

DEVELOPMENT OF TEMPERATURE REGULATION IN NEWBORN REINDEER

Temperaturreguleringens utvikling hos nyfødte reinkalver

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Abstract: Development of temperature regulation was investigated by determining the ability of newborn reindeer calves (*Rangifer tarandus tarandus*) to maintain a normal body temperature when exposed to an incrementally decreasing ambient temperature. Newborn calves (1 day old) can maintain their body temperature even at -15°C . They can increase their metabolic rate five- to sixfold. Heat production is primarily stimulated by the sympathetic nervous system. The response to exogenous administration of noradrenaline and propranolol was investigated.

RANGIFER 1(1): 29—38

HISSA, R., SAARELA, S. & NIEMINEN, M. 1981. Poronvasan lämmönsäätelyn syntymänjälkeinen kehittyminen. *Yhteenveto:* Vastasyntyneiden poronvasojen kylmänsietoa ja lämmönsäätelyä tutkittiin toukokuussa 1981 Inarin Kaamasessa Paliskuntain yhdistyksen koetarhassa. Tutkittavat vasat olivat 1-10 vuorokauden ikäisiä. Vasa asetettiin jäädytettävään mittauskammioon. Sen aineenvaihdunta, lämpötilat niin ihon eri kohdista kuin peräsuolesta, lihasvärinä ja sydänsyke rekisteröitiin jatkuvasti. Tulosten mukaan näyttää siltä kuin 1 vuorokauden ikäiselle vasalle $\pm 15^{\circ}\text{C}$ olisi ehdoton alaraja lämpötilan säätelyssä. Se kykeni kohottamaan hapenkulutusta tällöin 5-kertaisesti. Lihasvärinän merkitys on vähäinen verrattuna kemialliseen lämmöntuottoon kylmässä. Tämä voitiin osoittaa injisoimalla vasaan sympaattisen hermoston välittäjäainetta noradrenaliinia.

RANGIFER 1(1): 29—38

HISSA, R., SAARELA, S. & NIEMINEN, M. 1981. Temperaturreguleringens utvikling hos nyfødte reinkalver. *Sammendrag:* Temperaturreguleringens utvikling er studert ved å bestemme nyfødte reinkalvers evne til å opprettholde normal kroppstemperatur under påvirkning av gradvis synkende omgivelsestemperatur. Nyfødte kalver (1 døgn gamle) kan opprettholde sin kroppstemperatur selv ved $\pm 15^{\circ}\text{C}$. De kan øke sin omsetningshastighet fem til seks ganger. I starten er varmeproduksjonen stimulert av det sympatiske nervesystem. Virkningen av tilført noradrenalin og propranolol ble studert og skjelving synes å spille bare en mindre rolle umiddelbart etter fødselen.

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INTRODUCTION

In general, the endothermal maintenance of a stabilized and elevated body temperature is regarded as an evolutionarily adaptive feature in mammalian and avian physiology. However, in newborn homeotherms, the benefits of endogenous highly elevated heat production may be overcome by its high metabolic costs. Consequently newborns normally save energy for growth and body temperature is regulated at a lower temperature or they even may thermoregulate passively as ectotherms. However, the young of most ruminants are thermoregulatorily well developed from the moment of birth (see, e.g. Alexander & Williams 1968, Gemmel et al. 1972, Alexander et al. 1975).

A general comparison of the developmental characteristics of mammalian temperature regulation shows the existence of non-shivering thermogenesis (NST) which is associated with increased sensitivity to the calorogenic action of noradrenaline (NA). Furthermore, brown adipose tissue (BAT) is known to play an important role

in NST (Himms-Hagen 1967, Smith & Horwitz 1969, Janský 1973). Recent data suggest that BAT might be responsible for the major part of the NA-stimulated calorogenic response (Foster & Frydman 1978, 1979), thereby contributing substantially to their cold resistance (Hull & Segall 1965, Alexander 1970). The newborn young of most ruminants also have at least some multilocular BAT-tissue (see Alexander et al. 1975).

Arctic mammals, like caribou and reindeer, are well adjusted to cold (see rev. from Blix & Steen 1979). At the moment of birth the newly-born reindeer calves may survive exposure to a thermogradient which may exceed $50-60^{\circ}\text{C}$. How do they cope with this hostile moment? How efficiently can they elevate their metabolic rate? What pattern of heat production do they preferentially employ: Shivering or non-shivering thermogenesis?

Lentz & Hart (1960) studied the length and density of fur in 1—3 day old caribou calves. The effects of air velocity, direction and wetness of the

skin on heat loss were examined as well. Hart et al. (1961) studied the metabolic and thermal responses of infant caribou. The metabolic rate was doubled by a lowering of temperature to 0°C, but cold combined with wind and precipitation was observed to elevate the metabolic rate to over 5 times the resting value at 20°C.

It is previously (Krog et al. 1977, Wika et al. 1979 and Wika & Krog 1980) observed that newborn calves shivered immediately after birth. Fat taken from the interscapular region was richly vascularized and electronmicroscopically shows the anatomical characteristics of brown fat taken from newborn reindeer calves. Infrared thermograms revealed a warm spot on the back corresponding to the interscapular location of the brown adipose tissue. Furthermore, adrenergic nerve endings were also localized in EM-pictures.

Little information exists on the metabolism and development of temperature regulation in reindeer or caribou calves (see Nieminen et al. 1980a, b). The investigations described below were undertaken to delineate the relationship between heat production (oxygen consumption) of newborn reindeer calves (*Rangifer tarandus tarandus*) at large range of low ambient temperature. To assess the calorogenic action of NA as an index of NST, NA was injected subcutaneously into the dorsal axillary area. Since the calorogenic action of NA can be blocked pharmacologically with a β -receptor blockade, the effect of propranolol was investigated as well.

MATERIALS AND METHODS

The experiments were performed with 14 young 1–10 day old reindeer calves in Inari, Kaamanen, Finland (69° 10'). The time of delivery was carefully noted, with age being defined as time post-partum at commencement of an experiment. The calves were kept with their mother on the reindeer pasture and captured just before starting experiments in the near vicinity.

The calves were studied at four points in time postpartum: 1) at a mean age of 1 day (N=9), 2) 2 days (N=1), 3) 4 days (N=3) and 4) 10 days (N=1). (See Table 1).

The experiments were started on May 24 1981 and concluded on May 29. The daily mean ambient temperature and relative humidity varied between 1–14°C and 50–90% R.H. respectively. Younger calves underwent procedures in each experiment and each selected ambient temperature (T_a) for no more than 3–4 hours and the 10-day old for a maximum of 4–5 hours. The metabolic rate of calves was measured by determining oxygen consumption ($\dot{V}O_2$) (see Fig. 1). The calf was weighed and allowed to settle down in a metabolic chamber (40x55x90 cm, 198 l.). After at least 1/2–1 h for equilibration, evaluation began, using the prevailing air temperature as a starting ambient temperature. Calves were then exposed to a stepwise decreasing ambient temperature. One experiment with each calf took about 2–3 hours with equal time at each T_a . Exposure was commenced

Table 1. Body weight and age of reindeer calves investigated in the present study.
Tabell 1. Kroppsvekt og alder hos reinkalver i undersøkelsen.

Calf no.	Day of parturition	Body weight at birth	Day of experiment	Age in days	BW	Sex
Kalv nr.	Fødselsdato	Kroppsvekt ved fødsel	Forsøksdato	Alder dager	Kroppsvekt	Kjønn
1	23.5	3500 g	24.5	1	3500 g	♀
2	15.5	3900 g	25.5	10	6000 g	♂
3	23.5	4750 g	25.5	2	5300 g	♂
4	22.5	5150 g	26.5	4	7000 g	♂
5	22.5	5500 g	26.5	4	7000 g	♂
6	22.5	5100 g	26.5	4	5000 g	♂
7	26.5	4500 g	27.5	1	5000 g	♂
8	26.5	6000 g	27.5	1	5500 g	♂
9	27.5	4650 g	28.5	1	4500 g	♂
10	27.5	5100 g	28.5	1	5000 g	♂
11	27.5	4400 g	28.5	1	4400 g	♂
12	27.5	3850 g	28.5	1	4500 g	♂
13	28.5	4500 g	29.5	1	5000 g	♂
14	28.5	4850 g	29.5	1	5500 g	♂

when the body temperature and $\dot{V}O_2$ were stabilized. Results are calculated from each experiment of steady recording exceeding 15–30 min.

Compressed air was pushed through the chamber at a constant rate of 240 l per hour, as measured with a flowmeter (Rotameter 1100). The humidity of the chamber was not controlled. O_2 -consumption was analysed paramagnetically on a Beckman E2 oxygen analyzer and calculated according to Hill et al. (1972). Recordings were taken manually at 5 min. intervals.

Rectal temperature (T_{re}) at a depth of 5–6 cm, skin temperature of interscapular (T_{isc}), lumbal (T_{lb}), foot (T_f) and chamber (T_a) temperatures were measured by a copper-constantan thermocouple (Type 35, 2x0.2 mm, Bröckskes KG) on a Speedomax 250 recorder (Leeds & Northrup).

Three safety-pin electrodes were attached under the skin on both sides of the axillary region and the indifferent electrode to the skin on the mid-back to record muscle shivering (EMG-activity) and ECG. A two-channel signal processing system constructed in our laboratory was

used to record EMG and ECG. EMG-signal was fed into a differential amplifier and a band-pass filter. The high and low cut-off (-3dB) frequencies of the filter were 500 Hz and 10 Hz, respectively. The amplified and filtered signal was then passed into rectifying and averaging circuit providing either 4 or 8 s sliding time-average of the rectified EMG signal, which was recorded with a Rikadenki DP-6 (Tohshin) potentiometer. ECG-signals were continuously monitored with a Tektronix 502A dual beam oscilloscope.

In order to verify the ability of calves to perform NST, noradrenaline was injected subcutaneously at three different ambient temperatures in 1 day old calves. To avoid disturbances a remote injection technique outside the metabolic chamber was used. Noradrenaline (1-arterenol-bitartrate, Sigma, 0.2 or 0.4 mg per kg) was dissolved in 0.9% saline. Control animals received the same volume of saline. Propranolol (propranolol hydrochloride, Sigma) was likewise injected into one calf at $T_a \pm 0^\circ C$.

Conventional electron microscopy was used to describe the morphology of brown adipose tissue collected from cervical, prescapular, perirenal

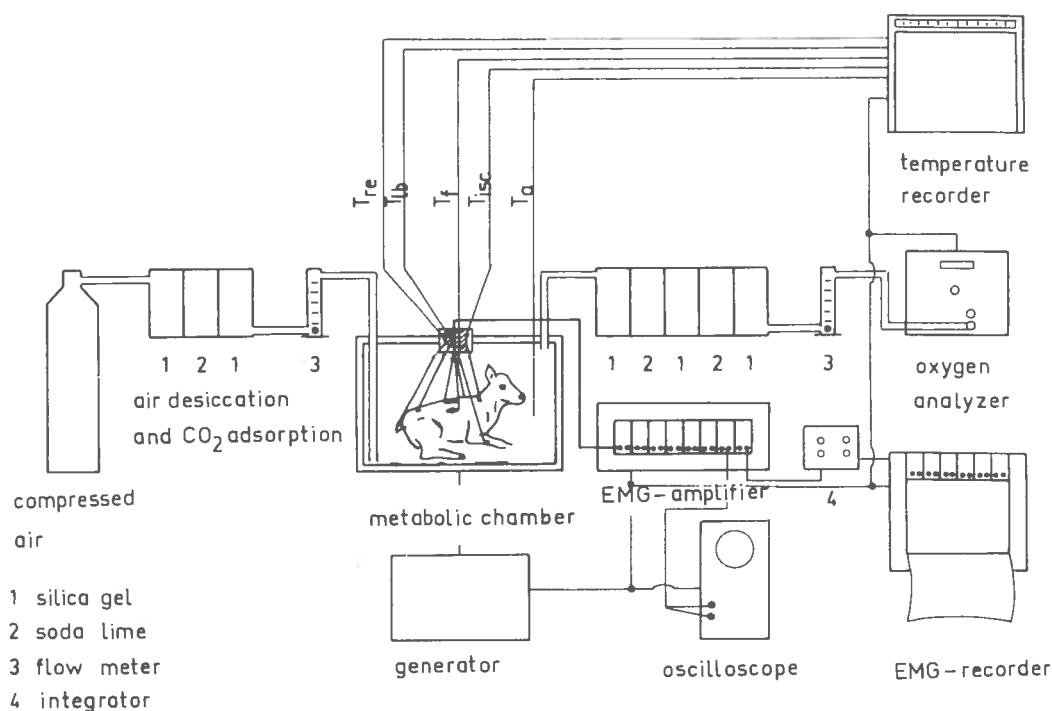


Fig. 1. A scheme of the system used in the present study. *Systemet benyttet i arbeidet skjematisk.*

and pericardial areas. Tissue samples were cut into small pieces and fixed with 3% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.4) at 4°C overnight and postfixed in 1% osmium tetroxide for 2 hours at 4°C. The blocks were dehydrated in ethanol, block-stained with 2% uranyl acetate in ethanol for ½ h and embedded in Epon for 2 days at 60°C. The specimens were poststained with lead citrate and uranyl acetate. They were viewed and photographed using a Jeol 100 B electron microscope.

RESULTS

Based on anatomic evidence BAT was present perirennally, pericardially and in pre- and subclavicular region. In one calf aged 1 day (5.4 kg) the total mass of BAT was 21.2 g, i.e. 0.39% of the total body mass.

After examination with electron microscope adipose tissue cells have a multilocular appearance typical of BAT (Fig. 2 A, B, C). However, only a few droplets of fat can be seen, probably due to exhaustion in the cold. Typically fat seems to be concentrated in large droplets in the adipocyte cells of the pericardial region. Blood vessels are seen adjacent to cells. In each cell a large concentration of mitochondria with densely packed cristae, similar to those found by Krog et al. 1977 and Wika & Krog 1980, are found, especially in the BAT of the pericardial region.

When calves were transferred to a metabolic chamber they settled down reluctantly. In all, only a very slight shivering was measured; this became more sustained and intense at the lower T_a (however only 32% above the resting level). Data obtained from the experiments are summarized in Fig. 3. T_{re} averaged between 39.6° and 40.5°C (Mean \pm SE: 40.0 \pm 0.07°C) at T_a ranging from +11° to -15°C. The foot temperature decreased from 37.8° to 25.5°C. Heart rate varied between 123 and 180 beats per min and breathing rate from 30 to 35 per minute. The lowest $\dot{V}O_2$ (5.7 ml/kg.min) was measured at +11°C. As shown in Fig 4 lowering of T_a induced a linear increase in $\dot{V}O_2$. The highest value (32.2 ml/kg. min in the calf No. 9) was reached at -15°C; this means a five-sixfold increase in $\dot{V}O_2$ over the lowest value. A general pattern of steady-state body temperatures show that the infant reindeer can maintain its body temperature even in the coldest experimental T_a i.e. of -15°C.

A much larger number of measurements is needed of course to demonstrate how long they

can stand the exposure to cold, for instance, as well as the transition of maximal capacity in the course of development down in temperature scale. With further morphological development the cold-induced $\dot{V}O_2$ is naturally reduced concurrently with the acquisition of a better insulation and a decrease of relative surface area. The question of the difference between the magnitude of the maximal (summit) and minimal (basal) metabolism can not be answered here, since the precise location of thermoneutral zone on the temperature scale was not studied.

After NA injection T_{re} reached maxima from 39.5° to 41.1°C in 30 min in one young (No. 13) and from 39.7° to 40.6°C in 35 min in another calf (No. 11). These experiments were performed at ambient temperatures of +10°C and 0°C, respectively. Injection at +11°C increased T_{re} from 39.3° to 41.9°C in 25 min and $\dot{V}O_2$ rose approximately fivefold above the preinjection level. At the same time the interscapular skin temperature (T_{isc}) increased approx. 3°C (2.9°C) above the preinjection level.

Characteristically, the response to NA was rapid and lasted at least one and a half hours after injection when the experiment was finished. Also the heart rate immediately was increased about 15% and alertness increased, probably due to elevated T_b .

An increase in T_{re} and $\dot{V}O_2$ after NA injection is apparently not due to shivering, since shivering was not significantly increased after NA injection.

As shown in Fig. 5 the substitutive effect between exogenous NA and cold stimulated endogenous NA release was clearly seen. The colder the T_a the smaller the NA-induced calorogenic response. The effect of subcutaneous administration of propranolol (1 mg/kg) at 0°C resulted in a clear elevation of EMG-activity. However, since it induced a violent alertness of the calf the experiment was stopped within 10 min of injection and during this time no changes in $\dot{V}O_2$ and T_{re} were measured.

DISCUSSION

Our results show that NST coupled with shivering provides the calf with a potential for increasing its metabolic rate five- to sixfold in the cold. The calves were not subjected to higher ambient temperature than +14 or +15°C in the present study, and it is apparent that the location of the thermoneutral zone was not yet achieved. Therefore the difference between summit and

basal metabolic rate may be even greater. The high metabolic rate and a well-developed insulation compared with other terrestrial mammals (Brody 1945), give the calf excellent cold resistance. Based on our results, we assume the newly born calves can cope with the weather normally prevailing at that time, i.e. at the end of May and beginning of June. However, of course, wetting of the pelt and wind may create a situation which is barely tolerated by infants (see e.g. Hart et al. 1961). According to our data it is likely that shivering plays only a minor role in the heat production of a newly born calf. NST, together with the high energy content of the milk (see Arman 1979), supports the surprisingly high body temperature and metabolic rate immediately after birth. A dense fur (see Lentz & Hart 1960) provides further support to keep body temperature normal in the cold. The heart rate presented in this work agrees well with observations in young reindeer calves by Timisjärvi et al. (1979).

The relatively high rectal temperature of the newborn calves presented in this work matches that observed by Krog et al. (1977), Wika & Krog (1980), Nieminen et al. (1980b). In discussing the reasons for higher metabolic rate in the work presented for infant caribou by Hart et al. (1961) the different techniques used for measuring the metabolism may give some clue. In their works the caribou calves were secured by a neck stanchion and held in a standing posture throughout the measurements. They also performed measurements under natural conditions at -1° to -4°C with wind velocities from 27 km to 37 km per hour. It was shown that several hours exposure to these conditions led to several degrees of hypothermia, which was most severe when the fur was wetted by drifting snow. It is clear that in a standing position calves are more sensitive metabolically to cooling factors in the environment. Hart et al. (1961) observed that the total increase in heat production of infant caribou was approximately fivefold from the mildest at approximately $+20^{\circ}\text{C}$ to most severe exposure at -1° to 4°C .

Since the maximum heat production is achieved in most cases only when body temperature is decreased several degrees centigrade (see Wang 1978) it seems also plausible that in reindeer calf the peak metabolism was not yet achieved. The speculation of this explanation is consistent with the observations reported in newborn mammals by Depocas et al.

(1957). According to Wang (1978) the limiting factors for maximum thermogenesis are primarily related to the following functions: 1) The maximum capability of the respiratory and cardiovascular systems for transport of oxygen and carbon dioxide, 2) the maximum rates governing substrate availability for NST and shivering and 3) the maximum rates for oxidative biochemical mechanisms of cells. We would conjecture that the substrate availability governing maximum thermogenesis is, in infant reindeer, the most likely critical factor, as also indicated by Wika (1979).

The distribution and proportion of BAT in the newborn lamb or bovine calf is approximately 1.5% of the total body mass (Alexander & Williams 1968, Gemmel et al. 1972). The smaller mass of BAT in infant reindeer presented in this study may be due to the fact that it was not found associated with the intestines as it is in lambs and bovine calves (Alexander et al. 1975). As in newborn lambs and bovine calves there appears to be very little white adipose tissue in the reindeer at birth (Wika & Krog 1980).

Whether the skeletal muscles play an important role in NST of calves is not known. Blix et al. (1979) have demonstrated that skeletal muscles of the fur seal probably play an important role in NST and the importance of skeletal muscles in NST of small mammals has repeatedly been shown (see e.g. Janský 1973, Foster & Frydman 1978, Feist 1980). How much skeletal muscles contribute the total NST during NA calorogenesis of the reindeer calf still remains open; Foster & Frydman (1978) indicated that muscles may contribute 12% of the total metabolic response to NA in the cold-acclimated rat. Since the total amount of BAT in the reindeer calf appears to be small, we assume that skeletal muscles contribute to a large part of total NST here.

It has been shown that thyroid hormones are also important in regulation of NST (Chaffee & Roberts 1971). Our recent results (Nieminen et al. 1980b) show relatively high plasma noradrenaline content in the infant reindeer. Likewise an initial high plasma T_4 content was relatively high immediately after birth, decreasing during the first 3 days. Therefore we assume that thyroid hormones are involved in the immediate response to cold in these calves.

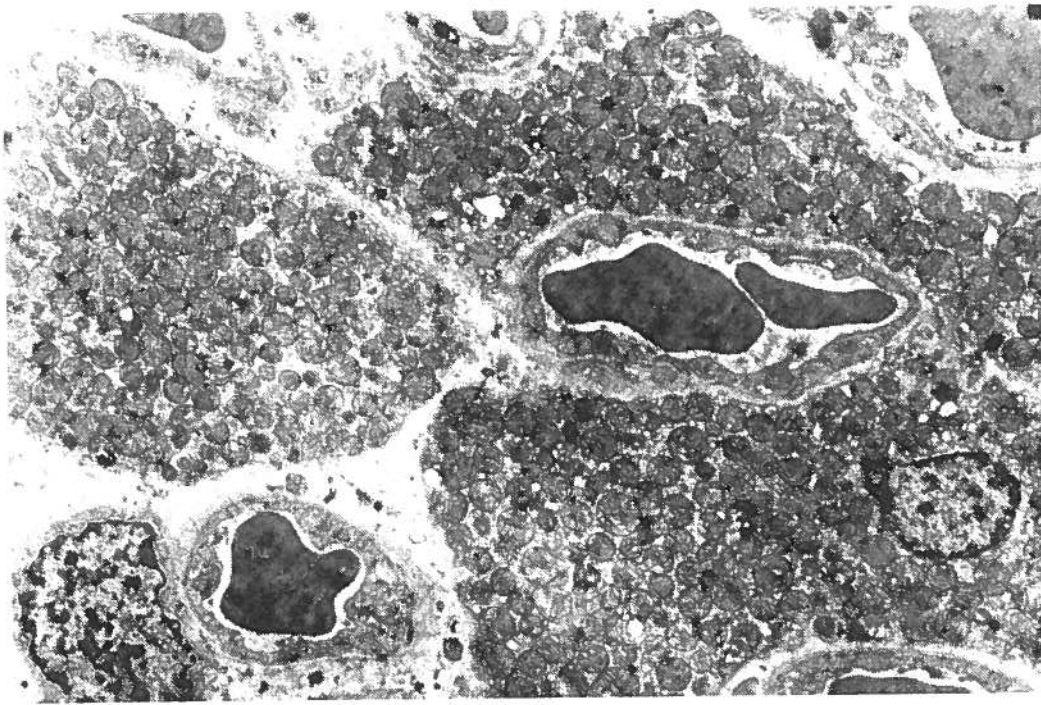
In summary, it seems justified to assume that thermogenesis produced by NA has a thermoregulatory significance in the newly-born reindeer

calf. The substitutive effect between exogenous NA and cold-stimulated endogenous NA release has been demonstrated in several adult mammalian species (see Janský 1973). On the basis of these results we conclude that the NA calorogenic effect is directly related to the sensitivity and magnitude of NST in newly born calves. The dependence between NA response and calf-age should be studied; e.g. in the lamb, a loss of response to NA has been seen within 2 weeks (Thomson & Jenkinson 1969).

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A

B

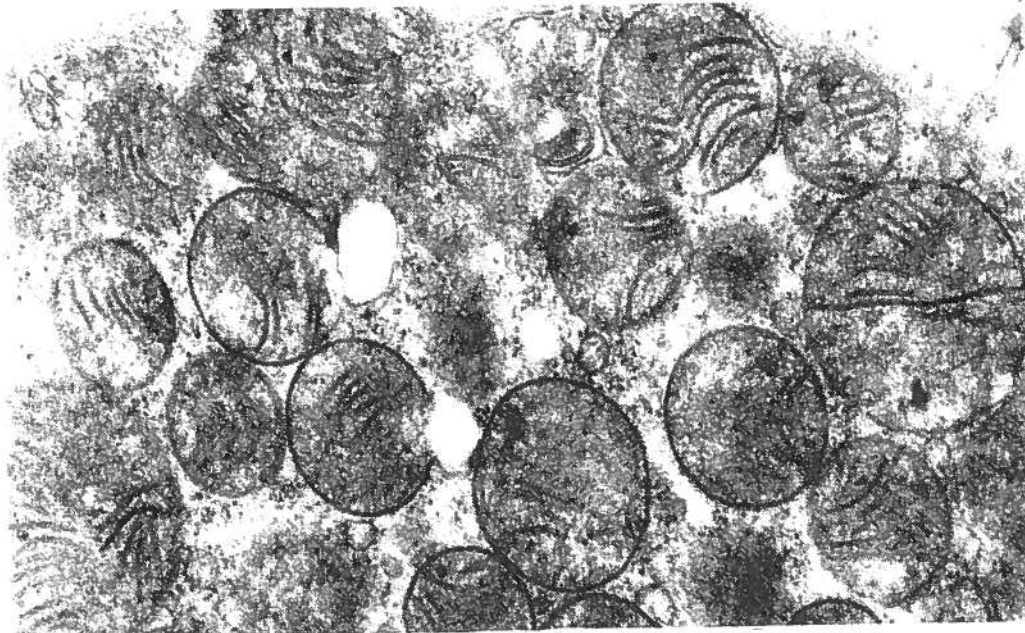


Fig. 2. A, B. Brown adipose tissue from the interscapular region of 1 day old reindeer calf, weighing 5.4 kg which had been exposed to the environmental temperature of appr. 5–10°C from birth. Typically the tissue contains few and small vacuoles of fat. Cells contain densely packed mitochondria with parallel cristae.

A, B. Brunt fettvev fra undersiden av skulderbladet hos en 1 dogn gammel reinsdyrkalf med knoppsvekt 5,4 kg, og som hadde vært utsatt for en omgivelsestemperatur på ca. 5–10°C fra fødselen. Typisk er at vevet inneholder små og få fettvakuoler. Cellene inneholder tettpakkede mitokondrier med parallelle ribber.

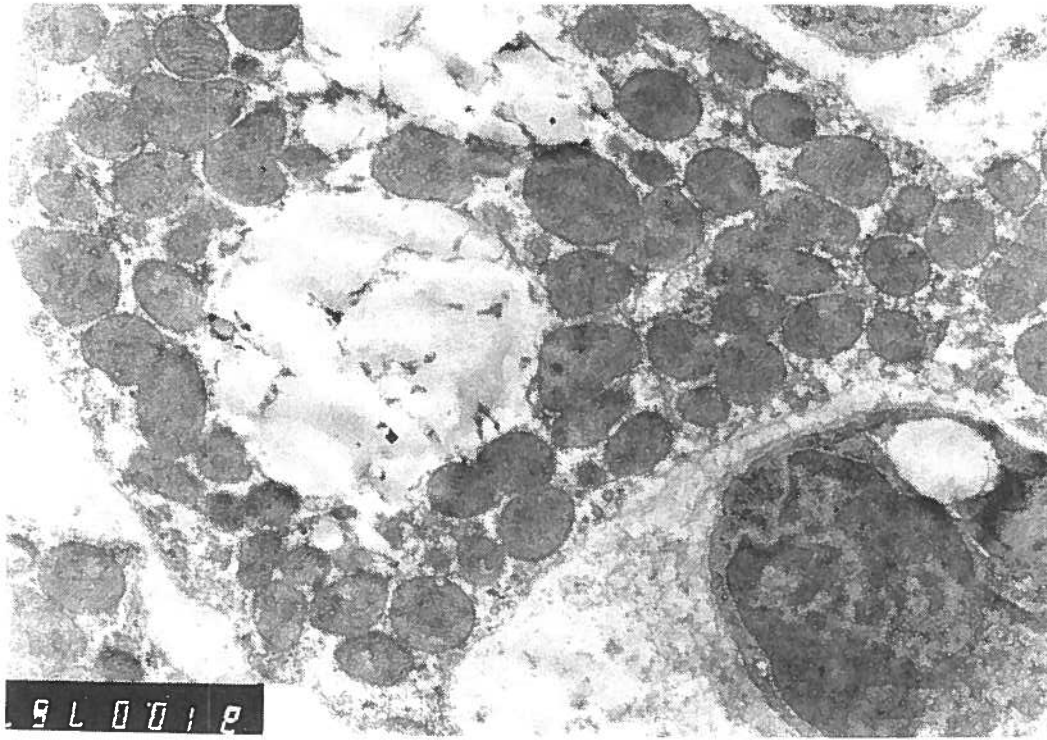


Fig. 2. C.

Brown adipose tissue from pericardial region showing only few large fat droplets. Typically cristae in mitochondria are much more densely packed than in the other two tissues.

C. Brunnt fettvev fra perikardialregionen med kun få, store fettdråper. Typisk er at ribber i mitokondriene er mer tettpakket enn i de andre to vev.

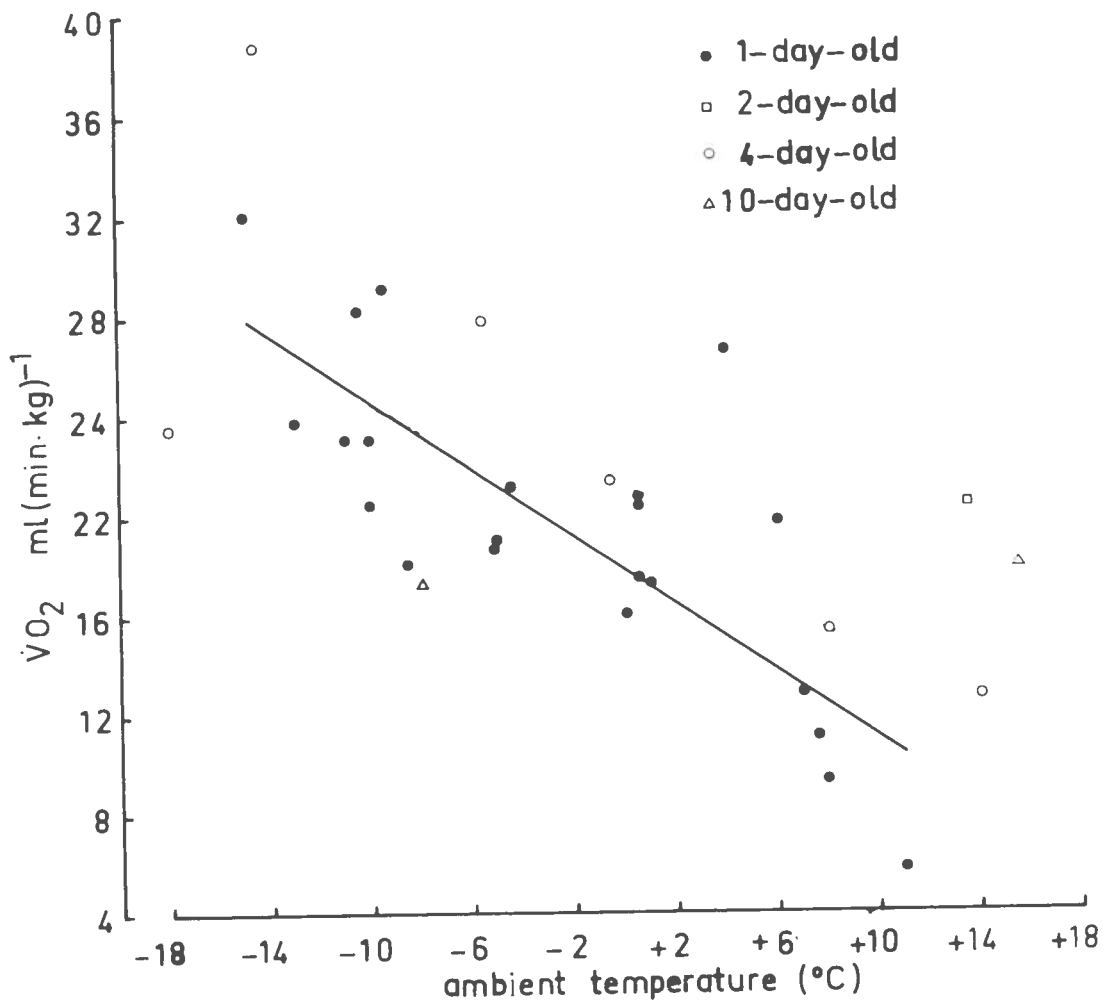


Fig. 4. Relationship between heat production ($\dot{V}O_2$) and ambient temperature in newborn reindeer calves. The linear regression equation: $y = 17.88 - 0.68x$, $r = 0.8136$, $P < 0.001$, ($N = 9$, 22 measurements) is calculated to all points of 1 day old calves by the method of least squares.

Sammenheng mellom varmeproduksjonen ($\dot{V}O_2$) og omgivelsestemperatur hos nyfødte reinsdyrkalver. Lineær regresjonsligning: $y = 17,88 - 0,68x$, $r = 0,8136$, $P < 0,001$ ($N = 9$, 22 målinger) er beregnet for alle punkter hos 1 dogn gamle kalver ved hjelp av metoden for minstekvadrat.

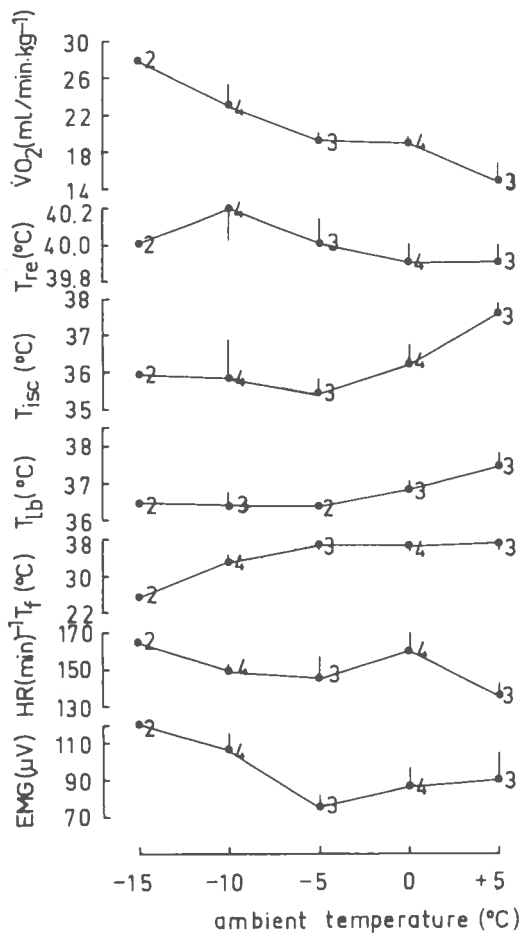


Fig. 3. Changes in oxygen consumption ($\dot{V}O_2$), body temperature (T_{re}), skin temperature above the interscapular (T_{isc}) and lumbar (T_{lb}) regions, foot temperature (T_f), heart rate (HR) and electromyographic activity (EMG) in 1 day old reindeer calves at various ambient temperatures. Number of measurements indicated at each symbol. Vertical bars represent standard errors of mean.

Forandringer i oksygenforbruket ($\dot{V}O_2$), kroppstemperatur (T_{re}), hudtemperaturen over skulder (T_{isc}) og lend (T_{lb}), fottemperatur (T_f), hjerterefrekkvens (HR) og elektromyografisk aktivitet (EMG) hos 1 dogn gamle reinsdyrkalver under forskjellige omgivelsestemperaturer. Antall malinger angitt ved hvert symbol. Vertikale staver representerer standardavvik paa midlet.

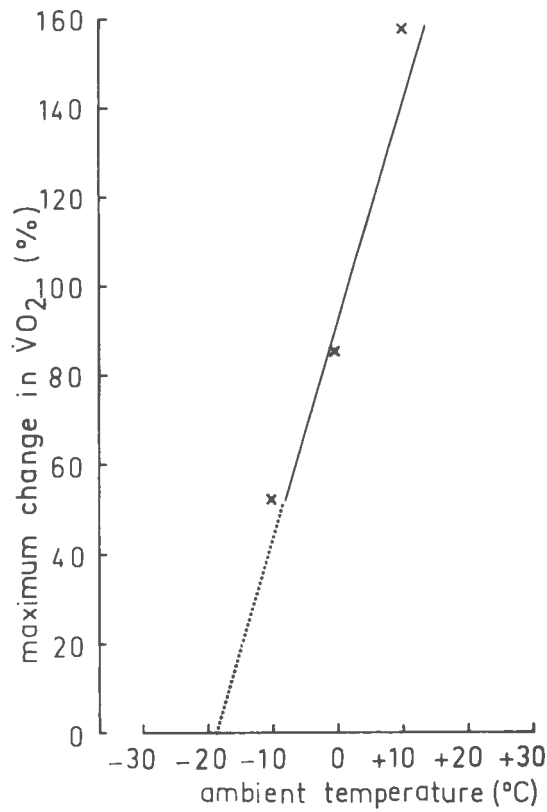


Fig. 5. The metabolic response to subcutaneous injection of noradrenaline (0.2 mg/kg) at 3 different ambient temperatures. The response was calculated by subtracting the increase in $\dot{V}O_2$ above preinjected levels after NA injection. The broken line described from the result shows the probable response to the same dosage of NA in the colder ambient temperature. ($y=98.4+5.25x$, $r=0.9765$, $P<0.001$).

Reaksjon paa omsetningen ved subkutan injeksjon av noradrenalin (NA) (0,2 mg/kg) ved 3 forskjellige omgivelsestemperaturer. Reaksjonen ble beregnet som differensen mellom $\dot{V}O_2$ for og etter injeksjonen av NA. Den brutte linje beskriver den sannsynlige reaksjon paa den samme dose av NA ved lavere omgivelsestemperatur. ($y=98,4+5,25x$, $r=0.9765$, $P<0.001$).