or non-shivering thermogenesis (NST), is assumed to play an important part in cold resistance in neonates (Hissa *et al.*, 1981). Little is known about the heat tolerance of reindeer calves. Hot midsummer weather may cause them considerable heat stress,as it does for adult reindeer.

In this paper we report thermal and metabolic responses of reindeer calves to various ambient temperatures (Ta) during their first weeks of life (Soppela *et al.*, 1986). The structure and insulative properties of reindeer fur and blood chemical constituents that may have thermoregulatory significance are also studied based mainly on works by Nieminen *et al.* (1984) and by Timisjärvi *et al.* (1984).

Material and methods

Thermoregulatory capabilities of 51 (50M + 1F) reindeer calves aged 1 to 35 days were studied at the Kaamanen Reindeer Research Station, Finland (69°10' N) in 1981 and 1982. Calves were divided into four age classes: 1-4, 6-9, 16-18 and 27-35 days. Measurements were performed in a metabolic chamber, in which the temperature (Ta) was stepwise decreased or increased in the range —27 to +35°C. At each Ta, stabilized recordings of rectal temperature (Tre), skin temperature (Ts) at various locations, oxygen consumption (VO_2), heart rate and muscle shivering (EMG) were monitored (Hissa *et al.*, 1981; Soppela *et al.*, 1986). Heat loss was estimated by calculating thermal conductance according to the equation of McNab (1980). Non-shivering thermogenesis (NST) was tested by injecting noradrenaline (NA) subcutaneously in newborn and growing reindeer calves at different Ta's.

Fur structure in six adults and four newborn calves was examined using light and scanning electron microscopy. Skin samples were collected from the back, abdomen and foreleg in adults and from the back in calves. Rectal (Tre) and skin temperatures (Ts) at four locations (foreleg, back, abdomen and muzzle) were measured for 216 animals (74 hinds, 142 calves, F, M) at varying Ta's (—28 to +15°C) and seasons in several reindeer herding districts during 1977-82. Ts on excised skin samples were measured *in vitro* attached to a heat sink in the laboratory (Timisjärvi *et al.*, 1984).

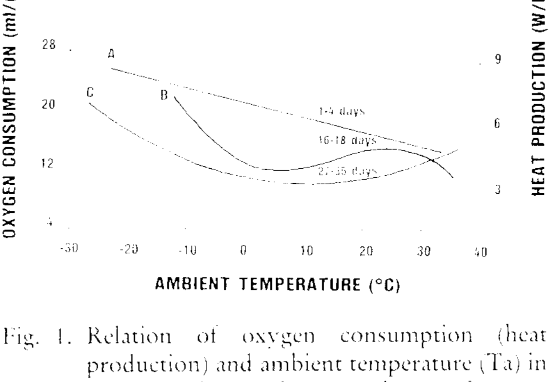

Fig. 1. Relation of oxygen consumption (heat production) and ambient temperature (Ta) in reindeer calves in three age classes, after a 30 min exposure to a given Ta. The goodness of fit of polynomial regression was checked by an F-test after each increment of the polynomial degree. (y = oxygen consumption and x = Ta)(modified from Soppela *et al.* (1986)).

Blood glucose and lactate, serum total lipid and triglyceride, thyroxine (T4), adrenaline (A) and NA concentrations and serum dopamine-ß-hydroxylase activity (DBH) were studied in 61 hinds and 81 calves at the Research Station and in several reindeer herding districts during 1977-78. Calves varied in age from 1 day to 10 months; hinds 3-10 years. Ta varied from —28°C to +14°C. Reindeer were penned outside with ample fodder or they grazed freely on pastures. Blood samples were taken from the jugular vein and kept frozen at —20°C until analyzed (Nieminen *et al.*, 1984).

Results

Calves aged 1-4 days maintained a high Tre (+40.2°C) even at —22.5°C by increasing oxygen consumption (VO_2) linearly as Ta decreased (Soppela *et al.*, 1986) (Fig. 1, $r=-0.396$, $n=66$, $P<0.001$). VO_2 varied from 5.7 ml/(min.kg) at +11.0°C to 38.8 ml/(min.kg) at 14.5°C. In calves 16-18 and 27-35 days old VO_2 rose at a lower Ta than in the newborns, but increased 3-fold above the resting level (Fig. 1). Tre remained independent of the Ta. Ts on the forefoot, lumbar and interscapular areas, however, followed changes in Ta. Thermal conductance values in calves aged 1 to 35 days were low at low Ta's, but rose strongly as Ta increased above +10°C (Fig. 2). At Ta above +20°C, VO_2 and heart rate increased sharply and Tre rose approximately 1°C. Calves panted rapidly when removed from the metabolic chamber. Compared with the resting level, VO_2 of calves aged 1-4 days increased 4- to 5-fold and nearly 2-fold in older calves.

Shivering thermogenesis in calves aged 1-4 days was weak and infrequent but it became stronger at low Ta's and attained 50-60 µV. Injection of NA caused a sharp increase in both Tre and VO_2 (Soppela *et al.*, 1986). The colder the Ta, the smaller the effect of NA on heat production. The endogenic NA-induced non-shivering thermogenesis of newborn calves was highest at —15.7°C, which thus appears to be their critical Ta (cf. Hissa *et al.*, 1981). The responses of older calves (7, 16 and 27 days) to NA injection were less than in the newborns.

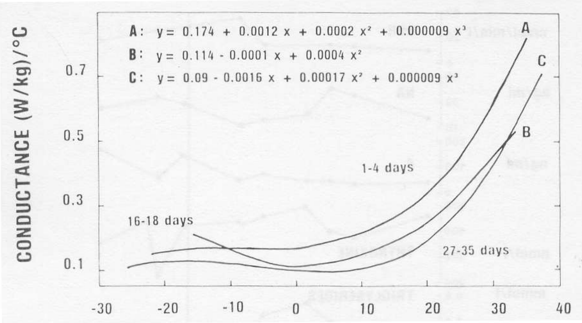

Fig. 2. Relation of thermal conductance to ambient temperature (Ta) in reindeer calves in three age classes, after 30 min exposure to a given Ta. The goodness of fit to polynomial regression was checked by an F-test after each increment of the polynomial degree. (y = thermal conductance and x = Ta)(modified from Soppela *et al.*, (1986)).

NA sensitivity disappeared during the first 3-4 weeks of life (Fig. 3, r=-0.954, n=8, $P<0.001$). Mean Tre over the Ta range +8 to +22°C was highest in newborn calves (+40.3±0.15°C, n=17). It decreased significantly ($P<0.001$) during the first 2 weeks but rose again to +40.0±0.23°C (n=5) in calves about 1-month old (Fig. 3). Mean thermal conductance was greatest (0.32±0.026 (W/kg)/°C, n=11) in calves aged 1-4 days, whereafter it decreased significantly (P <0.001) to the lowest value of 0.17±0.077 (W/kg)/°C, n=5) in calves 1-month of age.

The winter fur of adult reindeer consisted of thick guard hairs with air-filled cavities and an underfur of thin and woollen hairs. There was no variation in thickness between the back and abdomen fur, but foreleg fur was thinner (P <0.001). The density and length of guard hairs varied considerably and averaged 2000/cm^2 and 12 mm on the legs, 1000/cm^2 and 30 mm on the abdomen and 1700/cm^2 and 30 mm on the back (Timisjärvi *et al.*, 1984). The corresponding counts on the back of calves were 3200/cm^2 and 10 mm. The guard and woollen hairs in calves could not be discriminated. All hairs were wool-like and hollow. The Tre of adults averaged +38.9.±0.2°C and was independent of Ta. Decreases in Ta were followed by decreases in Ts, which were largest in the foreleg and muzzle areas. The behaviour of Ts in calves was similar to that of adults. Ts *in vitro* showed a linear dependence on Ta (Fig. 4). When the wind (10 m/sec) blew along the lay of the back fur, Ts decreased by 1.6°C at +20°C, by 6.7°C at 0°C and by 9.5°C at —20°C. Ts was lowest when the wind blew against the fur at an angle of 45° or perpendicular to the fur. There was a close correlation between surface Ts and thickness of the fur.

Seasonal blood composition (Fig. 5) revealed that blood glucose and lactate concentrations did not correlate with age, weight or Ta. No correlation was found between serum total lipid or triglyceride concentration and age, weight or Ta (Nieminen *et al.*, 1984). In adults total lipids and triglyceride were lowest in spring and highest in autumn ($P<0.001$). Serum total lipids increases significantly ($P<0.01$) in the neontal reindeer. Serum thyroxine (T4) level was not correlated with weight, age or Ta. In adults T4 showed significant ($P<0.001$) seasonal differences except between autumn and winter. T4 was high at birth, whereafter it decreased during the first weeks, then increased towards autumn ($P<0.05$). Serum adrenaline (A) correlated

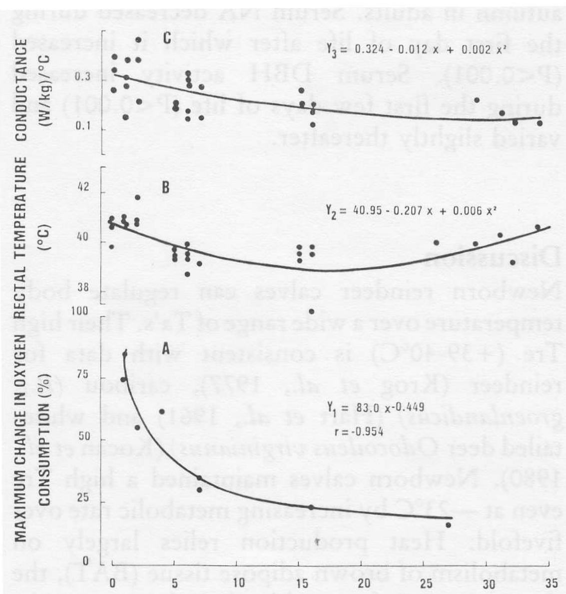

Fig. 3. A. Metabolic response to subcutaneous injection of noradrenaline (0.2 or 0.4 mg/kg) in 1 to 27 days old reindeer calves at 0°C.
B. C. Changes in rectal temperature (Tre) and thermal conductance with age in 1 to 35 days old calves at +8-22°C. (y1 = maximum change in oxygen consumption, y2 = Tre, y3 =thermal conductance and x = age in days)(modified from Soppela *et al.*, (1986)).

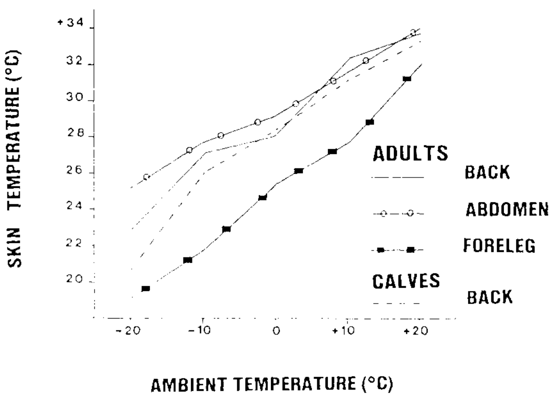

Fig. 4. Skin temperature of excised fur samples of adult reindeer and reindeer calves at various ambient temperatures.

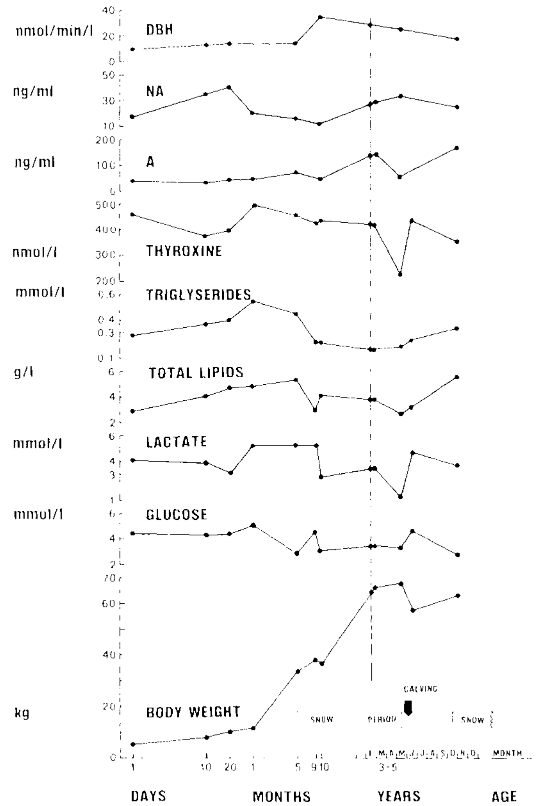

Fig. 5. Changes in body weight and blood constituents in reindeer with age and season. Filled circles represent measurement means.

positively with body weight (P<0.001), age (P<0.001), and total lipids (P<0.05), but not with Ta. Serum A varied (P<0.001) seasonally in adults. Serum NA was not correlated with other parameters. Both NA and dopamine-ß-hydroxylase (DBH) were highest in spring (P<0.01 and P<0.001) and decreased towards autumn in adults. Serum NA decreased during the first day of life after which it increased (P<0.001). Serum DBH activity increased during the first few days of life (P<0.001) and varied slightly thereafter.

Discussion

Newborn reindeer calves can regulate body temperature over a wide range of Ta's. Their high Tre (+39-40°C) is consistent with data for reindeer (Krog *et al.*, 1977), caribou *(R.t. groenlandicus)* (Hart *et al.*, 1961) and white-tailed deer *Odocoileus virginianus)* (Kocan *et al.*, 1980). Newborn calves maintained a high Tre even at —23°C by increasing metabolic rate over fivefold. Heat production relies largely on metabolism of brown adipose tissue (BAT), the tissue source of non-shivering thermogenesis, which is stimulated by the cold-induced NA release. The high energy content of reindeer milk supports a high metabolic rate and rapid growth. Shivering thermogenesis seems to be less important in the heat production of calves, as only weak shivering was found, mainly in newborns. Newborn reindeer calves shiver intensively immediately after birth until their birth fur is dry (Krog *et al.*, 1977).

Disappearance of NA sensitivity during the first month of life possibly reflects the concomitant loss of BAT. Growing reindeer calves appear to be more stressed by heat than by cold exposure as indicated by the increase in Tre at high Ta's. Poor heat tolerance was seen also in the strong increase in oxygen consumption and heart rate in a warm environment. Precise Ta leading to heat stress can not be given, since there is no real thermoneutral zone in a neonatal animal. In yearling reindeer Yousef and Luick (1975) found +35°C to be a critical Ta, when water was available *ad libitum*. Most of the heat load in reindeer, as in many other mammals with thick fur, is dissipated by evaporation through the respiratory tract. The great increase in oxygen consumption in reindeer calves at high Ta may result from the high energy demands of panting.

The reindeers birth fur is composed mainly of hollow, woollen hairs. Hair density is similar to that of the caribou calf (Lentz and Hart, 1960). The low and rather constant thermal conductance values at low Ta's reflect the good insulation capacity of the fur. Wind and wetting may, however, increase heat loss by as much as 50% (Lentz and Hart, 1960). Changes in conductance are not directly related to fur insulation (McNab, 1980). Strict comparisons must consider mass, changes in blood circulation and other aspects. The replacement of the birth fur commences in late June at an age of one month, and by late autumn it is adult in structure.

The thickness of winter fur (30 mm) was less than reported by Berge (1950) (35 mm) or by Scholander *et al.*, (1950)(50 mm), and less than in many other cervids (see Berge, 1950; Timisjärvi *et al.*, 1984). The length of individual guard hairs exceeded fur thickness since the hairs were not perpendicular to the skin. They still can be raised to an erect position. Piloerection reduces heat loss in the caribou calf by 30% (Lentz and Hart, 1960). The density of guard hairs varied between animals and depended on the sampling site. Our figures generally exceeded those reported by Berge (1950). The thick underfur is very important, since it effectively prevents air movement within it and thus reduces heat dissipation.

The Tre of adult reindeer agrees with earlier observations (e.g. Irving and Krog, 1955). It is within the normal range of +37-41°C, described for most Cervidae species. A rise in Tre resulting even from slight physical restraint is common in reindeer because of the fur insulation. Ts of extremities in both living animals and excised skin samples showed a strong dependence on Ta. The decrease in surface Ts *in vitro* was due to increased convection at low Ta's. The effect of Ta on Ts was further intensified by wind. A clear difference existed in fur thickness and Ts, the foreleg samples showing the lowest temperatures. A positive correlation between fur thickness and insulation value in arctic mammals has been reported by Scholander *et al.*, (1950).

Many physiological regulative mechanisms present in living animals are lost in excised skin samples. Reindeer are able to regulate leg Ts by adjusting blood circulation, invoking a counter current heat exchange mechanism. This mechanism is also utilized to prevent snow melting on the surface of the legs (Irving, 1951). A resting reindeer chooses a position in which the wind blows against the fur (Skjenneberg and Slagsvold, 1968) to shelter its head and minimize heat loss.

Blood constituents showed few correlations with Ta. Their seasonal differences are more indicative of nutrition than climate. Discrepancies may also arise from different methods of capturing and handling the animals. Serum total lipid and triglyceride concentrations were highest in autumn and may reflect the anabolism of adipose tissue. Autumn is also the rutting season of the reindeer, with associated high levels of gonadal steroids and adrenaline. High serum total lipids and triglycerides in calves may result from the high fat content of milk.

Thyroid secretion appears to elevate in the cold, but the magnitude of increase is species specific. Ringberg *et al.*, (1978) found the highest T4 levels in reindeer in summer and lowest in winter, whereas Yousef and Luick (1971) found no significant seasonal variation. In our work T4 was lowest in spring, indicating an overall lowered metabolic rate. NA was not correlated with other parameters, but A concentration was correlated with age, weight and total lipids, and also showed seasonal variation. No correlation was found with Ta. The high NA concentration in newborn calves supports high endogenous non-shivering thermogenesis. In adult reindeer the role of catecholamines may be involved in the mobilization of energy reserves under stress situations or starvation and may also reflect the body condition. In conclusion, the results suggest that the prime mechanism by which adult reindeer thermoregulate in a cold environment is insulation.

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