

ENERGY METABOLISM OF YOUNG, UNADAPTED CALVES

CENTRALE LANDBOUWCATALOGUS



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Promotoren: **Dr. J.P.T.M. Noordhuizen**
Hoogleraar in de veehouderij

Dr. ir. M.W.A. Verstegen
Buitengewoon hoogleraar op het vakgebied van de veevoeding in het
bijzonder de voeding van de eenmagigen

Co-promotor: **Dr. A. Arieli**
Senior lecturer in ruminant nutrition at the Faculty of Agriculture,
Hebrew University of Jerusalem, Israel

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ENERGY METABOLISM OF YOUNG, UNADAPTED CALVES

J.W. Schrama

Proefschrift

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Schrama, J.W. Energy metabolism of young, unadapted calves (Energiestofwisseling van jonge, niet aangepaste kalveren).

Calves reared for veal or other meat production are usually purchased before 2 weeks of age. The first weeks at the rearing unit represent a critical phase regarding their health. During this period calves are fed at a very low level. In this thesis, the energy metabolism of young, newly purchased calves, as affected by feeding level and ambient temperature, was studied. It was found that such calves are highly dependent upon body energy reserves due to restrictive feeding, their high maintenance requirements, and the low availability of nutrients from the diet. During this period, the response of these animals to temperature is not consistent with the current concept of thermoregulation. Thermal requirements are affected by the calf's posture (standing or lying). The influence of temperature on heat production of calves varies within a day. Part of this circadian fluctuation is related to the within day variation in time spent standing. The first 2 weeks after arrival the calves are not in a steady-state regarding their energy metabolism. Both the relationship between heat production and feeding level and heat production and temperature, change with time after arrival.

Ph.D. thesis, Department of Animal Husbandry and Department of Animal Nutrition, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands.

STELLINGEN

I

De invloed van voerniveau en omgevingstemperatuur op de energiestofwisseling verandert bij jonge, niet aangepaste kalveren in de tijd.

Dit proefschrift.

II

Het door Mount (1974) geformuleerde concept van thermoregulatie bij homeotherme dieren is niet van toepassing op zeer jonge kalveren.

Mount, L.E. 1974. The concept of thermal neutrality. In: J.L. Monteith, and L.E. Mount (Ed.) Heat Loss from Animals and Man. p 425. Butterworths, London.

Dit proefschrift.

III

Ook niet-specifiek thermoregulatoire activiteit beïnvloedt de temperatuursbehoefte van dieren.

Dit proefschrift.

IV

De suggestie van Webster et al. (1978), dat de ondergrens van de thermoneutrale zone (de onderste kritieke temperatuur) geen scherp omlijnd punt is maar een zone, wordt bevestigd in het onderhavige onderzoek.

Webster, A.J.F., J.G. Gordon, and R. McGregor. 1978. The cold tolerance of beef and dairy type calves in the first weeks of life. Anim. Prod. 26:85.

Dit proefschrift.

V

Optimale klimaatscondities voor jonge kalveren gedurende de eerst twee weken na transport zijn van belang om extra mobilisatie van energiereserves te voorkomen.

Dit proefschrift.

VI

Het optreden van voedingsdiarree bij jonge kalveren door een hoge voergift kan ook het gevolg zijn van het overschrijden van de capaciteit om de verteerde nutriënten te verwerken.

VII

In toekomstig wetenschappelijk onderzoek bij landbouwhuisdieren zal meer aandacht besteed moeten worden aan de gevolgen van veranderingen in omgevingscondities.

VIII

Door veel kenmerken te meten en/of te berekenen binnen één experiment wordt de kans op het vinden van niet bestaande biologische effecten vergroot.

IX

Onderzoek naar en ontwikkeling van duurzame produktiesystemen is nutteloos, indien dit niet ondersteund wordt door een duurzaam beleid.

X

Het politieke belang van de agrarische sector in een land is negatief gerelateerd aan de gemiddelde bedrijfs grootte.

XI

Voor goed boeren is ruimte nodig.

XII

Wie geen fouten maakt, kan best wat harder gaan werken.

J.W. Schrama

Energy metabolism of young, unadapted calves

Wageningen, 10 december 1993

VOORWOORD

Dit proefschrift is het resultaat van 4 jaar onderzoek bij de vakgroepen Veehouderij en Vervoeding van de Landbouwuniversiteit te Wageningen.

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Dear Ami, despite my stay in Rehovot, I am not a master in Hebrew. So for you the above words of thanks in English. First of all, I would like to thank my promotors, Prof. dr. J.P.T.M. Noordhuizen and Prof. dr. ir. M.W.A. Verstegen and my co-promotor Dr. A. Arieli. Dear Jos, Martin and Ami, the inspiring meetings, your comments and advices, but especially our discussions were of great value to me. You were around whenever necessary. Thanks for the support in good and bad times.

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CONTENTS

	Page
GENERAL INTRODUCTION	1
CHAPTER 1. Alteration of energy metabolism of calves fed below maintenance during 6 to 14 days of age	11
CHAPTER 2. Responses of young calves to low ambient temperatures at two levels of feeding	25
CHAPTER 3. Evidence of increasing thermal requirement in young, unadapted calves during 6 to 11 days of age	45
CHAPTER 4. Thermal requirements of young calves during standing and lying	59
CHAPTER 5. Circadian fluctuation in heat production of young calves at different ambient temperatures in relation to posture	77
GENERAL DISCUSSION	95
SUMMARY	125
SAMENVATTING	131
LIST OF PUBLICATIONS	137
CURRICULUM VITAE	139

General Introduction

GENERAL INTRODUCTION

In The Netherlands, almost all male and some of the female calves (those surplus to the requirements as herd replacements) born on dairy farms, are sold at about 1 to 2 weeks of age. These calves represent the major source of calves purchased for veal and other type of beef production. Some of the calves to be reared for veal are imported, depending on the market price. The common practice of the transfer of calves to the rearing units, comprises their collection from various dairy farms, followed by transportation to central collection points (dealers' premises or markets). At the collection points, calves are mixed and selected for transportation to either the rearing farm or another collection point.

The vigour of the calves after arrival at the rearing unit is dependent upon: 1) factors determining their vitality before leaving the dairy farm; 2) the duration and the nature of the complex of acute stressors imposed upon them during the transfer; and 3) the complex of alterations in environmental conditions between the dairy farm and rearing unit imposed on them after the transfer. Amongst others, some determinants of the calf's vitality before transfer are the ease of the birth process, the colostrum quantity and quality, the moment of colostrum ingestion, and other management factors on the dairy farm (e.g., hygiene, and the applied feeding level). The imposed stress complex of transit can be summarized as: climatic stressors (temperature, air velocity, etc.); deprivation of milk (and water) leading to hunger, thirst, and dehydration; exposure to unfamiliar, pathogenic micro-organisms (high infection risk because of the mixing of calves from different sources); others (e.g., handling during loading and unloading, exposure to noise and vibrations during transportation). After exposure to these acute stressors of transit, the purchased calves are exposed to changes in: housing system (e.g., straw bedding vs wooden slatted floor); social richness of surroundings (contact with dam vs individual housing); climate; feeding level and dietary composition (whole milk vs liquid milk replacer) between the farm of birth and the rearing unit.

Apart from perinatal mortality, high mortality rates occur in preweaned calves in both dairy and beef herds (Oxender and Adams, 1979; Perez et al., 1990; Lance et al., 1992; Azzam et al., 1993). Reported mortality rates from birth to weaning vary between 5 and 25%. The first weeks after birth are thus a critical phase in the life of calves. The transfer of calves to be reared for meat production during this critical phase in life, is considered to be very unfavourable with regard to their health (Roy, 1980; Webster, 1984, Broom, 1991). Staples and Haugse (1974) observed a higher mortality rate in calves purchased during the first 2 weeks of life than in older calves. In The Netherlands, mortality over the total growing period of veal calves is below 5% and occurs primarily during the

first three weeks after arrival at the rearing unit (Postema, 1985). Calves are particularly susceptible to respiratory and gastrointestinal diseases (Perez et al., 1990; Broom, 1991; Webster, 1991). During the total growing period, morbidity is higher during the first few weeks after arrival at the rearing unit due to both respiratory and enteric disorders (Postema, 1985; Webster et al., 1985), the latter being the main cause (Postema, 1985).

The period of 2 to 3 weeks after arrival at the rearing unit, can thus be considered as the most critical phase in veal and other types of meat production. In practical veal production, the priority during this period is not to optimize (or maximize) growth, but to control and minimize the occurrence of health disorders. In order to reduce the risk of gastrointestinal disorders, very low feed allowances are applied in practice. Commonly, calves are fed an electrolyte solution as the first meal after arrival, and a liquid milk replacer thereafter.

In Figure 1 a scheme is depicted, of the partition of dietary energy as used by an animal. The utilization of ingested food energy (gross energy intake, **GE**) by the animal involves several kinds of losses. Part of the GE intake is lost through excretion of energy in faeces, urine and combustible gases (the latter being of minor importance for young pre-ruminant calves). The remaining part of the GE intake, the metabolizable energy (**ME**), is used firstly for the supply of the energy requirements for maintenance. The part of ME used for maintenance, comprises the ATP required for sustaining primary life processes, and the heat increment of utilization of ME for maintenance. This part of ME is fully dissipated as heat. If GE intake (feeding level) is higher than the maintenance requirement, the part of the ME surplus to the maintenance requirement (the ME available for production) is retained in the body as energy (**ER**; growth). During growth, part of the available ME for production is lost due to the heat increment of the utilization of ME for growth. Thus, ER is the difference between ME and the total heat production. If GE intake is below the maintenance requirement, energy reserves from the body are mobilized (negative ER) to cover the deficit in ME for sustaining primary life processes. In conclusion, the ER of an animal depends on the feeding level (GE intake), the availability of energy in the diet (ratio between ME and GE) and the heat production by the animal (depending on the maintenance requirement and the heat increment of ME for maintenance and for growth).

Calculations of ME available for growth by Postema (1985), demonstrated that the quantities of feed offered during the first 2 to 3 weeks after arrival at the rearing unit, were insufficient to cover the calves' energy requirements for maintenance. So, after the period of transportation, during which the animals are not fed, a period follows in which the calves are partially dependent upon their body energy reserves. For some calves, this period of

dependency upon body energy reserves (negative ER) may even start at the dairy farm before transport. Dairy farmers may practice, to some extent, a strategy of excessive feed restriction to calves, which will be sold, in order to reduce the risk of gastrointestinal disorders, which may delay the sale of those calves at an early age. In pre-ruminant calves, energy metabolism in relation to feeding level has mostly been studied in animals older than 2 weeks, fed above maintenance, and after a certain period of adaptation to experimental facilities (van Es et al., 1969; Johnson and Elliott, 1972a,b; Holmes and Davey, 1976). There is a lack of information concerning energy metabolism, which is representative of young calves during the first weeks after arrival at the rearing unit (immediately after transportation and restrictively fed).

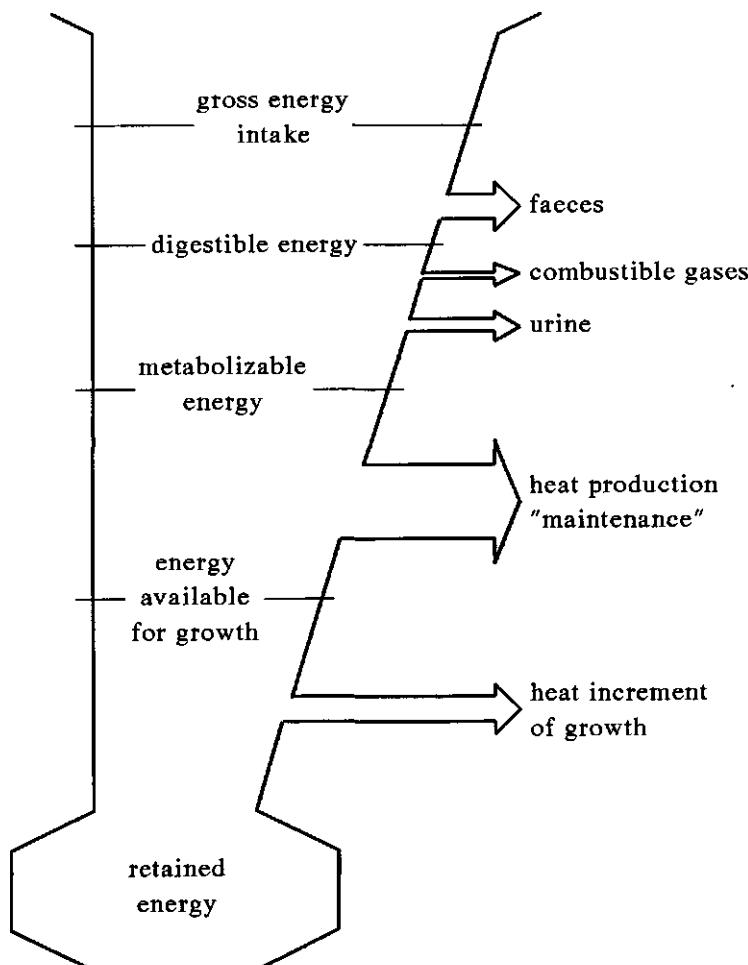


FIGURE 1. Scheme of a calf's partitioning of dietary energy (after: Young, 1975).

Homeothermic animals sustain a constant body temperature within relatively narrow limits at various climatic conditions, by balancing heat production and heat loss (Mount, 1979). Figure 2 shows the relation between heat production and ambient temperature. Within the ambient temperature zone between A and C' (or C''), the homeothermic zone, animals are able to maintain constancy of body temperature irrespective of the ambient temperature. Ambient temperatures below A and above C' (or C'') will cause hypothermia and hyperthermia, respectively. Between the ambient temperatures B' and C' (or B'' and C''), the thermoneutral zone, heat production is not affected by ambient temperature, but depends on other factors such as the level of nutrition. The lower limit of this zone (B' or B'') is called the lower critical temperature and the upper limit (C' or C'') the upper critical temperature. Below the lower critical temperature, the mechanisms of heat loss regulation are depleted and homeothermia is maintained by increasing heat production in order to counterbalance the increased heat loss. The feeding level influences the relation between heat production and ambient temperature. An increase in feeding level will result in an increase of the heat production in the thermoneutral zone, and will consequently lead to a decrease both in the lower and upper critical temperatures (Figure 2). In Figure 3, the relation between ER and ambient temperature is represented (derived from the situation in Figure 2). Within the thermoneutral zone ER is not modified by ambient temperature. Below the lower critical temperature (B' or B''), ER declines with decreasing ambient temperatures as a consequence of the increased energy requirements for maintaining constant body temperature, which is reflected by the increased heat production.

Like other young animals (NRC, 1981), young calves are more prone to cold stress than adult cattle (Webster, 1976), which is indicated by the higher lower critical temperature of young animals. Thermal requirements of young calves, have mostly been studied at feeding levels above the maintenance requirements (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978). It could be expected, that young calves are even more sensitive to low ambient temperatures during the first weeks after arrival at the rearing farm, because of the very low levels of nutrition during this period. As a consequence of this restricted feeding after arrival, the lower critical temperature of these calves could be higher (Figure 2). Exposure to cold stress (temperatures below the lower critical temperature), resulting in an increased maintenance requirement for sustaining homeothermia, could be considered as unfavourable for these calves. The increased energy requirements will result in an enhanced catabolism of body energy reserves in young, newly purchased calves because of the very low feed allowances.

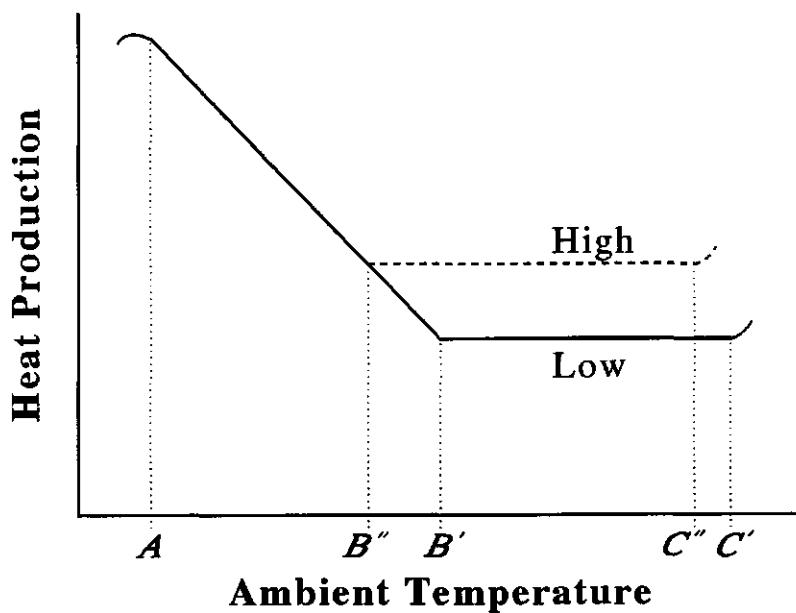


FIGURE 2. Relation between heat production and ambient temperature at two different feeding levels (according to Mount, 1979; Curtis, 1983).

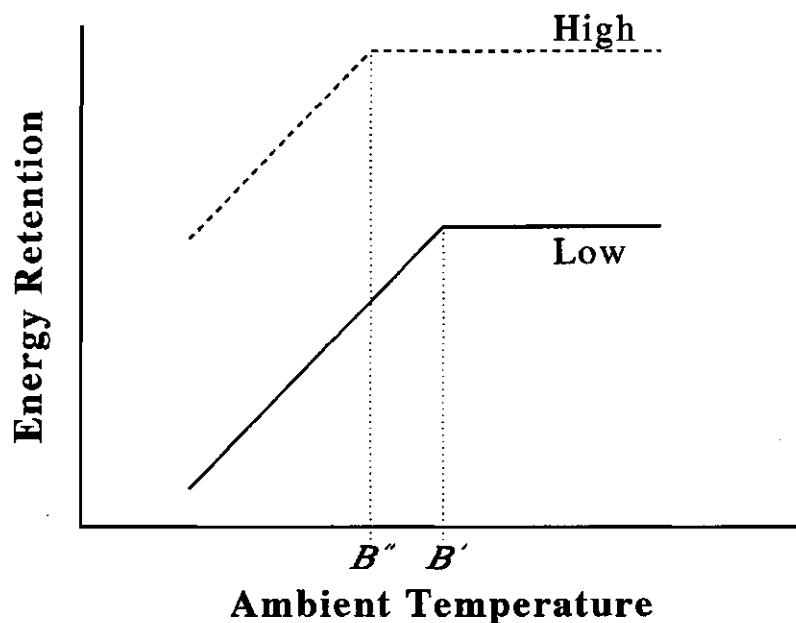


FIGURE 3. Relation between energy retention and ambient temperature at two different feeding levels within the homeothermic zone (derived from Figure 2).

The present study concerns the energy metabolism of young, restrictively fed calves during a period of 1 to 2 weeks after transportation. In the first experiment, the effect of feeding level on energy metabolism was assessed under thermoneutral conditions during the period of 4 to 12 d after transport (Chapter 1). In the second experiment, the effect of feeding level on thermal requirements was evaluated during the period 4 to 14 d after transport, by alteration of the ambient temperature between days, during this period (Chapter 2). The two applied feeding levels (referred to as 'high' and 'low') were chosen to be representative of feeding levels used in practice for young calves during the first 2 weeks after transportation. The low and high feeding levels were designed to be 0.7 and 1.1 times the ME requirements for maintenance, respectively.

These two experiments demonstrated that these calves were not in a steady-state with regard to their energy metabolism. During the period after transportation, heat production was altered with time. The second experiment showed that ambient temperature affected the alteration in heat production over time (days). This led to the hypothesis that thermal requirements change with time after arrival. This premise was investigated in the third experiment in which young calves were fed at the 'low' feeding level during the first 5 d after transportation (Chapter 3).

In Chapter 2 and 3, the effect of ambient temperature on heat production during a whole day (24 h) was assessed. Calves to be reared for veal are commonly housed individually. Consequently, the physical activity of these calves is restricted mainly to the selection of their posture (standing or lying). Heat production is higher during standing than during lying of animals (ARC, 1980; Blaxter, 1989). It can be hypothesized that the posture (standing or lying) of animals may influence both their heat production and their heat loss (thermal insulation). With the data from the third experiment, the thermal requirements in relation to the calf's posture (standing vs lying) were assessed in Chapter 4.

Like many other physiological traits, heat production, heat loss and body temperature of homeothermic animals exhibit circadian rhythms (Aschoff et al., 1974). With the data from the third experiment, a study was conducted to determine whether the relationship between heat production and ambient temperature varied within a day (Chapter 5). Furthermore, circadian fluctuations in this relationship were assessed for their relation to fluctuations in time spent standing within a day.

Finally, the major findings of the Chapters 1 to 5 are discussed in the general discussion. Firstly, the mean results over the period of 1 to 2 weeks after transportation are discussed with regard to the partitioning of energy at thermoneutrality, and with regard to the thermal effect on energy metabolism of young, newly purchased calves. Concerning the latter aspect, the whole day thermal requirements and the impact of behaviour on thermal

requirements are discussed separately. The final part of the general discussion deals with time-related alterations in energy metabolism in young, newly purchased calves after transportation.

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Chapter 1

Alteration of Energy Metabolism of Calves Fed Below Maintenance during 6 to 14 Days of Age

**J.W. Schrama^{*,#}, W. van der Hel^{*}, A. Arieli[†],
and M.W.A. Verstegen[#]**

Departments of ^{*}Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

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ALTERATION OF ENERGY METABOLISM OF CALVES FED BELOW MAINTENANCE DURING 6 TO 14 DAYS OF AGE

J.W. Schrama^{*#}, W. van der Hel^{*}, A. Arieli[†], and M.W.A. Verstegen[#]

Departments of ^{*}Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

Abstract: A study was conducted with seven groups of five to six Holstein-Friesian male calves to evaluate the effect of feeding level during 6 to 14 d of age on energy metabolism of unadapted young calves. Calves were transported at 2 to 3 d of age to their new environment. At 6 d of age measurements of heat production (H) and metabolizable energy (ME) intake started and continued over a period of 8 d. Calves were fed below (four groups) or near (three groups) the maintenance requirement (19 or 30 g of milk replacer powder.kg^{-0.75.d-1}). In contrast to ME intake, H decreased throughout the experimental period. This decrease was larger at the low than at the high feeding level (13.1 vs 3.6 kJ.kg^{-0.75.d-2}; $P < 0.001$). The relationship between H and ME intake was estimated as $H = 382 + 0.318 \times \text{ME intake (kJ.kg}^{-0.75.d}^{-1}\text{)}$. The decrease in H, together with the constant ME intake with time, resulted in a time-dependent relationship between H and ME intake. Estimated basal metabolic rate and efficiency of ME utilization below maintenance decreased with time, whereas the maintenance requirement remained virtually unchanged (560 kJ.kg^{-0.75.d-1}). The influence of feeding level on energy metabolism in young calves increased with time. For at least 12 d after transportation the energy metabolism of young calves had not reached steady-state levels.

Key Words: Adaptation, Calves, Energy Metabolism, Feed Restriction, Maintenance.

Introduction

Veal calves are usually brought to rearing farms at approximately 1 wk of age. Besides the stress of transportation, these calves are exposed to changes in housing system, climate, feeding level, and dietary composition. The first 2 wk after arrival is a critical period in veal production. Stress resulting from collecting animals from various sources and transportation can be regarded as the main cause of mortality in these calves (Roy, 1980).

Toullec (1989) suggested that the greater energy intakes and growth during the first weeks of life in young calves nursed by cows are due to the absence of stress caused by transportation and dietary alteration.

After arrival, feeding level normally increases from below to near the maintenance requirement in approximately 2 wk (Postema, 1985). Energy metabolism has been studied in pre-ruminant calves older than 2 wk and fed above maintenance (van Es et al., 1969; Johnson and Elliott, 1972a,b; Holmes and Davey, 1976). Information regarding energy metabolism of young calves immediately after transportation and fed below or near maintenance requirements is lacking.

The present study was thus designed to evaluate the effect of feeding level on energy metabolism in unadapted young calves immediately after transportation.

Materials and Methods

Animals and Housing. Seven groups of six Holstein-Friesian intact male calves, 2 to 3 d old, weighing approximately 45 kg each, were assigned to one of two feeding level treatments, four groups to a low (FL) and three groups to a high feeding level (FH). One calf assigned to the FH group was removed before the start of the experimental period because of leg problems. All calves were obtained from different commercial dairy farms, where they were fed colostrum. The six calves of each group were collected successively from the different farms and were transported together to the laboratory. The average distance travelled per calf was approximately 100 km. On the day of transportation, the average daily and maximum outdoor temperature was 7°C (SEM = 1.4, df = 6) and 12°C (SEM = 1.5, df = 6), respectively. At arrival the calves had been without food for about 6 to 12 h.

The experiment consisted of a 3.5-d preliminary period succeeded by an 8-d experimental period. The preliminary period was applied to allow calves to be treated for *E. coli* and to adjust them to wearing faecal collection bags.

Because of their different origins, calves were treated for *E. coli* with antibiotics on arrival (Belcomycine® S, Rhône Mérieux, Lyon, France, or Leotrox® injectable 24%, Leo Pharmaceutical Products B.V., Weesp, The Netherlands). Calves with blood haemoglobin values (Hb) < 10 g/100 mL were treated with Fe-dextran to avoid anaemia (Hb 9 to 10 g/100 mL: 400 mg of Fe i.m.; Hb 8 to 9 g/100 mL: 600 mg of Fe i.m.; Hb 7 to 8 g/100 mL: 800 mg of Fe i.m.). In total, nine FL calves (38%) and six FH calves (35%) were treated with Fe-dextran.

On arrival, each group was placed in a large open-circuit, indirect climatic respiration chamber (Verstegen et al., 1987). Each calf was fitted with a faecal collection bag and maintained individually in a metabolism cage (dimensions, 1.15 m × 0.46 m). Environmental temperature was kept constant at 15°C, which was assumed to be above the lower critical temperature (Roy, 1980; Schrama et al., 1991). Relative humidity was maintained at approximately 65%. Lights were on from 0745 to 1945.

Feeding. Calves were fed a commercial starter milk replacer (Nukamel Starter, n.v. Nukamel s.a., Olen, Belgium), which contained 23% crude protein and 20 kJ of gross energy (GE) per g of powder. Dietary protein originated from dairy products (Table 1). Amounts of powder offered to FL and FH were 19 and 30 g of powder.kg^{-0.75.d-1}, respectively, and were intended to be 0.7 and 1.1 times the ME requirement for maintenance (ME_m), respectively. Feeding levels chosen are representative of feeding levels used in practice for young veal calves during the first 2 wk after arrival. Feeding levels were kept constant during the experimental period and were calculated for each calf based on initial body weight (BW) and a ME_m requirement of 460 kJ.kg^{-0.75.d-1} (van Es et al., 1969). During the preliminary period, feed intake increased from arrival up to the FH level. At the beginning of the experimental period the feeding level of the FL group was lowered abruptly, whereas the FH group remained at the high level.

Milk replacer was fed at a temperature of 40°C at 0800 and 1900. Warm (35°C) water was offered at 1330, providing a total daily liquid input originating from both milk replacer and warm water of 10% of BW. Water and milk replacer were offered through a rubber teat.

TABLE 1. Composition of milk replacer powder^a

Ingredient	%
Skim milk powder	50.0
Sweet whey powder	23.0
Delactosed whey powder	7.5
Pre-gelatinized starch	2.5
Fat bland	16.0
Vitamin and mineral premix	1.0

^aDry matter basis.

Measurements. At the beginning and end of the experimental period individual BW were measured at 0900 and adjusted for milk replacer intake at 0800. Daily feed intake for each calf was corrected for feed refusals. Faeces and urine were collected daily, composited

for each calf, and sampled. Gross energy values were determined by adiabatic bomb calorimetry. Energy metabolizability (ME/GE) per calf during the experimental period was calculated from energy contents of feed, faeces and urine. In pre-ruminant calves methane production is very low (Gonzalez-Jimenez and Blaxter, 1962; Meulenbroeks et al., 1986); therefore, methane energy losses were not taken into account. Daily ME intake was calculated from feed intake and calculated ME/GE ratio during the total experimental period. Rectal temperature was measured daily at 0830. Heat production (H) of each group was determined daily from continuous measurements (every 9 min) of exchange of CO_2 and O_2 (Verstegen et al., 1987), according methods described by Brouwer (1965). Because of collection procedures in the chamber, measurements of H started 1 h after the morning feeding (23 h/d in total).

Statistical Analysis. Statistical evaluations of data were performed using SAS (1985). Rectal temperature, GE intake, and ME intake are averaged over the experimental period for each calf because no time effects were present for these variables. Initial BW, rate of BW change, rectal temperature, GE intake, ME/GE ratio, and ME intake were analyzed by one-way analysis of variance.

Daily H within groups were repeated measurements. Therefore, orthogonal polynomials of day number were used in the analysis for the effect of feeding level, time, and their interaction on H. The model used was as follows:

$$Y_{ijk} = \mu + F_i + e_{1,ij} + \beta \times (d_k - \bar{d}) + \beta_i \times (d_k - \bar{d}) + e_{2,ijk} \quad [1]$$

where Y_{ijk} = H at feeding level i, group j, and day number k; μ = overall mean; F_i = the effect of feeding level i ($i = 1, 2$); $e_{1,ij}$ = error term 1, which represents the random effect of group j within feeding level i ($j = 1, \dots, N_i$; N_i = number of groups within feeding level i); d_k = day number during the experimental period ($k = 1, \dots, 8$); \bar{d} = average day number during the experimental period; β = overall regression coefficient of H on d; β_{1i} = regression coefficient of H on d within feeding level i, representing the interaction effect between time and feeding level; and $e_{2,ijk}$ = error term 2.

Effect of feeding level was tested for significance against error term 1. The other two effects were tested against error term 2.

Heat increment of utilization of ME below maintenance ($1 - k_m$), ME_m , and basal metabolic rate (BMR) were estimated by linear regression of H on ME intake; values of H and ME intake were averages of the experimental period per group. Similar regressions were calculated for values of H and ME intake per day and per group.

TABLE 2. Number of calves, number of groups, means, SEM and significance level of initial body weight (BW), rate of BW change, rectal temperature, gross energy (GE) intake, metabolizability (ME/GE), and metabolizable energy (ME) intake of young calves differing in feeding level

Item	Feeding level		SEM	<i>P</i> -value ^b
	Low	High		
No. of calves	24	17	---	---
No. of groups	4	3	---	---
Initial BW, kg	43.7	43.6	0.80	NS
Rate of BW change, kg/d	-0.33	-0.09	0.031	***
Rectal temperature ^a , °C	38.53	38.77	0.078	*
GE intake, kJ.kg ^{-0.75.d-1}	369	551	5.5	***
ME/GE	0.74	0.78	0.020	NS
ME intake, kJ.kg ^{-0.75.d-1}	274	431	9.8	***

^aTwo thermometers were used; therefore, rectal temperatures are adjusted for effects of thermometer.

^bNS = not significant, *P* > 0.05; * *P* < 0.05; *** *P* < 0.001.

Results

Mean values for various traits are shown in Table 2. Orts were < 4% of the offered feed. Considerable variation among calves in ME/GE was noted; the SEM of ME intake was approximately twice that of GE intake. Intake of ME differed between feeding levels (*P* < 0.001) and, consequently, rate of BW change, which was negative at both feeding levels, was also different (*P* < 0.001). Rectal temperature was normal but was higher (*P* < 0.05) at FH.

Average *H* during the experimental period was higher (50 kJ.kg^{-0.75.d-1}) at FH than at FL (*P* < 0.05; Table 3). Heat production decreased with time (*P* < 0.001), whereas ME intake was constant during the experimental period (Figures 1 and 2). The slope of the regression of *H* over time differed between feeding levels (*P* < 0.001); the linear decrease in *H* was highest for FL (Figure 1, Table 3). There were no nonlinear components of time effect on *H* (*P* > 0.05).

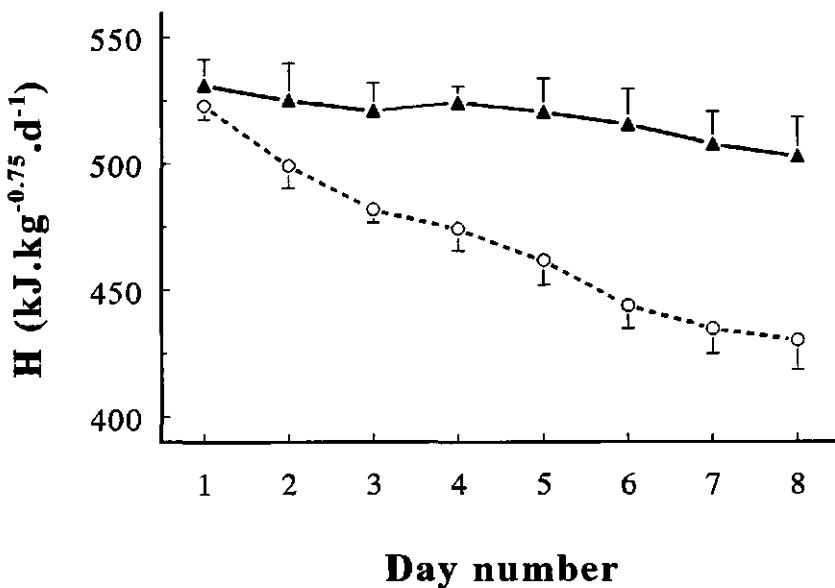


FIGURE 1. Mean daily heat production (H) of young calves on a low (FL; ---○---) or a high feeding level (FH; —▲—) during the experimental period. Vertical bars represent SE.

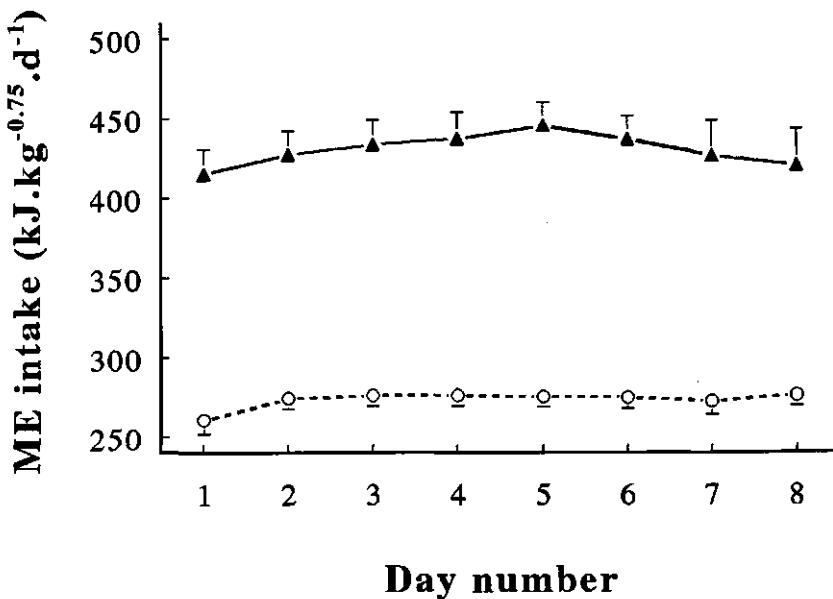


FIGURE 2. Mean daily metabolizable energy intake (ME) of young calves at a low (FL; ---○---) or a high feeding level (FH; —▲—) during the experimental period. Vertical bars represent SE.

TABLE 3. Mean heat production (H) and daily change in H during the experimental period in young calves differing in feeding level^a

Item	Feeding level		SEM	P-value ^b
	Low	High		
Mean H, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	469	519	9.6	*
Change in H, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-2}$	-13.1	-3.6	0.70	***

^a R^2 , standard deviation in H between groups and standard deviation in H between days were 0.96, 17.6 and 8.4, respectively.

^b* $P < 0.05$; *** $P < 0.001$.

For the total experimental period, H was related to ME intake (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) by the following equation:

$$H = 382 (\pm 24.6) + 0.318 (\pm 0.070) \times \text{ME intake} \quad R^2 = 0.80 \quad [2]$$

From Equation [2] ME_m was estimated as $560 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, BMR as $382 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and k_m as 0.68.

Regression of H on ME intake per day showed that the relationship between H and ME intake changed with time such that estimated BMR and k_m decreased, whereas ME_m remained similar (Figure 3).

Discussion

The present study demonstrated a clear alteration in level of H by young calves during the 12 d after transportation to the experimental facilities. Besides the transportation itself, calves had to adapt to the housing system and to feed quality and quantity. The adaptation, which was affected by feeding level, seemed to play an important role in determining metabolic rate in these calves.

On both feeding levels calves lost weight, indicating that feeding levels were below ME_m . The estimated ME_m in this study of $560 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ was higher than the range of 390 to $460 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ reported for young, milk-fed calves (van Es et al., 1969; Johnson and Elliott, 1972a,b; Holmes and Davey, 1976). In the present study, however, calves were younger and feeding levels were lower than those described in previous reports. Furthermore, estimations of ME_m by extrapolation to zero energy retention are negatively related to feeding level, because of the nonlinear relationship between H and ME (Blaxter, 1989).

The efficiency of utilization of ME below maintenance (k_m) of 0.68 was lower than the range of 0.80 to 0.90, which is often assumed for nonruminant animals (ARC, 1980; Blaxter, 1989). Despite the higher estimate of ME_m and the lower estimate of k_m , estimated BMR ($382 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) was similar to earlier estimates (ARC, 1980).

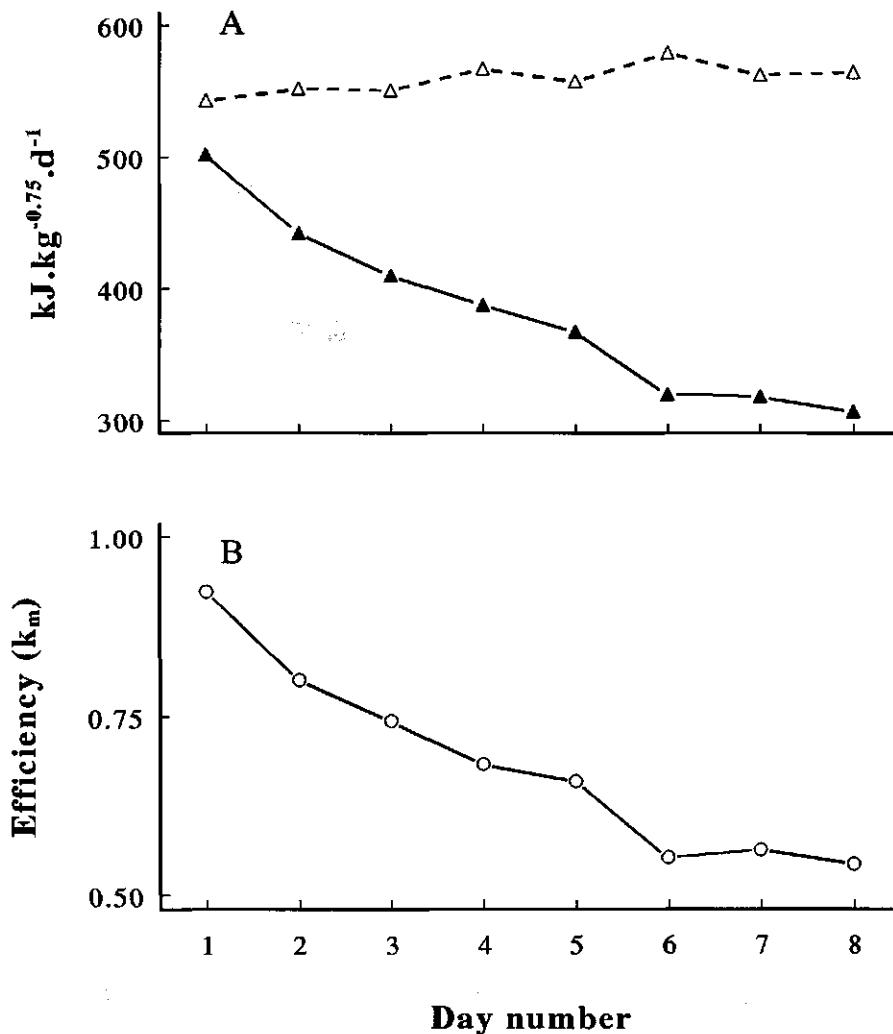


FIGURE 3. Daily estimations of (A) maintenance requirements (ME_m ; ---Δ---), basal metabolic rate (BMR; —▲—), and (B) efficiency of utilization of metabolizable energy below maintenance (k_m ; —○—) during the experimental period.

Figure 1 shows that H decreased with time. Comparable data regarding H and alteration of H by young, feed-restricted calves immediately after transportation are lacking. The decline in H with time was higher at FL than at FH (Figure 1, Table 3), suggesting that H depended more on ME intake. Over time k_m decreased from 0.93 to 0.55 (Figure 3); k_m during the last 4 d of the experimental period were lower than values in previous experiments (ARC, 1980; Blaxter, 1989). In Figure 3 it was assumed that ME/GE was constant throughout the experimental period. The ME/GE of the milk replacer (0.76) was low, although it was comparable to that in other studies with very young calves (Neergaard, 1980). The low ME/GE could be related to incomplete development of the digestive tract at this age (Toullec and Guilloteau, 1989). Recalculation of the relationship between H and ME intake, assuming that ME/GE increased gradually from 0.71 at d 1 to 0.81 at d 8, however, altered each of the values of BMR, k_m and ME_m by less than 5%.

In the present study metabolic adjustment of young calves to the new environment immediately after transportation was investigated. Although effects of transportation and change in housing, climate, and diet quality were similar among both feeding levels, the effect of reduction in feeding level at the start of the experimental period was only present at FL. The observed decline in H might be regarded as a carry-over effect of the feeding level in the preliminary period, as well as to an initial high metabolic rate before transportation. However, the present reduction in H at FL would lead to an unrealistically low value of H (approximately $150 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) in the steady-state situation following the theory of Turner and Taylor (1983), assuming that the change in H of $13.1 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-2}$ is 3.5%/d of the total change in metabolic rate after an alteration in feeding level.

The observed alteration in the relationship between H and ME intake with time (Figure 3) cannot be fully explained by an increase in ME/GE with age and by a carry-over effect of the prior feeding level. To interpret the decrease in k_m and BMR (Figure 3) the sources from which H originated should be considered. For animals fed below ME_m (as in the present study) H can be separated (Holmes and Davey, 1976) into 1) the "true" net energy cost of maintenance (tNE_m), representing the energy equivalent of ATP required for sustaining primary life processes and 2) the heat produced during the utilization of dietary ME ($1 - k_1$) and the utilization of body energy stores (BES; defined as the amount of energy mobilized from body stores) ($1 - k_2$) to meet tNE_m . Hence:

$$H = tNE_m + (1 - k_1) \times ME + (1 - k_2) \times BES \quad [3]$$

Below maintenance both endogenous (BES) and exogenous energy (ME intake) are used

to meet tNE_m :

$$tNE_m = k_1 \times ME + k_2 \times BES,$$

which equals:

$$BES = (tNE_m - k_1 \times ME) / k_2 \quad [4]$$

Substituting Equation [4] into [3] gives the relationship between H and ME intake for feeding levels below maintenance:

$$H = (1/k_2) \times tNE_m + (1 - k_1/k_2) \times ME \quad [5]$$

Below maintenance the following expressions can be derived from Equation [5]:

$$k_m = k_1/k_2 \quad [6]$$

$$BMR = (1/k_2) \times tNE_m \quad [7]$$

$$ME_m = (1/k_1) \times tNE_m \quad [8]$$

Thus, k_m appears to be a ratio between k_1 and k_2 (Equation [6]), which is equal to the ratio, used for calculating k_m theoretically (Armstrong, 1969; Blaxter, 1989), of the enthalpy of combustion/mol ATP of tissue spared from oxidation ($1/k_2$) to the enthalpy of combustion/mol ATP of nutrients supplied by the diet ($1/k_1$). According to Equation [7] BMR estimated by regressing H on ME intake or measured in fasting animals is always higher than tNE_m .

The alteration with time in the relationship between H and ME intake in the present study could be related to variation in k_1 , k_2 , and/or tNE_m according to Equations [6], [7], and [8]. The decrease in BMR and k_m , but not in ME_m (Figure 3), might indicate that there is an increase in k_2 (efficiency of utilization of energy from body stores) with time. The suggested increase in k_2 (resulting in a decrease in k_m and BMR) with time might be related to exhaustion of body energy reserves, which are actually low in newborn calves (Roy, 1980). The reduction of thyroid hormone level found in feed-restricted, young pre-ruminants lambs (Wrutniak and Cabello, 1987) might also be involved in the present decrease in metabolic rate (i.e., decrease in k_m and BMR). However, the present increase in k_2 with time (expressed by a decrease in k_m and BMR, Figure 3) might also be the result of restoration of an earlier reduction in k_2 directly after arrival induced by exposure to

stressors. In addition to the stress of transportation, the calves in the present study were exposed to changes in housing system, climate, feeding level, and dietary composition. The hormonal responses to stress exposure enable the animal to mobilize its energy reserves quickly for metabolic processes (Dantzer and Mormède, 1983). This enhanced mobilization of energy reserves might be related to a possible reduction of the efficiency of utilization of BES (k_2) directly after arrival.

From the results of the present study it is impossible to distinguish whether the change in relationship between H and ME intake is due to the process of aging or is a manifestation of a mechanism of adaptation to variables such as restricted feeding level or exposure to stressors. The present study shows that young calves (6 to 14 d of age) are not in a steady-state with respect to energy metabolism.

Implications

After arrival, young veal calves are usually fed below maintenance. Because these calves have a high maintenance requirement and feed intake is restricted, they are very dependent on stores of body energy. Furthermore, young veal calves are exposed to several concomitant stressors. For practical animal husbandry it is important to understand the processes of adaptation in relation to susceptibility to disturbances. The influence of adaptation processes on thermal requirement and energy metabolism is not well known.

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Chapter 2

Responses of Young Calves to Low Ambient Temperatures at Two Levels of Feeding

**J.W. Schrama^{*#}, A. Arieli[†], M.J.W. Heetkamp^{*},
and M.W.A. Verstegen[#]**

Departments of ^{*}Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

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RESPONSES OF YOUNG CALVES TO LOW AMBIENT TEMPERATURES AT TWO LEVELS OF FEEDING

J.W. Schrama*,[#], A. Arieli[†], M.J.W. Heetkamp*, and M.W.A. Verstegen[#]

Departments of *Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

Abstract: Seven groups of five or six Holstein-Friesian male calves were transported to an experimental farm at 2 to 3 d of age. At 6 d of age, heat production (H) and metabolizable energy (ME) intake were measured for an 8-d period. During this period, calves were exposed to various ambient temperatures: 6, 9, 12 and 15°C. Ambient temperature was constant within days, but changed between days. Calves were fed below (four groups) or near (three groups) the maintenance requirements (290 or 460 kJ of ME.kg^{-0.75.d-1}). From 6 to 14 d of age the lower critical temperature (LCT) was 12.5°C and H increased by 8.4 kJ.kg^{-0.75.d-1} per °C fall in ambient temperature below LCT. Both LCT and increase in H below LCT were not affected by feeding level. Rectal temperature was lower at low ambient temperatures. The decrease in rectal temperature with ambient temperature was greatest at the low feeding level. During the experimental period, calves were not in a steady-state regarding energy metabolism. Heat production decreased with time. This decrease was affected by feeding level and ambient temperature. After arrival, the influence of both ambient temperature and feeding level on the energy metabolism of young calves increased with time.

Key Words: Calves, Energy Metabolism, Food Intake, Heat Production, Thermoregulation.

Introduction

In The Netherlands, calves to be reared for veal are usually brought on farm at an age of about 1 wk. In addition to the stress of transportation, these calves are exposed to changes in housing system, climate, feeding level and dietary composition. The first few weeks after arrival are a critical phase in veal production in relation to the health of the calves (Webster et al., 1985).

Restricted feeding schedules are applied immediately after arrival on the veal farm

to reduce gastrointestinal disorders. At low feeding levels however, animals are less cold-tolerant (Webster, 1976), with an increase in the lower critical temperature (LCT). The energy requirements are increased in animals exposed to ambient temperatures below LCT (Mount, 1974). Schrama et al. (1992) observed during the first 2 wk after arrival an increased maintenance requirement in calves kept at thermoneutral conditions (15°C). As a result of the initial low feeding level and higher maintenance requirements of veal calves after arrival, it is important to avoid any increase in energetic demand due to exposure to cold conditions.

So far, the thermal requirements of young calves have mostly been studied at feeding levels above the maintenance requirements (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978). The metabolizable energy (ME) intake in these studies ranged from 750 to 950 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. Except from a preliminary study by Schrama et al. (1991), no information is available on the thermal requirements of young calves at low feeding levels and during the critical phase after transportation.

The present study was designed to evaluate the effect of feeding level on the thermal requirements of young calves during the first 2 wk after arrival on the veal farm.

Materials and Methods

Animals and Housing Seven groups of six Holstein-Friesian male calves were assigned in a 2×2 factorial arrangement of treatments to one of two feeding levels and to one of two ambient temperature sequences. One calf was removed before the start of the experimental period, due to omphalitis. Upon arrival, calves were 2 to 3 d old and weighed about 45 kg (Table 1). Each calf was obtained from a different dairy farm, where it was fed colostrum. The six calves per group were each collected successively from the farms and were transported together to the experimental facility. The average distance travelled per calf was about 100 km. On the day of arrival, the daily average and maximum outdoor temperatures were 7°C (SEM = 1.4) and 12°C (SEM = 1.5), respectively. Upon arrival the calves had been without food for 6 to 12 h.

Upon arrival, calves were treated with antibiotics (Belcomycine® S, Rhône Mérieux, Lyon, France, or Leotrox® inj. 24%, Leo Pharmaceutical Products B.V., Weesp, Holland) to reduce the risk of enteric infections. Additionally, calves with blood haemoglobin values (Hb) below 10 g/100 mL were treated with Fe-dextran to avoid anaemia (Hb 9 to 10 g/100 mL: 400 mg Fe i.m.; Hb 8 to 9 g/100 mL: 600 mg Fe i.m.; Hb 7 to 8 g/100 mL: 800 mg Fe i.m.). In total, 16 calves (39%) were treated with Fe-dextran.

Each group was housed in a large open-circuit indirect climatic respiration chamber (Verstegen et al., 1987). Each calf was fitted with a faecal collection bag and maintained individually in a metabolism cage (dimensions 1.15 m × 0.46 m). Relative humidity was maintained at about 65% and air velocity was below 0.20 m/s. Lights were on from 0745 to 1945.

Preliminary Period. The experiment consisted of a 3.5-d preliminary period followed by an 8-d experimental period. The preliminary period was applied to allow calves to be treated for possible *E. coli* infections and to adjust to the wearing of faecal collection bags. Food intake at both the 'low' (FL) and 'high' feeding level (FH) was progressively raised during the preliminary period to 1.1 times the maintenance requirement. At the LF groups, the feeding level was abruptly lowered to 0.7 times the maintenance requirement at the start of the experimental period. For the groups of calves exposed to the temperature sequence starting at an ambient temperature of 15°C (TS₁₅₋₆₋₁₅), ambient temperature in the preliminary period was 15°C. Ambient temperature was reduced by 3°C per day during the preliminary period for those groups of calves, which were exposed to the temperature sequence starting at 6°C (TS₆₋₁₅₋₆) (Figure 1).

Feeding. Calves were fed a commercial starter milk replacer (Nukamel Starter, n.v. Nukamel s.a., Olen, Belgium); four groups at a 'low' (FL) and three groups at a 'high' feeding level (FH). The milk replacer contained 230 g crude protein and 20 MJ gross energy (GE) per kg powder. Dietary protein originated from dairy products (Schrama et al., 1992).

Amounts of powder offered to FL and FH were 19 and 30 g of powder.kg^{-0.75.d-1}, respectively, and were intended to be 0.7 and 1.1 times the ME requirements for maintenance, respectively. Feeding levels were kept constant during the experimental period, and were calculated for each calf based on initial body weight (BW) assuming the value of 460 kJ.kg^{-0.75.d-1} for maintenance requirement (van Es et al., 1969).

Milk was offered at a reconstitution rate of 150 g of powder/kg of milk and at a temperature of 40°C at 0800 and 1900. Warm (35°C) water was offered at 1330, providing a total daily liquid input originating from both milk replacer and warm water, of proportionately 0.1 of BW. Water and milk replacer were offered through a rubber teat.

Ambient Temperature. During the experimental period four ambient temperatures were applied: 6, 9, 12 and 15°C, on the assumption that young calves fed below or near the maintenance requirements have a lower critical temperature (LCT) between 12 and 15°C

(Schrama et al., 1991). Each day ambient temperature was changed by 3°C at 0900. Two groups at FL and one group at FH were exposed to a temperature sequence starting at 15°C, decreasing to 6°C and increasing back to 15°C ($TS_{15-6-15}$). The remaining groups were exposed to a reversed sequence starting at 6°C, increasing to 15°C and decreasing back to 6°C (TS_{6-15-6}) (Figure 1). These two temperature sequences were used to account for any effects of sequence of temperature change on the relation between ambient temperature and heat production (H) itself.

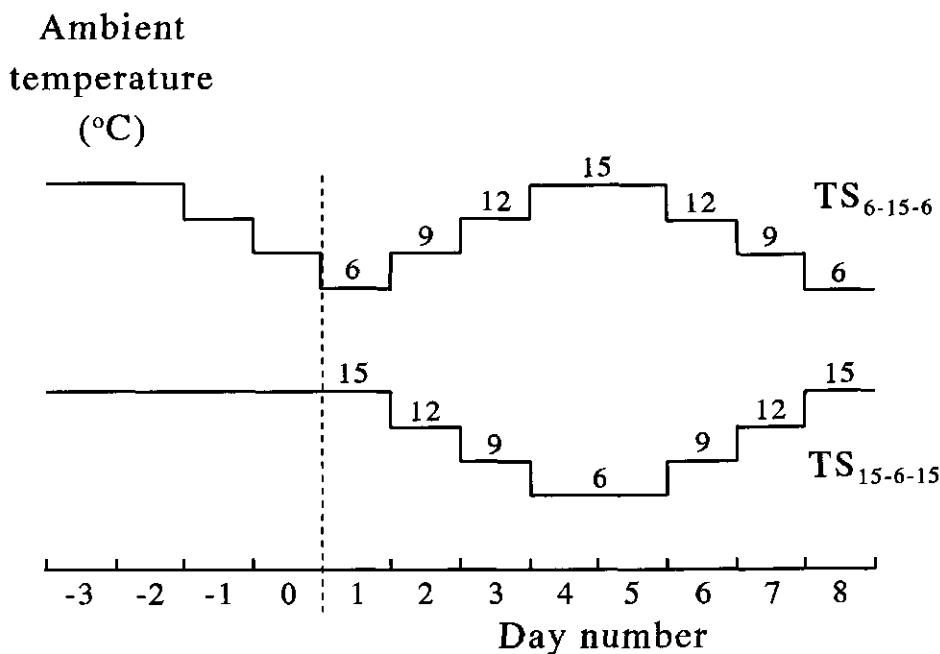


FIGURE 1. Experimental design of ambient temperature with time of the two temperature sequences (TS_{6-15-6} and $TS_{15-6-15}$).

Measurements. At the beginning and end of the experimental period calves were weighed at 0900. The individual BW were adjusted for milk intake at 0800. Daily food intake for each calf was corrected for feed refusals. Faeces and urine were collected daily during the experimental period and were bulked and sampled per calf. Calorific values were determined by adiabatic bomb calorimetry. Metabolizability (ME/GE) of energy intake per calf during the experimental period was derived from energy content in food, faeces and urine. In pre-ruminant calves methane production is very low (Gonzalez-Jimenez and Blaxter, 1962; Meulenbroeks et al., 1986), so methane energy losses were not taken into account. Rectal temperature (T_{rec}) was measured daily at 0830. Heat production (H) of each group was determined daily from continuous measurements (every 9 min) of exchange of

CO_2 and O_2 (Verstegen et al., 1987), according to Brouwer (1965). Measurements of H started 1 h after the morning feeding (23 h/d in total). Data on ME and H were expressed in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$.

Statistical Analysis. Data on initial BW, rate of BW change, GE intake, ME/GE and ME intake were tested for the effect of feeding level and temperature sequence by using a two-way analysis of variance.

The effect of feeding level, temperature sequence and ambient temperature on H were tested by means of F -tests using a split-plot model (procedure GLM; SAS, 1985), with data of daily H within groups taken as repeated measurements. Day number during the experimental period was included as a covariate in the analysis. Schrama et al. (1992) found that the effect of time (day number during the experimental period) on H of young calves after transportation was influenced by feeding level. Hence, the interaction effects of time with feeding level, temperature sequence and ambient temperature were included in the model:

$$Y_{ijklm} = \mu + F_i + TS_j + e_{1,ijk} + T_l + (F \times T)_{il} + (TS \times T)_{jl} \\ + \beta(d_m - \bar{d}) + \beta_i(d_m - \bar{d}) + \beta_j(d_m - \bar{d}) + \beta_l(d_m - \bar{d}) + e_{2,ijklm} \quad [1]$$

where Y_{ijklm} = daily H per group; μ = overall mean; F_i = fixed effect of feeding level ($i = 1, 2$); TS_j = fixed effect of temperature sequence ($j = 1, 2$); $e_{1,ijk}$ = error term 1, which represented random effect of group within the feeding level and temperature sequence ($k = 1, 2$); T_l = fixed effect of ambient temperature ($l = 1, \dots, 4$); d_m = day number during the experimental period ($k = 1, \dots, 8$); \bar{d} = average day number during the experimental period; β = overall regression coefficient of H on d_m ; β_i = regression coefficient of H on d_m within feeding level i ; β_j = regression coefficient of H on d_m within temperature sequence j ; β_l = regression coefficient of H on d_m within ambient temperature k ; $e_{2,ijklm}$ = error term 2, which represented random effect within group between day number.

The effects of feeding level and temperature sequence were tested for significance against the effect of group within the feeding level and temperature sequence (error term 1). The other effects were tested against the random effect between day number within group (error term 2).

Daily values of T_{rec} per calf were analyzed by the same model used for H (Equation [1]). The random effect of group was now replaced by the random effect of calf.

The lower critical temperature (LCT), extra thermal heat production (ETH) below LCT and heat production at thermal neutrality (H_{th}) were estimated for each group from

the daily values of H and ambient temperature by using a model based on that of van der Peet et al., (1987) (using the DUD non-linear regression method of the procedure NLIN; SAS, 1985):

$$H_i = H_{th} + \log_e [1 + e^{(ETH \times [LCT - T_i])}] \quad [2]$$

where H_i = heat production (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) at day i ($i=1, \dots, 8$); H_{th} = the heat production in the thermoneutral zone; ETH = extra thermoregulatory heat production (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot \text{C}^{-1}$); T_i = ambient temperature (in $^{\circ}\text{C}$) at day i ; LCT = lower critical temperature.

The estimated values per group of LCT , ETH and H_{th} were tested for the effect of feeding level and temperature sequence by using a two-way analysis of variance.

Results

Least square means for various traits at both feeding levels are depicted in Table 1. Food refusals were proportionately less than 0.03 of the offered food. Metabolizability (ME/GE) was not influenced by feeding level ($P > 0.05$). Intake of GE was constant during the experimental period. Consequently, ME intake was also constant with time assuming that ME/GE did not alter. The difference in ME intake between feeding levels was 164

TABLE 1. Number of calves, number of groups and least square means of initial weight (BW), rate of BW change, gross energy (GE) intake, metabolizability (ME/GE) and metabolizable energy (ME) intake of young calves at different feeding levels^a

Item	Feeding level		SEM	Significance of feeding level ^b
	Low	High		
No. of calves	23 ^c	18	---	---
No. of groups	4	3	---	---
Initial BW, kg	43.3	43.8	1.00	NS
Rate of BW change, kg/d	-0.34	-0.07	0.038	***
GE intake, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	373	558	11.2	***
ME/GE	0.78	0.81	0.014	NS
ME intake, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	291	455	13.1	***

^aThe effect of temperature sequence and interaction between temperature sequence and feeding level were not significant for all traits.

^bNS = not significant, $P > 0.05$; *** $P < 0.001$.

^cOne calf at TS₆₋₁₅₋₆ removed before the beginning of the experimental period, due to omphalitis.

$\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ($P < 0.001$). Calves lost weight at both feeding levels. The rate of BW change was different between feeding levels ($P < 0.001$; Table 1). Rate of BW change, GE intake, ME/GE and ME intake were not affected by temperature sequences.

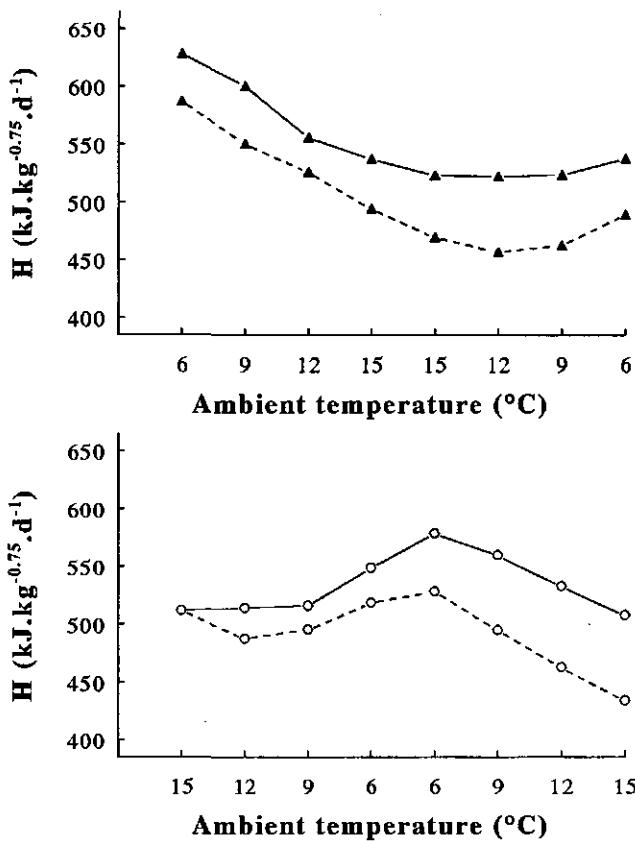


FIGURE 2. Heat production (H) at the experimental ambient temperatures during successive days of young calves at two different feeding levels and two different temperature sequences (TS): —, high feeding level; ----, low feeding level; ▲, TS₆₋₁₅₋₆; ○, TS₁₅₋₆₋₁₅.

Heat Production. Data on H at each ambient temperature are shown in Figure 2. Average H during the experimental period was higher at FH compared with FL ($P < 0.05$; Table 2 and 3). The mean H during the experimental period was influenced by ambient temperature ($P < 0.001$; Table 2). Heat production was increased at low ambient temperatures (Table 3 and Figure 2). The interaction between feeding level and ambient

temperature was not significant (Table 2). The difference in H between FH and FL was about $46 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ at each ambient temperature (Table 3). Temperature sequence had no significant influence on the mean H (Table 2).

TABLE 2. Results of the statistical analyses of the effects of feeding level (F), temperature sequence (TS), group number (e_1), day number (d), temperature (T) and interactions on heat production and on rectal temperature with day number taken as a linear covariable

Effect	Heat production ^a			Rectal temperature ^{bc}		
	d.f.	Mean squares	F probability	d.f.	Mean squares	F probability
F ^{ab}	1	28443.8	0.024	1	27.230	<0.001
TS ^{ab}	1	3333.8	0.291	1	1.461	0.129
e_1	4	2251.7	<0.001	38	0.605	<0.001
T	3	7386.4	<0.001	3	2.841	<0.001
F × T	3	41.6	0.858	3	0.477	0.008
TS × T	3	6.5	0.989	3	0.101	0.467
d	1	21310.9	<0.001	1	4.501	<0.001
d × F	1	2382.9	<0.001	1	3.763	<0.001
d × TS	1	9544.2	<0.001	1	0.387	0.072
d × T	3	903.9	0.003	3	2.841	0.008
e_2	34	163.4	---	272	0.118	---

^aEffect of feeding level (F) and temperature sequence (TS) on heat production were tested against the random effect of group number (e_1).

^bEffect of feeding level (F) and temperature sequence (TS) on rectal temperature were tested against the random effect of animal (e_1).

^cTwo different thermometers were used, therefore rectal temperatures were adjusted for the effect of thermometer.

TABLE 3. Adjusted least square means of heat production (H) at different ambient temperatures at both feeding levels, difference in H between feeding levels and average of both levels (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$)^a

Ambient temperature, °C	Feeding level		Difference between high and low	Average of high and low
	Low	High		
6	531 ^x	573 ^x	42	552 ^x
9	501 ^y	551 ^y	50	526 ^y
12	484 ^{yz}	531 ^{yz}	47	507 ^z
15	478 ^z	521 ^z	43	499 ^z
SEM	4.5	5.4	7.0	3.5

^aThe values are adjusted for the effect of time to the average day number during the experimental period (i.e., the mean H value of the two replicates at each ambient temperature).

^{x,y,z}Values in columns with different superscripts are significantly different ($P < 0.05$).

Heat production altered with time during the experimental period ($P < 0.001$; Table 2). Thus, within feeding level and temperature sequence, H at each ambient temperature was different between the first and second exposure (Figure 2). When averaged over feeding levels, temperature sequences, and ambient temperatures, H decreased with time by $8.9 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$.

The effect of time on H was significantly affected by feeding level, ambient temperature, and temperature sequence (Table 2 and 4). Heat production decreased with time by 11.8 and $6.0 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$ at FL and FH, respectively ($P < 0.001$). The decline in H with time was 3.7 , 6.2 , 9.6 and $16.0 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$ at 6 , 9 , 12 and 15°C , respectively ($P < 0.01$). The decrease in H was higher at TS_{6-15-6} by $19 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$ compared with $\text{TS}_{15-6-15}$ ($P < 0.001$).

Feeding level and temperature sequence did not influence the estimates of LCT and ETH per group. Averaged over all groups, LCT was 12.5°C (SEM = 0.57) and ETH was $8.4 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-1} \cdot {}^\circ\text{C}^{-1}$ (SEM = 0.99). H_{th} was higher at FH compared with FL ($P < 0.01$); being 521 and $478 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-1}$, respectively (SEM = 6.3).

TABLE 4. Effect of ambient temperature, feeding level and temperature sequence on change in heat production (H) and change in rectal temperature (T_{rec}) with time

Main effects	Change in H with time, $\text{kJ.kg}^{-0.75} \cdot \text{d}^{-2}$	Change in T_{rec} with time, ${}^\circ\text{C/d}$
Ambient temperature		
6°C	-3.7^y	-0.081^{yz}
9°C	-6.2^y	-0.107^z
12°C	-9.6^{yz}	-0.015^y
15°C	-16.0^z	-0.008^y
SEM	1.80	0.0120
Feeding level		
Low	-11.8^y	-0.101^y
High	-6.0^z	-0.005^z
SEM	1.09	0.0121
Temperature sequence		
$\text{TS}_{15-6-15}$	0.7^y	-0.078
TS_{6-15-6}	-18.5^z	-0.028
SEM	1.48	0.0164

^{y,z}Values in columns within each main effect, with different superscripts are significantly different ($P < 0.05$).

Rectal Temperature. Data on T_{rec} at various ambient temperatures are shown in Figure 3. Mean T_{rec} was higher at FH compared with FL, 38.68 and $38.08 {}^\circ\text{C}$ ($P < 0.001$; Table 2). Rectal temperature decreased with declining ambient temperature (Table 5 and

Figure 3). There was an interaction of feeding level and ambient temperature on T_{rec} ($P < 0.01$; Table 2). The decrease in T_{rec} with ambient temperature was larger at FL compared with FH. Therefore, the difference in T_{rec} between both feeding levels was highest at low ambient temperatures (Table 5 and Figure 3).

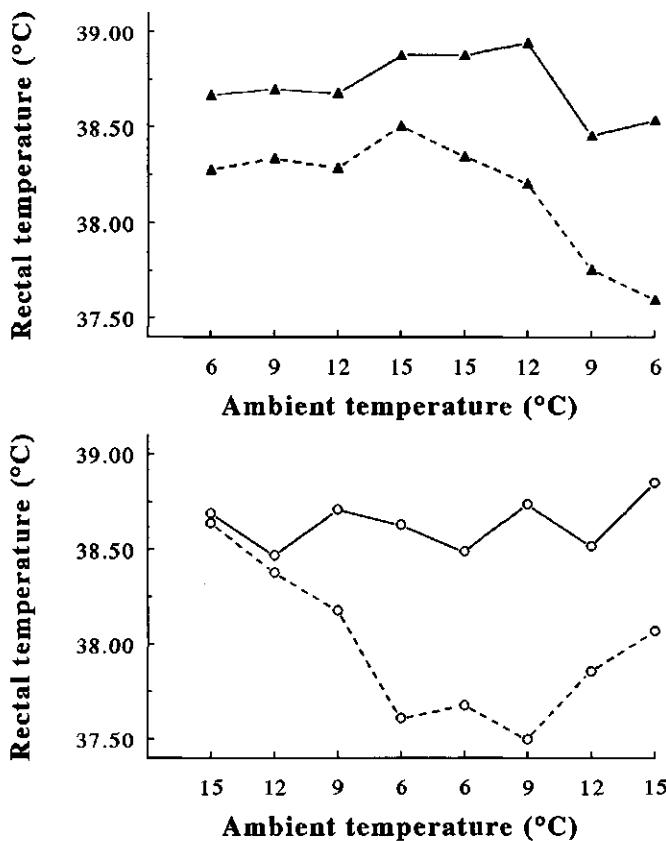


FIGURE 3. Rectal temperature at the experimental ambient temperatures during successive days of young calves at two different feeding levels and two different temperature sequences (TS): —, high feeding level; ----, low feeding level; ▲, TS₆₋₁₅₋₆; ○, TS₁₅₋₆₋₁₅.

Within feeding level and temperature sequence, T_{rec} at each ambient temperature was different between the first and second exposure (Figure 3). Rectal temperature decreased with time during the experimental period at a rate of 0.053 °C/d averaged over feeding levels, temperature sequences and ambient temperatures ($P < 0.001$; Table 2). The

effect of time on T_{rec} was influenced by feeding level ($P < 0.001$) and ambient temperature ($P < 0.01$) (Table 2 and 4).

TABLE 5. Adjusted least square means of rectal temperature (T_{rec}) at different ambient temperatures at both feeding levels, difference in T_{rec} between feeding levels and average of both levels (in $^{\circ}\text{C}/\text{d}$)^a

Ambient temperature, $^{\circ}\text{C}$	Feeding level		Difference between high and low	Average of high and low
	Low	High		
6	37.79 ^x	38.56 ^x	0.78 ^x	38.18 ^x
9	37.94 ^x	38.63 ^{xy}	0.69 ^{xy}	38.28 ^x
12	38.19 ^y	38.68 ^{xy}	0.49 ^{xy}	38.43 ^y
15	38.39 ^z	38.84 ^y	0.44 ^y	38.61 ^z
SEM	0.051	0.059	0.078	0.039

^aThe values are adjusted for the effect of time to the average day number during the experimental period (i.e. the mean T_{rec} value of the two replicates at each ambient temperature).

^{x,y,z}Values in columns with different superscripts are significantly different ($P < 0.05$).

Discussion

Young calves are particularly prone to cold stress shortly after arrival on a veal farm, since their feed is restricted. This study has focused on the effect of feeding level on the thermal requirements of such calves.

The lower critical temperature (LCT) can be estimated from either 1) thermoneutral heat production and whole-body conductance (K_b) at one ambient temperature below LCT (method 1; Blaxter, 1989) or 2) the slope of increase in H below LCT (method 2; Mount, 1974). For the latter method, data on H at two or more ambient temperatures below LCT are needed. Table 6 gives the estimates of LCT and the increase in H below LCT (K_b for method 1 and ETH for method 2) from the present as well as earlier reported studies. It appears that estimates of ETH are lower than K_b , and that estimates of LCT are higher when using method 2 as compared with method 1 (Table 6).

Our estimates of ETH for calves were not affected by their feeding level. The mean value ($8.4 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot {}^{\circ}\text{C}^{-1}$) is within the range of values obtained from other studies (Holmes and McLean, 1975; Schrama et al., 1991) and is similar to the value reported by Webster et al. (1978) (Table 6).

The mean value of 12.5°C for LCT at both feeding levels (by method 2) is comparable with values in the literature (Table 6). In the present study, LCT was not

affected by feeding level. According to the concept of thermoneutrality however, LCT changes with feeding level (Mount, 1979). In addition, we found a similar difference of about $46 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ in H at each temperature between both feeding levels (Table 2 and 3). Data of Schrama et al. (1991) also showed a trend of a constant difference in H between feeding levels at ambient temperatures below LCT. Moreover, T_{rec} was influenced by ambient temperatures (Table 5). Our finding that T_{rec} of young calves was lowered at a low ambient temperature and that this effect was higher at FL as compared with FH (Table 5), agrees with results found for young calves between 7 to 28 d of age by Scibilia et al., (1987).

TABLE 6. Different estimates of lower critical temperature (LCT) and increase in heat production below LCT (K_b in method 1 and ETH in Method 2) of young pre-ruminant calves in still air. Estimates ordered by the method used for estimating thermal requirements: method 1 by calculating whole-body conductance (K_b) at one ambient temperature below LCT; method 2 by estimation of the relationship between heat production and ambient temperature

Breed	Age, day	Weight, kg	ME intake, $\text{kJ} \cdot \text{kg}^{0.75} \cdot \text{per day}$	Method 1			Method 2			Ref. ^b
				K_b^a , $\text{kJ} \cdot \text{m}^{-2} \cdot \text{per day} \cdot \text{per }^\circ\text{C}$	$K_b^{0.75}$, $\text{kJ} \cdot \text{kg}^{0.75} \cdot \text{per day} \cdot \text{per }^\circ\text{C}$	LCT, $^\circ\text{C}$	ETH, $\text{kJ} \cdot \text{kg}^{0.75} \cdot \text{per day} \cdot \text{per }^\circ\text{C}$	LCT, $^\circ\text{C}$	Ref. ^b	
Ayrshire	2-22	40	730	218 ^c	14.6 ^c	10.3 ^c	---	---	---	1
Jersey	8-34	26 ^d	840 ^d	246 ^e	16.5	8.6	12.3 ^f	12.8 ^f	12.8 ^f	2
Friesian	8-34	38 ^d	760 ^d	215 ^e	13.8	7.4	7.8 ^f	12.4 ^f	12.4 ^f	2
British Friesian	4-56	65	950	279	18.0	10.4	5.3 ^g	---	---	3
Hereford ×										
British Friesian	4-56	60	950	262	17.0	8.4	5.3 ^g	---	---	3
Holstein-Friesian	5-12	43	320	---	---	---	7.0 ^f	13.3 ^f	13.3 ^f	4
Holstein-Friesian	5-12	45	640	---	---	---	4.2 ^f	12.6 ^f	12.6 ^f	4
Holstein-Friesian	6-14	43	290-460	---	---	---	8.4	12.5	12.5	5

^aFormula used for surface area (m^2) = $0.09 \times \text{BW}^{0.67}$ (kg) (Mitchell, 1928).

^bReferences: 1, Gonzalez-Jimenez and Blaxter (1962); 2, Holmes and McLean (1975); 3, Webster et al. (1978); 4, Schrama et al., (1991); 5, Present study.

^cEstimated at 12 d of age.

^dValues recalculated or extrapolated from reported data.

^eFormula used by authors for surface area (m^2) = $0.098 \times \text{BW}^{0.63}$ (kg) (Brody, 1945).

^fEstimated from reported data of heat production at different ambient temperatures by using a simplified model of van der Peet et al. (1987) (Equation [2], this paper).

^gEstimated by the authors using linear regression of heat production on ambient temperature combining the data of both breeds.

The present study demonstrated a clear change in H between 6 and 14 d of age. Heat production decreased with time (days) by an average of $71 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ during the 8-d experimental period. The decrease in H with time was influenced by both feeding level and ambient temperature (Table 4). Heat production decreased with time more at the low than

at the high feeding level (Table 4). This result is consistent with the results of a previous study with young calves kept at a constant ambient temperature (15°C) (Schrama et al., 1992). The decrease in H with time was larger at high compared with low ambient temperatures (Table 4). In young growing calves fed above maintenance Gonzalez-Jimenez and Blaxter (1962) found a reverse trend; namely a larger decrease at 3°C than at 23°C. This reverse trend and our higher values of decline in H with time compared with Gonzalez-Jimenez and Blaxter (1962) are probably related to the lower feeding levels in the present study. The effects of both feeding level and ambient temperature on the decline in H with time, indicate that the relation between H and feeding level, and the relation between H and ambient temperature, depend on time (age) after arrival. The effect of both feeding level and ambient temperature on H increased with time (Figure 4).

The observed alteration in energy metabolism with time may be related to the very young age of the calves in our study. Young mammals tend to have a higher minimal metabolic rate than adults (Poczopko, 1981). Okamoto et al. (1986) found no effect of colostrum feeding on resting and summit metabolism in 1-d-old calves. From Roy et al. (1957) we calculated that the fasting heat production in young calves between 6 to 14 d of age declined by $7.8 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-2}$. This suggests that the initial age of calves can have a major influence on metabolic rate irrespective of effects of feeding level and ambient temperature.

The observed difference in decline in H with time between treatments could also be related to a carry-over effect of feeding level in the preliminary period. Feeding level at the start of the experimental period was lowered only for the FL treatment. However, Schrama et al. (1992) calculated that the extent of a decline in H with time of $13.1 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-2}$ at a low feeding level was far too large to be completely explained by such a carry-over effect. Additionally, such a carry-over effect would not explain why the decrease in H with time depends on the ambient temperature.

Dantzer (1982) and Mormède et al. (1982) reported that blood glucose levels of 4- to 32-d-old calves were lowered upon arrival on the veal farm. Mormède et al. (1982) suggested that the observed hypoglycaemia upon arrival is the result of the effect of food deprivation and of an increased energetic demand induced by transportation and handling of the calves. Plasma cortisol levels, which are used as an index of stress, are elevated in response to transportation (Johnston and Buckland, 1976; Crookshank et al., 1979; Kent and Ewbank, 1983, 1986a,b). In general, through hormonal responses (catecholamines and corticosteroids) a stress-exposed animal is able to mobilize its energy reserves quickly for metabolic processes (Dantzer and Mormède, 1983). The observed decline in H with time in the present study, may be related to the exposure of the calves to stressors, occurring at

the moment of transportation. In addition to the stress of transportation, the calves in the present study were exposed to changes in housing system, feeding level and dietary composition. Shortly after arrival, the effects of feeding level and ambient temperature on H might have been overruled by the exposure to stressors.

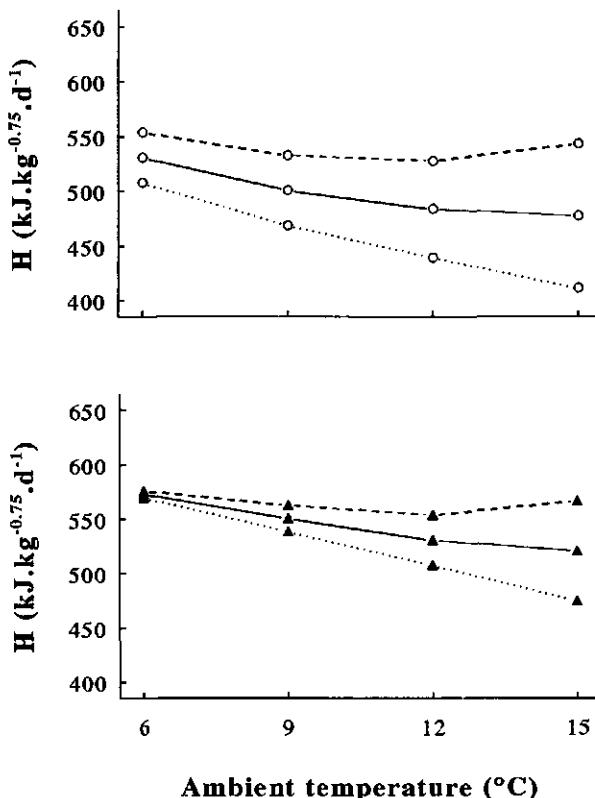


FIGURE 4. Relationship between heat production (H) and ambient temperature of young calves at different days during the experimental period and at different feeding levels: ----, day 1; —, day 4.5;; day 8; ○, low feeding level; ▲, high feeding level.

In summary, both LCT and ETH of young transported calves during the period of 6 to 14 d of age were not affected by feeding level. Over this entire period, LCT was 12.5°C and ETH was $8.4 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$. During this period, these young calves were not in a steady-state with regard to energy metabolism. The observed changes in energy

metabolism could be related to a combination of the process of aging and(or) a manifestation of a mechanism of adaptation to variables such as restricted feeding level or exposure to stressors. During 6 to 14 d of age, there was an alteration in the relation between H and feeding level, and between H and ambient temperature. The latter might be an indication that during this period the thermal requirements changed with time. Due to the restricted feeding level of young veal calves after arrival on the veal farm, it is important to have knowledge of the thermal requirements of these calves, in order to prevent the increased catabolism of body energy reserves by exposure to cold. More research is required into alterations of thermal requirements with time of young, unadapted animals.

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Chapter 3

Evidence of Increasing Thermal Requirement in Young, Unadapted Calves During 6 to 11 Days of Age

**J.W. Schrama^{*,#}, A. Arieli[†], W. van der Hel^{*},
and M.W.A. Verstegen[#]**

Departments of ^{*}Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

EVIDENCE OF INCREASING THERMAL REQUIREMENT IN YOUNG, UNADAPTED CALVES DURING 6 TO 11 DAYS OF AGE

J.W. Schrama*,[#], A. Arieli[†], W. van der Hel*, and M.W.A. Verstegen[#]

Departments of *Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

Abstract: Changes in thermal demand in restrictively fed, unadapted, young calves were studied during the first days after transportation. Twenty-three 6-d-old Holstein-Friesian male calves were assigned to one of four ambient temperature treatments: 5, 9, 13, or 18°C. Calves were fed at a constant level below the maintenance requirement (300 kJ of metabolizable energy.kg^{-0.75}.d⁻¹). After arrival, heat production (H) and energy and nitrogen balance were measured for each calf for 5.5 d. At ambient temperatures of 5 and 9°C, H was increased compared with temperatures of 13 and 18°C ($P < 0.001$). As a consequence, energy retention was decreased at low ambient temperatures ($P < 0.05$). At temperatures of 5 and 9°C, body fat mobilization was increased compared with that at temperatures of 13 and 18°C ($P < 0.001$). Energy retained as protein was not affected by ambient temperature. During the experimental period, H decreased with time. Ambient temperature affected this decrease ($P < 0.001$), indicating that the relationship between H and ambient temperature changed with time. The rate of increase in H below the lower critical temperature was not affected by time, averaging 9.5 kJ.kg^{-0.75}.d⁻¹.°C⁻¹. Lower critical temperature, however, increased with time by 0.89°C/d ($P < 0.05$). The changing relation between H and ambient temperature with time in young, unadapted calves after transportation is thus reflected in an alteration in thermal requirement with time.

Key Words: Adaptation, Calves, Energy Metabolism, Temperature.

Introduction

In The Netherlands, calves to be used for veal are usually brought to the farm at approximately 1 wk of age. Besides the stress of transportation, these calves are exposed to changes in housing system, climate, feeding level, and diet composition. The first few weeks after arrival is a critical phase in relation to the health of the calves (Webster et al.,

1985).

Exposure to cold conditions has an adverse effect on growth performance of young calves (McKnight, 1978; Williams and Innes, 1982; Scibilia et al., 1987). Thermal requirement has been studied in young calves fed above the maintenance requirement (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978). Shortly after arrival at the farm, veal calves are, however, mostly fed below maintenance to reduce gastrointestinal disorders. Low feeding levels reduce the tolerance of animals to cold (Webster, 1976).

After transportation, energy metabolism of young, restrictively fed calves alters with time (Schrama et al., 1992a,b). Schrama et al. (1992a) showed that the alteration in heat production was affected by ambient temperature. This suggests that thermal requirements change with time after arrival.

This study was designed to quantify whether the thermal demand of young, restrictively fed calves alters with time after arrival.

Materials and Methods

Animals and Treatments. Twenty-three 6-d-old Holstein-Friesian intact male calves, weighing approximately 44 kg, were obtained from different commercial dairy farms. Calves were fed colostrum during the first 3 d of life and thereafter a liquid milk replacer. The average distance travelled per calf was 28 km (SEM = 4.4, df = 22). On the day of transportation, the average daily and maximum outdoor temperature were 12°C (SEM = 1.0, df = 22) and 18°C (SEM = 1.1, df = 22), respectively. At arrival, the calves had been without food for approximately 6 to 8 h.

On arrival, calves were assigned to one of four constant ambient temperature treatments: 5, 9, 13, or 18°C. The experimental period started immediately on the afternoon of arrival of the calves at the experimental facilities and lasted for 5.5 d. Calves were housed individually in one of two similar open-circuit, indirect climatic respiration chambers (Verstegen et al., 1987). Calves were tethered and kept on a wooden, slatted floor. In the chambers relative humidity was maintained at approximately 65% and air velocity was < 0.20 m/s. Lights were on from 0745 to 1945.

A commercial starter milk replacer (Nukamel, n.v. Nukamel s.a., Olen, Belgium) was fed at a level of 19 g of powder. $\text{kg}^{-0.75} \cdot \text{d}^{-1}$. The milk replacer contained 23% crude protein and 20 kJ of gross energy (GE) per g of powder (Schrama et al., 1992b). The feeding level was representative of the amount of feed given to young calves after their

arrival at a veal farm in The Netherlands. The feeding level was kept constant during the experimental period and was calculated for each calf based on its body weight (BW) at arrival.

Milk was fed at a reconstitution rate of 150 g of powder/kg of milk and at a temperature of 40°C at 0800 and 1900. Warm (35°C) water was offered at 1330, providing a total daily liquid input originating from both milk and water of 10% of BW. Water and milk were offered through a rubber teat.

Measurements. Initial BW of each calf was measured immediately after its arrival. Final BW was measured at the end of the experimental period (at 0900) and was adjusted for feed intake at 0800. Rectal temperature was recorded daily shortly after the water was offered. Faeces were collected from each calf and sampled at the end of the experimental period. Urine was collected daily and composited and sampled for each calf. Gross energy values of feed, faeces, and urine were determined by adiabatic bomb calorimetry and nitrogen contents by the Kjeldahl method. Intake of metabolizable energy (ME) was calculated as the difference between GE intake and energy losses in faeces and urine. In pre-ruminant calves methane production is very low (< 0.0001 mL/L of air; Gonzalez-Jimenez and Blaxter, 1962; Meulenbroeks et al., 1986); therefore, methane energy losses were not taken into account. Daily heat production (H) of each calf was calculated from continuous measurements (every 9 min) of exchange of CO₂ and O₂ (Verstegen et al., 1987), according to the equation of Brouwer (1965). Measurements of H started the morning after arrival at 0900 and lasted for 5 d. Respiratory quotient per day was calculated as the ratio between CO₂ production and O₂ consumption. Energy retention (ER) over the total experimental period was calculated by subtracting mean H from mean ME intake. Energy retained as protein (ER_p) was obtained from protein gain (nitrogen gain × 6.25) multiplied by 23.6 kJ/g (the energetic value of body protein; ARC, 1980). Energy retained as fat (ER_f) was derived from ER by subtracting ER_p.

Statistical Analysis. Rectal temperature and respiratory quotient were averaged over the experimental period for each calf because no time trend was present in these traits. The effect of ambient temperature on these two traits and all other non-repeated measured traits were tested by means of an F-test using an one-way analysis of variance.

The effect of time and ambient temperature on H were tested by means of F-tests using a split-plot model (GLM procedure; SAS, 1985), with daily H values within calves taken as repeated measurements:

$$Y_{ijk} = \mu + T_i + e_{1,ij} + \beta \times (d_k - \bar{d}) + \beta_i \times (d_k - \bar{d}) + e_{2,ijk} \quad [1]$$

where Y_{ijk} = daily H per calf; μ = overall mean; T_i = fixed effect of ambient temperature ($i = 1, \dots, 4$); $e_{1,ij}$ = error term 1, which represents the random effect of calf within ambient temperature ($j = 1, \dots, N_i$; N_i = number of calves within ambient temperature i); d_k = day number during the main period ($k = 1, \dots, 5$); \bar{d} = average day number during the experimental period; β = overall regression coefficient of H on d; β_i = regression coefficient of H on d within ambient temperature i , representing the interaction effect between time and ambient temperature; and $e_{2,ijk}$ = error term 2, which represents the random effect within calf between day number.

The effect of ambient temperature on H was tested for significance against error term 1. The effect of time and interaction between time and temperature on H were tested against error term 2.

Lower critical temperature (LCT), extra thermal heat production (ETH) below LCT, and heat production at thermal neutrality (H_{th}) were estimated for the total group of calves from values of H and ambient temperature by using a model based on that of van der Peet et al. (1987) (using the DUD non-linear regression method of the NLIN procedure; SAS, 1985):

$$H_i = H_{th} + \ln[1 + e^{(ETH \times [T_i - LCT])}] \quad [2]$$

where H_i = heat production (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) of calf i ($i = 1, \dots, 23$); H_{th} = the heat production in the thermoneutral zone; ETH = extra thermoregulatory heat production (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$); T_i = ambient temperature (in $^\circ\text{C}$) of calf i ; and LCT = lower critical temperature. Different from the model of van der Peet et al. (1987), the heat production in the thermoneutral zone (H_{th}) was made independent of the ME intake in Equation [2]. This was because the feeding level was similar for all calves in the present study. Furthermore, the influence of BW on H was adjusted in Equation [2] by expressing H in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, whereas in the model of van der Peet et al. (1987) H was expressed in kJ/d and the effect of BW was included in that model.

Daily values of LCT, ETH, and H_{th} were estimated from daily values of H and ambient temperatures. Linear regression of LCT, ETH, and H_{th} on day number ($n = 5$) were performed; the effects of time were tested against the error term.

TABLE 1. Effect of ambient temperature on weight gain, rectal temperature, and energy intake of young calves

Item	Ambient temperature, °C				SEM	P-value ^a
	5	9	13	18		
No. of calves	6	5	6	6	---	---
Initial BW, kg	44.5	42.2	42.7	45.4	1.94	NS
Rate of BW change, kg/d	-0.38	-0.21	-0.13	-0.22	0.075	NS
Rectal temperature, °C	38.51	38.59	38.38	38.62	0.062	*
GE intake, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	370	368	366	368	1.3	NS
ME/GE	0.82	0.82	0.81	0.80	0.039	NS
ME intake, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	304	301	297	295	14.3	NS

^aNS = not significant, $P > 0.05$; * $P < 0.05$.

Results

None of the offered food was refused, resulting in similar GE intake at all temperature treatments (Table 1). Apparent digestibilities of nitrogen and energy were similar among temperature treatments ($P > 0.05$); overall means were 0.73 (SEM = 0.024) and 0.87 (SEM = 0.013), respectively (data not shown). These digestibility values might be overestimated, because of some contamination of urine with faeces. Metabolizability of energy (ME/GE) was not affected by temperature treatment, and thus ME intake was similar at all ambient temperatures (Table 1). At all ambient temperatures, calves lost weight. The effect of ambient temperature on BW change was not significant, because a considerable between-calf variation was present (Table 1). Rectal temperature was affected by ambient temperature ($P < 0.05$), although no systematic trend of rectal temperature in relation to ambient temperature was present (Table 1).

TABLE 2. Effect of ambient temperature on mean heat production (H) and daily change in H of young calves during the experimental period^a

Item	Ambient temperature, °C				SEM	P-value ^b
	5	9	13	18		
Mean H, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	529 ^y	515 ^y	453 ^z	450 ^z	9.6	***
Change in H, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-2}$	-5.0 ^y	-10.2 ^{yz}	-4.2 ^y	-18.1 ^z	2.20	***

^aR², standard deviation in H between animals and standard deviation in H between days were 0.90, 21.6, and 16.7, respectively.

^b*** $P < 0.001$.

^{y,z}Means within rows lacking a common superscript differ significantly ($P < 0.05$).

TABLE 3. Effect of ambient temperature on energy retention (ER), energy retained as protein (ER_p) and as fat (ER_f), and respiratory quotient (RQ) of young calves

Item	Ambient temperature, °C				SEM	P-value ^a
	5	9	13	18		
ER, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	-225	-213	-156	-155	18.0	*
ER_p , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	5	6	2	-20	9.9	NS
ER_f , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	-229 ^y	-219 ^y	-159 ^z	-135 ^z	12.5	***
RQ	0.79 ^y	0.79 ^y	0.80 ^{yz}	0.81 ^z	0.003	**

^aNS = not significant, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

^{y,z}Means within rows lacking a common superscript differ significantly ($P < 0.05$).

Mean H during the experimental period was affected by ambient temperature ($P < 0.001$) and was highest at low ambient temperatures (Table 2). At all temperatures, ER was negative. The magnitude of ER was affected by ambient temperature ($P < 0.05$, Table 3). Ambient temperature did not influence ER_p (Table 3). The increase in H at ambient temperatures below LCT resulted in lower ER_f values at low than at high ambient temperatures ($P < 0.001$, Table 3). The effect of ambient temperature on ER_f was reflected by the respiratory quotient. Respiratory quotient was lower in calves at low than in those at high ambient temperatures ($P < 0.01$, Table 3), although the differences were small (0.02 between 5 and 18°C).

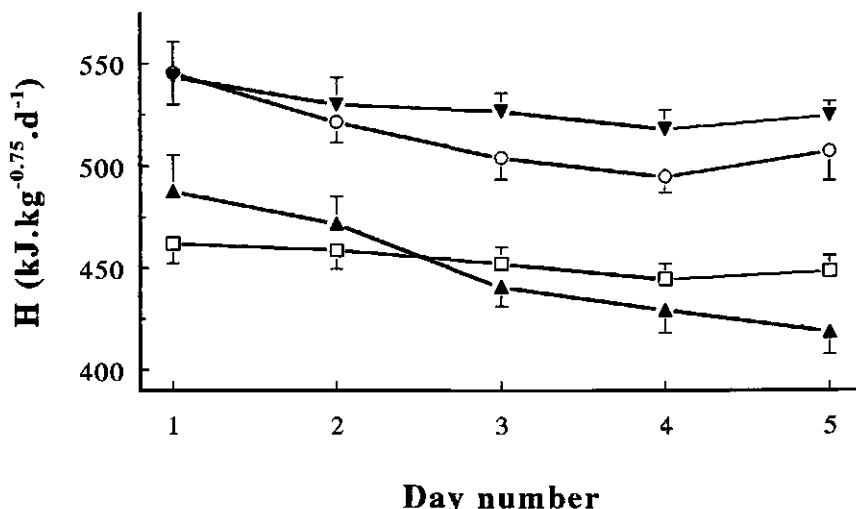


FIGURE 1. Mean heat production (H) of young calves at different ambient temperatures during successive days after transport (▼, 5°C; ○, 9°C; □, 13°C; ▲, 18°C). Vertical bars represent SE.

Heat production was not constant during the experimental period (Figure 1), despite the fixed feeding level. The average linear decline in H over all treatments was $9.4 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$ ($P < 0.001$). The linear component of time effect on H was different among ambient temperatures ($P < 0.001$; Table 2). The linear decrease in H with time at 18°C was higher by $11.3 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$ than the average decrease at 5 , 9 , and 13°C ($P < 0.001$).

The effect of ambient temperature on the change in H with time (Figure 1, Table 2) indicated that the relationship between H and ambient temperature altered with time. The alteration in this relationship is also shown by the daily estimations of LCT, ETH, and H_{th} (Table 4). The altering relationship is expressed by a decrease in H_{th} and an increase in LCT with time; the linear coefficients of H_{th} and LCT on day number were $-16.5 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-2}$ ($P < 0.01$) and $0.89 \text{ }^\circ\text{C/d}$ ($P < 0.05$), respectively (Table 4). No time effect was present on ETH ($P > 0.05$). The average daily ETH during the experimental period was $9.5 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-1} \cdot {}^\circ\text{C}^{-1}$ (Table 4).

TABLE 4. Extra thermal heat production (ETH), lower critical temperature (LCT), and thermoneutral heat production (H_{th}) during successive days, and the linear relationship between these traits and day number^a

Item	ETH, $\text{kJ.kg}^{-0.75} \cdot \text{d}^{-1} \cdot {}^\circ\text{C}^{-1}$	LCT, ${}^\circ\text{C}$	H_{th} , $\text{kJ.kg}^{-0.75} \cdot \text{d}^{-1}$	RSD ^b	R^2
Day 1	9.50	13.1	481	41.2	0.38
Day 2	8.77	13.1	470	30.9	0.48
Day 3	9.49	14.8	441	23.5	0.72
Day 4	9.61	15.0	430	23.1	0.73
Day 5	10.04	16.6	419	25.4	0.76
Int ^c	$9.5 (\pm 0.2)$	$14.5 (\pm 0.2)$	$448 (\pm 2.5)$	---	---
Lin ^d	$0.19^{\text{NS}} (\pm 0.14)$	$0.89^* (\pm 0.16)$	$-16.5^{**} (\pm 1.8)$	---	---

^aThe following regression model was used: $Y_i = \mu + \beta \times (d_i - \bar{d}) + e_i$, where d_i = day number i during the experimental period ($i = 1, \dots, 5$) and \bar{d} = average day number during the experimental period.

^bRSD = residual standard deviation of the model used for estimating ETH, LCT, and H_{th} (Equation [2]).

^cInt designates the intercept estimates with SEM between parentheses.

^dLin designates the linear regression coefficient estimates with SEM between parentheses.

*Regression estimate is significantly different from 0 ($P < 0.05$).

**Regression estimate is significantly different from 0 ($P < 0.01$).

NSRegression estimate is not significantly different from 0 ($P > 0.05$).

Discussion

In practice, veal calves are brought to the farm at a young age and are fed restrictively after arrival. Apart from transportation, these calves have to adapt to the new housing system and to changes in feed quality and quantity. After arrival, young calves are

not in a steady-state concerning their energy metabolism (Schrama et al., 1992a,b). The decrease in H with time in the present study (Table 2, Figure 1) also reflects that these calves were not in a steady-state. In accordance with the findings of Schrama et al. (1992a), the present study shows that the decline in H with time is affected by ambient temperature (Table 2, Figure 1), indicating that the relation between H and ambient temperature altered with time. However, in contrast to the results of Schrama et al. (1992a), no gradual increase in this H decline with increasing ambient temperature was observed in the present study. In the study of Schrama et al. (1992a) the daily thermal requirements were not estimated.

The present study shows that the changing relation between H and ambient temperature in unadapted, young calves is also expressed in an altering thermal requirement with time. During the experimental period, LCT increased ($0.89\text{ }^{\circ}\text{C/d}$) and H_{th} decreased ($16.5\text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-2}$), but ETH remained constant with time (Table 4). The extra heat loss per $^{\circ}\text{C}$ fall in ambient temperature below LCT (ETH) is equivalent to the overall conductance of an animal. Therefore, the reciprocal of ETH is a measure of the overall insulation of an animal (Mount, 1979). Over a longer period of time (several weeks), LCT in young animals declines as a function of age (NRC, 1981). In young, growing calves fed at a constant level, the decline in LCT with age (between 2 to 22 d of age) has been related to the increase in whole-body insulation with age (Gonzalez-Jimenez and Blaxter, 1962). The constant ETH values in the present study indicated, however, that the whole-body insulation of these unadapted calves remained constant during the experimental period (Table 4). Furthermore, the observed time-related change in LCT is opposite to the long-term (during several weeks) decline in LCT observed in animals acclimating to cold exposure (Young et al., 1989). This decline in LCT caused by adaptive responses to cold is related to an increased whole-body insulation and to an increased H in the thermoneutral zone (H_{th}) (Young et al., 1989). The time-related change in thermal requirement in the present study cannot be regarded as an acclimation response to cold, because ETH was constant with time and H_{th} decreased with time (Table 4).

In young calves fed above the maintenance requirement, LCT ranged from 8 to 11°C (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978). In our study, the estimated value of LCT of 13°C at the first day of the experimental period was only slightly above this range. The difference in LCT between the present study and these earlier studies is relatively small considering the difference in feeding level between our study and these studies. In line with this small difference in LCT between studies, Schrama et al. (1992a) reported that LCT estimated over a period of 8 d in young calves after transportation was not affected by feeding level. In the present study, LCT increased with time (Table 4) and became consequently higher than the reported values in the

literature for young, growing calves. Because ETH is constant with time (Table 4), this increase in LCT with time is mainly caused by the larger decline in H at thermoneutral conditions (18°C) than at ambient temperatures below LCT (5, 9, and 13°C) (Table 2). The observed alteration in the relation between H and ambient temperature in young calves after transportation might be a reflection of a changing effect of feeding level on H under thermoneutral conditions. Such an increase in the effect of feeding level on H with time has been found in young, transported calves kept at 15°C (Schrama et al., 1992b).

To sustain vital life processes, calves in the present study were partially dependent on the mobilization of body energy reserves. This was reflected by the negative ER (Table 3). Because of the increased H below LCT, ER was negatively influenced by low ambient temperatures (Table 3). As demonstrated by Graham et al. (1959) in sheep, the values of ER_f , ER_p , and respiratory quotient in the present study (Table 3) showed that fat was the primary tissue substrate used for the increase in H below LCT. Because of the low body fat content of young calves (ARC, 1980), feeding levels below maintenance in combination with low ambient temperature might have caused exhaustion of body energy reserves in our calves. In the present study, however, ER_p was similar between treatments. Moreover, no time trend was present in both rectal temperature and respiratory quotient. This indicates that body energy reserves were not entirely depleted during the experimental period. Consequently, exhaustion of body energy reserves is unlikely to be the reason for the observed alterations in the relationship between H and ambient temperature with time.

The decrease in H with time at ambient temperatures below LCT (Table 2) without concomitant changes with time in both ETH (Table 4) and rectal temperature suggested that the calves become more efficient with time in covering the heat losses to the environment. Newborn calves are able to increase H during cold exposure by non-shivering thermogenesis because of the presence of brown adipose tissue (Alexander et al., 1975). Ter Meulen and Molnar (1975) noted the presence of brown adipose tissue at 25 d of age in calves raised under cold condition. In general, the response in non-shivering thermogenesis to cold exposure increases with increasing duration of the cold exposure (Janský, 1973). The increased energetic efficiency below LCT with time in our calves might be related to an increase in non-shivering thermogenesis, but also variation in physical activity may play a role.

In conclusion, the present study shows that the altering relation between H and ambient temperature with time in young calves after transportation is also reflected in an alteration in thermal requirement with time. During a 5-d period after transportation, LCT increases with time by $0.89\text{ }^{\circ}\text{C}/\text{d}$. During this period, ETH remains constant at a level of $9.5\text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}\cdot\text{}^{\circ}\text{C}^{-1}$.

Implications

After arrival, young veal calves are particularly dependent on body reserves to meet their energy requirement because of limited feed allowances. Ambient temperature should not be lower than 14°C immediately after arrival, to prevent extra mobilization of energy reserves. Furthermore, lower critical temperature increases with time after arrival as a consequence of adaptation to the new environment. The consequences of the increased thermal requirement can be compensated by increasing the feeding level. If the feeding level cannot be increased in the 1st wk after arrival, because of the risk for gastrointestinal disorders, adjustment of ambient temperature may be needed.

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Chapter 4

Thermal Requirements of Young Calves During Standing and Lying

J.W. Schrama *#, **A. Arieli[†]**, **H.A. Brandsma ***, **P. Luiting[§]**,
and M.W.A. Verstegen[#]

Departments of *Animal Husbandry, [#]Animal Nutrition and [§]Animal Breeding,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

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THERMAL REQUIREMENTS OF YOUNG CALVES DURING STANDING AND LYING

J.W. Schrama*, #, A. Arieli†, H.A. Brandsma*, P. Luiting§, and M.W.A. Verstegen#

Departments of *Animal Husbandry, #Animal Nutrition and §Animal Breeding, Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands and †Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

Abstract: A study of 23 6-d-old Holstein-Friesian male calves was conducted to evaluate the thermal requirements of young calves in relation to their posture (standing or lying). Calves were housed individually and were assigned to one of four ambient temperatures: 5, 9, 13, or 18°C. Heat production of each calf was measured continuously every 9 min by indirect calorimetry for 5 d. The posture during these 9-min periods was derived from the continuous measurement of physical activity. For both standing and lying, heat production was increased at 5 and 9°C compared with 13 and 18°C. This increase in heat production was larger during standing than during lying. Consequently, the energy cost of standing was affected by ambient temperature (173, 189, 144, and 114 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ at 5, 9, 13, and 18°C, respectively). The time spent standing was not affected by ambient temperature. The thermal requirements of the calves were dependent on the posture. Lower critical temperature was 13.5°C during lying and 17.0°C during standing. The rate of increase in heat production below the lower critical temperature was 7.47 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot \text{°C}^{-1}$ during lying and 11.24 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot \text{°C}^{-1}$ during standing. These results indicate that the increase in heat loss upon standing in the cold is greater than the increase in heat production upon standing at thermoneutrality. Consequently, young calves require to have increased cold-induced thermogenesis when standing.

Key Words: Calves, Cold-Induced Thermogenesis, Energy Cost of Standing, Energy Metabolism, Lower Critical Temperature, Physical Activity.

Introduction

Exposure to cold conditions causes an increase in metabolic rate in homeothermic animals (Mount, 1979). The thermal requirements of farm animals have been extensively studied because of the negative influence on production (NRC, 1981). In contrast to adult

cattle, young calves are particularly prone to cold stress (Webster, 1976).

Thermal requirements are mostly estimated during a certain time span (e.g., a day) and provide only average thermal characteristic values without considering the variations in physical activity during this period (Blaxter, 1989). Part of the energy expenditure of animals is related to physical activity. In rats, it has been demonstrated that exercise-induced thermogenesis can substitute for cold-induced thermogenesis (Hart and Jansky, 1963; Arnold et al., 1986). The energy cost of standing over lying (EC_{st}) in both cattle and sheep has been studied disregarding ambient temperature (T_a) or at assumed thermoneutrality (ARC, 1980). It can be hypothesized that the posture (standing or lying) of animals may influence both their heat production and their heat loss (thermal insulation).

Therefore, in the present paper the thermal requirements of young calves in relation to their posture (standing or lying) were investigated.

Materials and Methods

Animals. In this study, 23 Holstein-Friesian male calves were used. Calves were obtained at 6 d of age from different commercial dairy farms. They were fed colostrum during the first 3 d of age and thereafter a commercially available liquid milk replacer. The average distance each calf was transported was 28 km (SEM = 4.4, df = 22). On the day of transportation to the experimental facilities, the average daily and maximum outdoor temperatures were 12°C (SEM = 1.0, df = 22) and 18°C (SEM = 1.1, df = 22), respectively. Upon arrival, the calves had been without food for approximately 6 to 8 h and weighed approximately 44 kg.

Housing and Temperature Treatment. The calves arrived in the afternoon and were housed individually for a period of 5.5 d in one of two open-circuit indirect climate respiration chambers (Verstegen et al., 1987). Calves were tethered and kept on a wooden slatted floor. The inner dimensions of the chambers (available for each calf) were 1 m length \times 0.8 m width \times 0.97 m height. Calves could move freely to stand up and lie down.

Calves were assigned to one of four constant ambient temperature (T_a) treatments: 5, 9, 13, and 18°C (with six, five, six, and six calves per treatment, respectively). Relative humidity inside the chambers was maintained at approximately 65% and air velocity was below 0.20 m/s. Lights were on from 0745 to 1945.

Feeding. A commercial starter milk replacer (Nukamel, n.v. Nukamel s.a., Olen,

Belgium) with a gross energy content of 20 kJ/g of powder and a crude protein content of 23% was fed (for composition see Schrama et al., 1992b). Calves were fed according to their metabolic body weight at a level of $19 \text{ g of powder} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. The feeding level was kept constant during the experimental period and was calculated for each calf from its initial body weight (BW). Averaged over all T_a treatments, the measured metabolizable energy intake was $299 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (Schrama et al., 1993). This very low feeding level (being below the energy requirements for maintenance) was applied to reduce the risk of gastrointestinal disorders, which frequently occur in such young calves after being transported (Webster et al., 1985b).

Milk was reconstituted to 150 g of powder/kg of milk and was fed at a temperature of 40°C at 0800 and 1900. Warm (35°C) water was offered at 1330 providing a total daily liquid input originating from both milk and water of 10% of their BW. Water and milk were offered through a rubber teat.

Measurements. Initial BW of each calf was measured immediately upon arrival. Final BW was measured at the end of the experimental period (at 0900) and was adjusted for feed intake at 0800. Rectal temperature was measured directly after the intake of water at 1330. Heat production (H) of each calf was determined indirectly from measurements of the exchange of CO_2 and O_2 per chamber during successive 9-min intervals, and was calculated according to Brouwer (1965). Results were expressed in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. Methane production as a result of fermentation processes in the rumen, was considered negligible, because methane production is very low (< 0.0001 mL/L of air) in pre-ruminant calves (Gonzalez-Jimenez and Blaxter, 1962; Meulenbroeks et al., 1986). Physical activity of each calf was measured continuously by Doppler-radar activity meters (Radar MD5, Suther, Vierpool, Amsterdam, The Netherlands) (Wenk and van Es, 1976; Verstegen et al., 1987). Every change of the surface of the animal due to movement, resulted in a change of wave length of the reflected ultrasound waves emitted by the meters. The changes were recorded as counts over a 3-min period. The measurements of H and physical activity started the morning after arrival of the calves at 0900 and lasted for 5 d.

Data on energy and nitrogen balances, rectal temperature, and the analysis of the relation between the 24-h mean H and T_a have been reported previously (Schrama et al., 1993).

Estimation Procedure of Standing and Lying. In the present study, the posture of the calf (standing or lying) was derived from analysis of the frequency distributions of the 3-min physical activity measurements. These activity measurements were distributed into

classes with intervals of 25 counts. The total number of 3-min observations in each class was counted. An example of a typical frequency distribution for one calf during a day is presented in Figure 1. Such distributions were made for each calf during each day of the experimental period. These distributions showed many observations appearing in classes with low activity counts. A second, lower peak occurred at higher activity counts. Between both peaks a minimum was observed, which was assumed to be the distinction between standing and lying (Figure 1). The physical activity value (i.e., distinction value) at this minimum was derived from a fifth-order polynomial function, which described the frequency distribution. This distinction value was estimated separately for each calf and for each day during the experimental period. An example of such a polynomial function with distinction value is given in Figure 1. A calf was assigned to be standing during a 3-min period when its physical activity exceeded the distinction value. A calf was considered to be standing during a 9-min period associated with measurement of H , when it was standing during at least two 3-min periods within this 9-min period. During all other 9-min periods the calf was assumed to be lying. The validation of this procedure for deriving the posture of the calf from the physical activity measurements is given below.

Derived Variables. Total daily heat production (H_{tot}) was calculated as the mean of the 9-min values of H during a day. Heat production during standing (H_{st}) was obtained by averaging the H values of the 9-min periods when the calf was standing and heat production during lying (H_{ly}) by averaging the H values when the calf was lying. Energy cost of standing over lying (EC_{st}) was derived by subtracting H_{ly} from H_{st} . The daily percentage of time spent standing (f_{st}) was obtained from the daily number of 9-min periods when the calf was standing. The extra daily amount of energy expenditure due to standing (H_{fxECst}) was obtained by multiplying EC_{st} with f_{st} . Values of H_{tot} , H_{ly} , H_{st} , EC_{st} , f_{st} , and H_{fxECst} were calculated per calf and per day. To avoid possible bias by inclusion of the heat increment associated with food ingestion or with stress (rectal temperature measurement) on estimations of H_{ly} , H_{st} , EC_{st} , and H_{fxECst} , the 9-min measurements during the 1st h after offering milk (0800 to 0900 and 1900 to 2000) and offering water (1330 to 1430), were excluded from the calculations of all traits (including H_{tot} and f_{st}). The presence of this possible bias was checked by estimating EC_{st} separately for the light and dark period during a day. The $7 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ higher EC_{st} during the dark period was not significantly different from EC_{st} during the light period.

Data on H_{tot} , H_{ly} , H_{st} , EC_{st} , and H_{fxECst} were expressed in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. The results of these traits were not influenced by the units applied ($\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, $\text{kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ or $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$), because BW was similar for different T_a treatments.

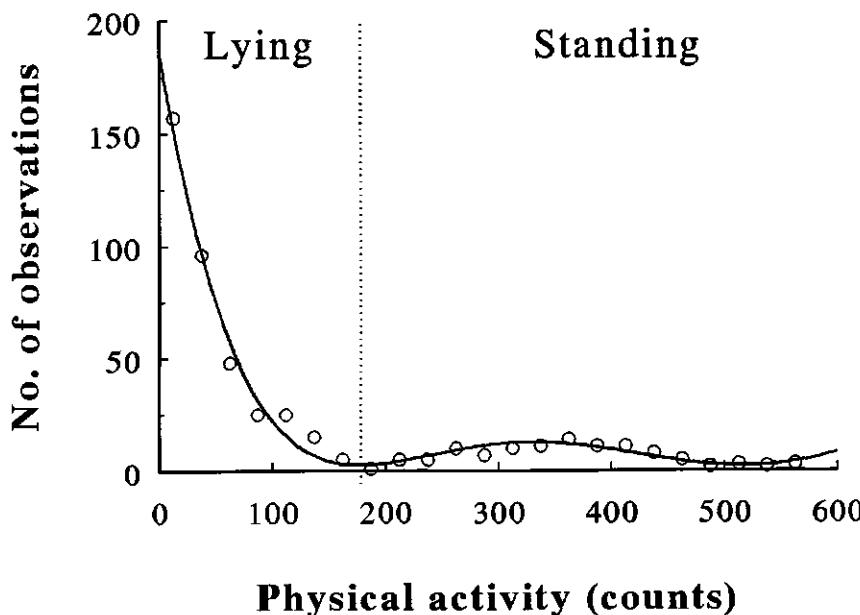


FIGURE 1. An example of a frequency distribution of a calf over a 1-d period. Points (O) represent the observed number of 3-min observations within the defined classes of physical activity. The solid line (—) is the estimated fifth-order polynomial function describing the relationship between number of observations within each class (Y) and the mean value of physical activity counts of each class (X); $Y = 187 - 3.0 X + 0.018 X^2 - 0.49 \times 10^{-4} X^3 + 0.60 \times 10^{-7} X^4 - 0.28 \times 10^{-10} X^5$, $R^2 = 0.99$, $n = 23$. The vertical dotted line (····) is the distinction value between standing and lying.

Statistical Analysis. Daily values of H_{tot} , H_{st} , H_{ly} , EC_{st} , f_{st} , and $H_{f \times ECst}$ were averaged per calf over the experimental period. Effects of T_a on these traits averaged per calf were tested by means of F -tests using one-way analyses of variance. Least square mean differences were used for the pairwise comparison between different T_a with an overall confidence level of 0.95.

Lower critical temperature (LCT), extra thermal heat production below LCT (ETH), and heat production at thermal neutrality (H_{th}) during the total day, during standing, and during lying were estimated from the mean values of H_{tot} , H_{st} , and H_{ly} per calf, respectively. Estimations of LCT, ETH, and H_{th} were made by using a modification of the model according to van der Peet et al. (1987) (using the DUD non-linear regression method of the procedure NLIN; SAS, 1985):

$$H_i = H_{th} + \ln[1 + e^{(ETH \times [LCT - Tai])}] \quad [1]$$

where H_i = mean heat production (H_{tot} , H_{st} , or H_{ly} , in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) over the experimental period of calf i ($i = 1, \dots, 23$); H_{th} = heat production at thermoneutrality (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$); ETH = extra thermal heat production (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$); T_{ai} = ambient temperature (in $^\circ\text{C}$) of calf i ; LCT = lower critical temperature (in $^\circ\text{C}$).

The model describes the relation between heat production and T_a according to the concept of thermoneutrality in homeothermic animals (Mount, 1974). According to the model, heat production decreases linearly with increasing T_a below LCT and is independent of T_a above LCT (thermoneutrality).

Validation of Estimation Procedure of Standing and Lying. The above described procedure for deriving the posture of the calf was validated on a second data set from another experiment with calves (our unpublished observations). In that experiment 24 calves were assigned in a 2×2 factorial arrangement of treatments to one of two feeding levels and to one of two T_a . Calves were of similar age and weight, and were transported and housed in a similar way as in the present experiment. In addition to measurements of H and physical activity, the posture of the calves was determined with a photo-electric cell (Telemecanique, XUG-F04031, Technische Unie, Arnhem, The Netherlands). In each chamber a photo-electric cell was located in one corner and the infrared beam emitted by this photo-electric cell was aimed at a reflector located in the opposite corner. If a calf was lying the infrared beam was recorded by the photo-electric cell. During standing, the beam was intercepted by the calf and consequently not recorded by the photo-electric cell. The posture of the calf was continuously recorded during each 9-min period associated with measurement of H .

TABLE 1. Validation of the estimation procedure of standing and lying on heat production (H) and posture traits from a second data set (our unpublished observations)^a

Trait	Avg of measured values	Avg of estimated values	Linear regression coefficient ^b	Correlation coefficient ^c
H during standing (H_{st}), $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	629	626	0.88	0.94***
H during lying (H_{ly}), $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	480	478	1.00	1.00***
Energy cost of standing (EC_{st}), $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	150	148	0.51	0.64**
Time spent standing (f_{st}), %	19.5	20.3	0.59	0.53**
Standing related H ($H_{\text{f} \times \text{EC}_{\text{st}}}$), $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	29	30	0.78	0.74***

^aOne calf was excluded because of a technical failure of the photo-electric cell ($n = 23$).

^bLinear regression coefficient of estimated values on measured values.

^cSignificance level of correlation coefficient between estimated and measured values: ** $P < 0.01$; *** $P < 0.001$.

From these posture measurements, H_{st} , H_{ly} , EC_{st} , f_{st} , and H_{fxECst} were calculated per calf and per day. Furthermore, H_{st} , H_{ly} , EC_{st} , f_{st} , and H_{fxECst} were calculated using the estimated postures from the physical activity measurements according to the above described estimation procedure. For all these traits, the average estimated (by activity meter) values per calf were compared with the average measured (by photo-electric cell) values per calf (Table 1).

Differences between measured and estimated values expressed as percentages of measured values, were all below 4.2%. Correlation coefficients between the measured and estimated values were all positive. For H_{st} , H_{ly} , and H_{fxECst} correlation coefficients were larger than 0.7 and linear regression coefficients were close to unity (0.78 to 1.00). For f_{st} and EC_{st} both correlation (0.53 and 0.64, respectively) and regression coefficients (0.59 and 0.51, respectively) were lower (Table 1). By applying the procedure for estimating the posture of the calves from physical activity measurements, accurate estimations can be obtained for H_{st} , H_{ly} , and H_{fxECst} , but estimations for EC_{st} and f_{st} are less accurate.

Results

Initial BW of calves was similar for the different ambient temperature (T_a) treatments ($P > 0.05$, Table 2). Calves lost weight during the 5.5-d experimental period. The weight loss was not significantly affected by T_a but tended to be higher at 5°C than at 9, 13, and 18°C (Table 2).

Average daily total heat production (H_{tot} ; excluding the three 1st h after the supply of milk and water) was affected by T_a ($P < 0.001$), being highest at the two lowest T_a (Table 2). Heat production during both standing (H_{st}) and lying (H_{ly}) was greater at low T_a than at high T_a ($P < 0.001$; Table 2), but the increase in H_{st} at low T_a was larger than the increase in H_{ly} . At 5°C compared with 18°C, H_{st} was higher by $116 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and H_{ly} was higher by $56 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (Table 2). This larger difference for H_{st} than for H_{ly} was reflected in the energy cost of standing (EC_{st}), being highest at the two lowest T_a ($P < 0.001$; Table 2). At both 5 and 9°C, EC_{st} was higher by 59 and $75 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, respectively, than at 18°C ($P < 0.05$, Table 2).

The time spent standing during the defined 21-h period (f_{st}) was not different between T_a ($P > 0.05$, Table 2). During the excluded three h immediately after the supply of milk and water, the calves spent more time standing than during the defined 21-h period (data not shown). The total 24-h values of f_{st} were also not significantly affected by T_a , but tended to be lower at 18°C, being 27.8, 25.8, 26.4, and 23.6% (SEM = 2.81) at 5, 9, 13,

and 18°C, respectively. However, because of the difference in EC_{st} , H_{fxECst} during the 21-h period was influenced by T_a ($P < 0.05$, Table 2). Expressed as a percentage of H_{tot} , H_{fxECst} was 7.3, 6.9, 6.8, and 4.8% at 5, 9, 13, and 18°C, respectively.

TABLE 2. Heat production (H) as affected by posture in young calves at different ambient temperatures

Trait	Ambient temperature, °C				SEM	P-value ^a
	5	9	13	18		
No. of calves	6	5	6	6	---	---
Initial BW, kg	44.5	42.2	42.7	45.4	1.94	NS
Rate of BW change, kg/d	-0.38	-0.21	-0.13	-0.22	0.075	NS
Total H (H_{tot}) ^b , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	509 ^x	494 ^x	444 ^y	437 ^y	10.2	***
H during standing (H_{st}) ^b , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	646 ^x	649 ^x	557 ^y	530 ^y	17.6	***
H during lying (H_{ly}) ^b , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	472 ^x	460 ^{xy}	414 ^z	416 ^{yz}	10.5	***
Energy cost of standing (EC_{st}) ^b , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	173 ^x	189 ^x	144 ^{xy}	114 ^y	11.1	***
Time spent standing (f_{st}) ^b , %	21.9	19.3	20.5	19.1	2.71	NS
Standing related H (H_{fxECst}) ^b , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	37	34	30	21	3.8	*

^aNS = not significant, $P > 0.05$; * $P < 0.05$; *** $P < 0.001$.

^bThese traits have been calculated from the 9-min measurements during a 21-h period per day (data on the three 1st h after the supply of milk and water have been excluded).

^{x,y,z}Means within rows lacking a common superscript differ significantly ($P < 0.05$).

The estimated thermal requirement characteristics of the calves are shown in Table 3. The lower critical temperature (LCT) during standing was 3.5°C higher than during lying. While standing, ETH was 3.77 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$ higher than while lying. This difference in ETH was 50% of the ETH during lying. The total values of ETH and LCT over the defined 21-h period (with no distinction between postures of the calf) were intermediate to the values during standing and lying (Table 3) but closer to the lying values.

TABLE 3. Extra thermal heat production (ETH), lower critical temperature (LCT), and thermoneutral heat production (H_{th}) estimated from the average total daily heat production, from the average heat production during lying and from the average heat production during standing per calf^a

Item	ETH, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$	LCT, °C	H_{th} $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	RSD ^b	R^2
Total	8.40	14.6	437	25.6	0.62
Lying	7.47	13.5	416	26.1	0.51
Standing	11.24	17.0	530	46.6	0.55

^aThe average total daily heat production, heat production during standing and during lying used for estimation of ETH, LCT, and H_{th} have been calculated from the 9-min measurements during a 21-h period per day (data on the three 1st h after the supply of milk and water have been excluded).

^bRSD = residual standard deviation of the model used for estimating ETH, LCT, and H_{th} (Equation [1]).

Discussion

In the present study the effect of physical activity in terms of posture (standing vs lying) on the thermal requirement of young calves was investigated. The posture of the calves was not measured but deduced. The validation of the applied procedure for deriving the posture (Table 1) showed that accurate ($r > 0.7$) estimations can be obtained for H_{st} , H_{ly} , and H_{fxECst} . Estimations for EC_{st} and f_{st} will be less accurate. Because the corresponding regression coefficients were below unity, the differences between T_a in both EC_{st} and f_{st} will probably be underestimated in the present study.

Time Spent Standing (f_{st}). In the present study, calves were standing on average 25.9% and lying 74.1% of the total day (24-h period). This is in accordance with the value reported for lying (74%) by de Wilt (1985) and for standing idle (23%) by Webster et al. (1985a) on individually housed veal calves.

Energy Costs of Standing (EC_{st}). Apart from Vermorel et al. (1983), there are no other data in the literature on EC_{st} in young calves and on the effect of T_a on EC_{st} . Therefore, the EC_{st} at 18°C (thermoneutrality) of the present study, is compared with data from the literature on adult cattle and sheep, which are assumed to have been measured at thermoneutrality. This comparison of EC_{st} shows its dependency on the units in which EC_{st} is expressed (Table 4). When expressing EC_{st} as a percentage of H_{ly} , our value of 27% at 18°C is in good agreement with the average value of data reported for both cattle and sheep ($\bar{x} = 21\%$, ranging from 9 to 42%; Table 4). But when EC_{st} is expressed per BW, our value of $43.9 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ at 18°C is approximately twice the average value of reported data ($\bar{x} = 19.9 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$, ranging from 8.8 to $53.5 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$; Table 4). Compared with the recommended value for EC_{st} ($10 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$) by the ARC (1980), our value of EC_{st} at 18°C is threefold higher. In the present study, BW is low compared with the literature (Table 4). When using the unit $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, our value of EC_{st} at 18°C ($114 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) is relatively much less different than the average of reported values ($\bar{x} = 66 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, ranging from 33 to $152 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$; Table 4), than when using the unit $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$. This relatively small difference among studies, together with the observed effect of T_a on EC_{st} (present study) suggests that EC_{st} is a function of metabolic body size or body surface rather than of BW.

TABLE 4. Estimates of energy cost of standing (EC_{st}) from the literature (including the present study) in cattle and sheep expressed in percentage of energy expenditure during lying (H_{ly}), in $kJ \cdot kg^{-1} \cdot d^{-1}$ and in $kJ \cdot kg^{-0.75} \cdot d^{-1}$

Reference ^a	No. of animals	Age, mo	Weight, kg	Ambient temperature, °C	Feeding level ^b	EC_{st}		
						% of H_{ly}	kJ/kg per day	kJ/kg ^{0.75} per day
Cattle								
1	1	— ^d	468	—	0	25	15.2	71
2 ^c	24	22-45	461	—	>0 ^e	9	8.8	41
3	4	24	460	—	0	14	11.1	51
4	11	12-25	273	27-30	0	19	13.5	55
5	—	0.03	—	10	—	40-100	—	—
6	6	0.3	45	18	0.65	27	43.9	114
6	6	0.3	43	13	0.65	35	56.3	144
6	5	0.3	42	9	0.65	41	74.2	189
6	6	0.3	45	5	0.65	37	70.0	173
Sheep								
2	2	24	63	—	>0 ^e	9	12.2	34
7	4	—	60	—	1	13	11.8	33
8	4	—	65	25	1	42	53.5	152
9	12	14-72	62	—	1	33 ^f	32.7 ^f	92 ^f

^aReferences: 1, Forbes et al. (1927); 2, Hall and Brody (1933); 3, Clark et al. (1972); 4, Vercoe (1973); 5, Vermorel et al. (1983); 6, Present study; 7, Webster and Valks (1966); 8, Brockway et al. (1969); 9, Toutain et al. (1977).

^bFeeding level is expressed as the proportion of the energy requirements for maintenance.

^cThe presented values are the average of two different breeds (Holstein and Jersey).

^d— = value not reported.

^eAnimals were 'normally' fed, but the amount was not reported.

^fRecalculated values from the reported data without making a distinction between state of vigilance during lying of the animals.

Irrespective of the units in which EC_{st} is expressed, considerable variation in EC_{st} among studies (both cattle and sheep) does exist. Possible factors which may cause this variability, are differences in T_a , feeding level, physical activity within each posture and(or) state of adaptation of the animals between studies. The present study demonstrates that EC_{st} in young calves is affected by T_a (Table 2). With respect to an effect of feeding level on EC_{st} , the present study, and the studies of Brockway et al. (1969) and Toutain et al. (1977) suggest that in animals that have been fed, EC_{st} is increased compared with animals, that have been unfed (Table 4). However, data of Hall and Brody (1933) and Webster and Valks (1966) do not indicate such an effect. A higher EC_{st} in fed animals may, however, be due to confounding of the heat increment of food ingestion and of standing. Regarding physical activity within postures, Toutain et al. (1977) demonstrated in sheep that H_{ly} and thereby EC_{st} , were dependent on the alertness of the animals (awake or asleep). In man, both H_{ly}

and H_{st} were increased by small movements (Dauncey, 1990). As for the state of adaptation, Blaxter (1974) demonstrated in sheep that EC_{st} declined with the progress of training. Immediately after transportation, young calves are not in a steady-state regarding energy metabolism (Schrama et al., 1992a,b). Therefore, the calves of the present experiment were also unadapted (Schrama et al., 1993). Our relatively high value of EC_{st} value at 18°C compared with most of the reported values may, therefore, be related to the unadapted state of the calves.

Thermal Requirements during Standing and Lying. The present study shows that thermal requirements of calves are different for standing and lying. Both LCT and ETH were higher during standing than during lying by 3.5°C and $3.77 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$, respectively (Table 3). Therefore, the present study demonstrates that in young, unadapted calves EC_{st} does not substitute for cold-induced thermogenesis. This is in contradiction to the substitution of cold-induced thermogenesis by exercise-induced thermogenesis demonstrated in rats (Hart and Janský, 1963; Arnold et al., 1986). Similarly, Mount and Willmott (1967) showed that thermogenesis from spontaneous activity in mice (including both movement and posture) could substitute for cold-induced thermogenesis.

The approximately 50% higher ETH during standing (Table 3), indicates that below thermoneutrality, the minimal whole-body conductance in calves is larger during standing than during lying. This in good agreement with the observed difference in minimal conductance in mammals between day- and night-time, assumed to be related to a difference in physical activity (Aschoff, 1981). Possible factors causing the lower capacity of heat preservation in the cold during standing than during lying are a larger surface area, an increased peripheral vasodilatation, and an increased heat production in muscles close to the surface.

Influence of Time Spent Standing on Daily Thermal Requirements. The total heat production during a whole day (H_{tot}) is dependent on the energy expenditure associated with each of the states of physical activity and the duration of being in those states. This study demonstrated that the influence of T_a on H_{st} , is larger than on H_{ly} (Table 2), which was illustrated also by the difference in thermal requirements (both ETH and LCT) between standing and lying (Table 3). Consequently, the influence of T_a on H_{tot} and, thereby, also on daily thermal requirements are dependent on the proportion of time spent in each posture.

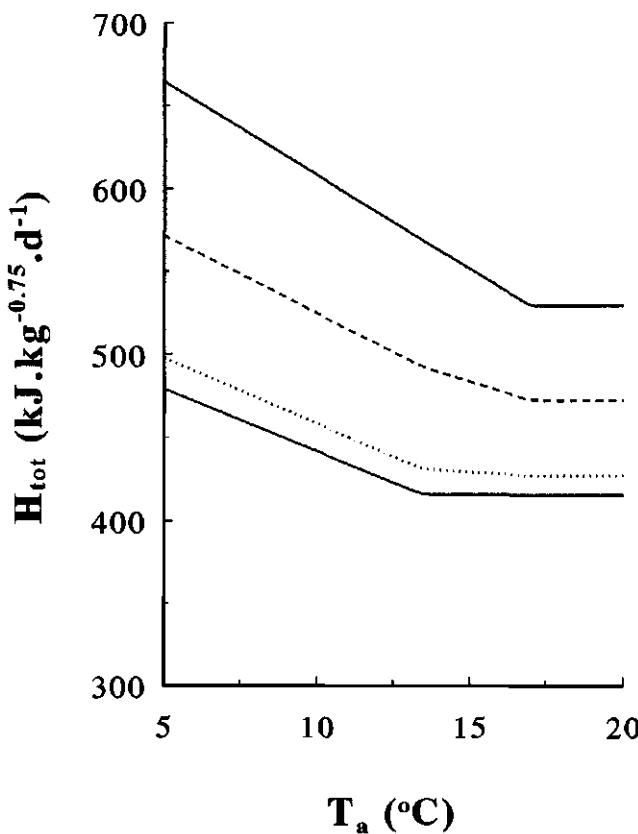


FIGURE 2. Influence of time spent standing (f_{st}) on the relationship between daily total heat production (H_{tot}) and ambient temperature (T_a) in the hypothetical situation that f_{st} is not affected by T_a (H_{tot} at a f_{st} level of 10%,; H_{tot} at a f_{st} level of 50%, ---). The top solid line is the estimated relationship between heat production and T_a during standing ($f_{st} = 100\%$) and the bottom solid line the relationship during lying ($f_{st} = 0\%$).

The influence of variation in f_{st} on daily thermal requirements is depicted in Figure 2 for the theoretical situation that f_{st} is not influenced by T_a . In that case, differences in f_{st} (e.g., in the present study there was a considerable variation in f_{st} among calves; Table 2) would result in differences in the daily mean ETH. This is because in that situation the daily mean ETH value is the average of ETH during standing and during lying, weighted by the duration of being in these postures. As for LCT, Figure 2 shows that if f_{st} is $> 0\%$ and $< 100\%$ the daily LCT is not a distinct point. This is in agreement with the suggestion of Webster et al. (1978) that LCT is the mid-point of a certain range of T_a . At T_a between the LCT of lying (13.5°C) and of standing (17.0°C), H_{tot} is influenced by T_a (Figure 2).

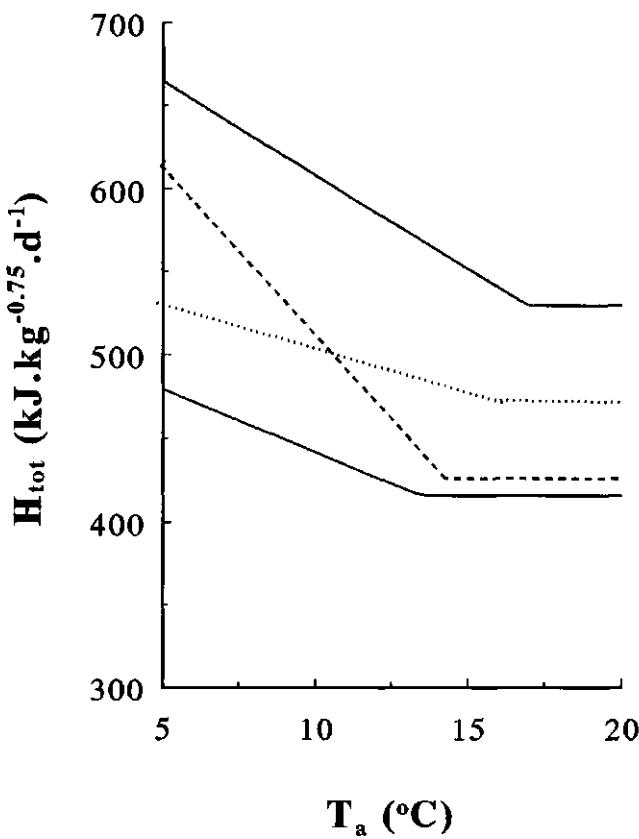


FIGURE 3. Influence of time spent standing (f_{st}) on the relationship between daily total heat production (H_{tot}) and ambient temperature (T_a) in the hypothetical situation that f_{st} is affected by T_a (H_{tot} when f_{st} increases with decreasing T_a , ----; H_{tot} when f_{st} decreases with decreasing T_a ,). The top solid line is the estimated relationship between heat production and T_a during standing ($f_{st} = 100\%$) and the bottom solid line the relationship during lying ($f_{st} = 0\%$).

In this study the 21-h value of f_{st} was not affected by T_a , but the 24-h value of f_{st} tended to be slightly lower at 18°C. If f_{st} is affected by T_a , the daily mean ETH will be dependent on the magnitude of the influence of T_a on f_{st} , as depicted for two hypothetical situations in Figure 3. The daily mean ETH can be even larger than the ETH of standing or smaller than the ETH of lying, if there is a relatively large increase in f_{st} or decrease in f_{st} with decreasing T_a , respectively (Figure 3). In these situations, the daily LCT observed from H_{tot} is dependent upon the relationship between T_a and f_{st} (Figure 3).

As Figures 2 and 3 demonstrate, the daily thermal requirements can be affected by the percentage of time spent in the different postures. This indicates that differences in

physical activity among animals may result in differences in thermal requirement. Therefore, it is important to have information on the physical activity of animals when comparing values of ETH and LCT from different studies. Furthermore, the significance of the results of studies on thermal requirements for practical animal husbandry will increase if information about the physical activity is present. For instance, an alteration in husbandry system leading to a change in physical activity may result in altered thermal requirements.

Implications

Young calves to be reared for veal are usually transported for 1 to 2 d, in the first 2 wk of age. These calves are prone to cold stress, because they are very young coupled with the fact that they are fed at a low feeding level directly after transport. The present experiment demonstrated that thermal requirements are higher during standing than during lying. Therefore, by changing their posture, calves are able to alter their thermal requirement. Husbandry conditions, which stimulate lying (e.g., type of bedding), will have a positive effect on the thermal requirements of these calves.

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Chapter 5

Circadian Fluctuation in Heat Production of Young Calves at Different Ambient Temperatures in Relation to Posture

**J.W. Schrama^{*,#}, J.P.T.M. Noordhuizen^{*}, A. Arieli[†], H.A. Brandsma^{*},
J.M. van der Linden^{*}, and M.W.A. Verstegen[#]**

Departments of ^{*}Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

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CIRCADIAN FLUCTUATION IN HEAT PRODUCTION OF YOUNG CALVES AT DIFFERENT AMBIENT TEMPERATURES IN RELATION TO POSTURE

J.W. Schrama*[#], J.P.T.M. Noordhuizen*, A. Arieli[†], H.A. Brandsma*,
J.M. van der Linden*, and M.W.A. Verstegen[#]

Departments of *Animal Husbandry and [#]Animal Nutrition,
Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
and [†]Department of Animal Science, Faculty of Agriculture, Rehovot, Israel.

Abstract: Circadian fluctuations in the effect of ambient temperature (T_a) on heat production (H_{tot}) and its relation to posture, were investigated in young calves. Twenty-three 6-d-old Holstein-Friesian male calves, were assigned to one of four T_a treatments: 5, 9, 13, or 18°C. Heat production was measured per calf continuously every 9 min, by indirect calorimetry for 5 d. The posture during these 9-min periods was derived from physical activity measurements by doppler-radar meters. Heat production varied within a day; being highest when calves were drinking (milk or water). The influence of T_a on H_{tot} was larger for the light (including feeding periods) than for the dark phase of the day; being related to the larger T_a effect during the feeding periods. Lower critical temperatures (LCT) were 14.1, 15.2 and 16.8°C and extra thermal heat productions below LCT (ETH) were 8.48, 8.28, and $11.55 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$ for the dark, the light (excluding feeding periods), and the feeding phase during the day, respectively. Time spent standing was not affected by T_a , but varied during the day. Averaged over T_a , 51% of the within day variation in H_{tot} was accounted for by the calf's posture. Correction of H_{tot} for the time spent standing, reduced the difference in both ETH and LCT between phases of the day. The present study demonstrates that in young calves, circadian fluctuations exist in the relation between heat production and ambient temperature, and are partially related to within day variation in time spent standing.

Key Words: Ambient Temperature, Calves, Circadian Rhythm, Heat Production, Lower Critical Temperature, Physical Activity.

Introduction

Homeothermic animals keep their body temperature constant (over periods ≥ 1 d), by balancing heat production and heat loss (Mount, 1979). Like many other physiological traits, heat production, heat loss, and body temperature of homeotherms, exhibit circadian rhythms (Aschoff et al., 1974).

In comparison with adult cattle, young calves are more sensitive to low ambient temperatures (Webster, 1976). In calves the effects of ambient temperature (T_a) on heat production have commonly been studied on mean values over a whole day (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978; Schrama et al., 1992a, 1993b). However in contrast to pigs (van der Hel et al., 1984; Verstegen et al., 1986; Kemp et al., 1990), there is no information on circadian fluctuations in the response of heat production to T_a in calves. Schrama et al. (1993a) demonstrated a larger response in heat production to T_a when a calf was standing than when lying. Consequently, circadian fluctuation in time spent standing may be a cause of circadian fluctuations in the effect of T_a on heat production.

In this paper, the influence of the time of day on the relation between heat production and T_a was investigated in young calves. Circadian fluctuations of this relationship were also examined for their relation to fluctuations in time spent standing.

Materials and Methods

Animals, Housing, Feeding and Temperature Treatment. The 9-min heat production and posture data of an earlier experiment (Schrama et al., 1993a,b) with young calves have been used for this investigation. In this experiment 23 6-d-old Holstein-Friesian male calves were assigned to one of four constant ambient temperature (T_a) treatments: 5, 9, 13 or 18°C (with six, five, six and six calves per treatment, respectively). Calves were obtained from different commercial dairy farms. Immediately following arrival in the afternoon, calves were housed individually for a period of 5.5 d in one of two open-circuit indirect climate respiration chambers (Verstegen et al., 1987b). Calves were tethered and kept on a wooden slatted floor. The inner dimensions of the chambers were 1 m length \times 0.8 m width \times 0.97 m height. Calves could move freely to stand up and lie down. During the experimental period, T_a was maintained constant at the respective treatment level, and relative humidity was kept at approximately 65%. Air velocity was < 0.20 m/s. Lights were on from 0745 to 1945.

Calves were fed a commercial starter milk replacer (for composition see Schrama et al., 1992b) according to their individual metabolic body weight, which had been recorded upon arrival. The feeding level was kept constant during the experimental period. The feeding level was set below the energy requirements for maintenance, in order to reduce the risk of gastrointestinal disorders, which frequently occur in such young calves after transport (Webster et al., 1985b). Averaged over all T_a treatments, the measured metabolizable energy intake per animal was $299 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (Schrama et al., 1993b). Milk was fed at a temperature of 40°C at 0800 and 1900. Warm (35°C) water was offered at 1330, providing a total daily liquid input originating from both milk and water of 10% of their body weight (BW). Water and milk were offered through a rubber teat, which was replaced daily after the intake of milk at 1900.

Measurements. Initial and final BW were measured, immediately upon arrival and at the end of the experimental period (at 0900), respectively. Final BW was adjusted for the previous feed intake at 0800. Rectal temperature was measured daily, immediately after the intake of water at 1330. The measurements of heat production (H) and physical activity began on the morning after the arrival of the calves at 0900, and lasted for 5 d. Heat production (H) was determined indirectly from measurements of the exchange of CO_2 and O_2 per chamber during successive 9-min intervals, and was calculated according to Brouwer (1965). Results were expressed in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. Methane production was considered negligible, due to the fact that its production is very low in pre-ruminant calves (Gonzalez-Jimenez and Blaxter, 1962; Meulenbroeks et al., 1986). The physical activity of each calf was measured continuously by Doppler-radar activity meters (Radar MD5, Suther, Vierpool, Amsterdam, The Netherlands) (Wenk and van Es, 1976; Verstegen et al., 1987b). The posture (standing or lying) of the calf during the 9-min period associated with measurement of H was derived from the physical activity measurements, according to the procedure described by Schrama et al. (1993a).

Results for energy and nitrogen balance, rectal temperature, and the analysis of the relation between the 24-h mean H and T_a as well as data on the thermal requirements of calves during standing and lying, have been reported elsewhere (Schrama et al., 1993a,b).

Calculations. The division of the day into time-periods, was made in two different ways. First, for looking at the difference in the influence of T_a on heat production between the dark and light phase, the day was divided into three time-periods: the night phase (NP; 2000 to 0745), the day phase (DP; 0745 to 1900, excluding the first 1-h periods after the supply of milk and water at 0800 and at 1330), and the feeding phase (FP; the first 1-h

periods after the supply of milk and water, 0800 to 0900, 1330 to 1430, and 1900 to 2000). Secondly, for looking at fluctuations within both the light and dark phases, the day was arbitrarily split into 17 time-periods; three 1-h periods (the first 1-h periods after the supply of milk and water) and 14 1.5-h periods (the remaining part of the day).

The heat production (H_{tot}) for each time-period was calculated as the mean of all of the 9-min values of H during that time-period. The percentage of time spent standing (f_{st}) was obtained from the number of 9-min intervals when a calf was standing during that time-period. For studying the influence of posture on circadian fluctuations in the response in H_{tot} to T_a , heat production corrected for the energy cost of standing (H_{cor}) during each of the defined time-periods was determined per calf as follows:

$$H_{cor} = H_{tot} - 0.01 \times f_{st} \times EC_{st} \quad [1]$$

where H_{tot} (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) and f_{st} (in %) are the calculated values during that time-period, and EC_{st} (the energy cost of standing; in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) is the mean estimated value of each calf over the experimental period. The value of EC_{st} (the difference between H during standing and H during lying) of each calf was estimated as described by Schrama et al. (1993a) from the 9-min values of H and posture, excluding the 9-min measurements during the first 1-h periods after the supply of milk and water (FP). The mean values of EC_{st} per T_a treatment used for calculating H_{cor} were 173, 189, 144, and 114 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ at 5, 9, 13, and 18°C, respectively. Circadian fluctuations in EC_{st} were not taken into account in the estimation of H_{cor} according to Equation [1], because EC_{st} was not different between the dark and light phase of the day (Schrama et al., 1993a).

Statistical Analysis. For each of the defined time-periods, the average H_{tot} , f_{st} and H_{cor} over the 5-d experimental period were calculated per calf. Statistical analyses of these data were performed, using the SAS software (1985).

For the data of H_{tot} , f_{st} and H_{cor} of the three phases of the day (NP, DP and FP), the effect of T_a treatment, phases of the day, and their interaction were tested by means of F -tests using a split-plot model (procedure GLM, SAS, 1985). The values of phases within calves were taken as repeated measurements:

$$Y_{ijk} = \mu + T_i + e_{1,ij} + P_k + (T \times P)_{ik} + e_{2,ijk} \quad [2]$$

where Y_{ijk} = value of the trait at temperature treatment i , for calf j , and phase k ; μ = overall mean; T_i = the effect of temperature treatment i ($i = 1, \dots, 4$); $e_{1,ij}$ = error term 1,

which represents the random effect of calf within temperature treatment ($j = 1, \dots, N_i$; N_i = number of calves within temperature treatment i); P_k = the effect of phase k ($k = 1, 2, 3$); $e_{2,ijk}$ = error term 2, which represents the random effect within calf between phases.

The effect of T_a treatment on these traits were tested for significance against error term 1. The effect of phase of the day and interaction between T_a treatment and phase of the day were tested against error term 2.

Lower critical temperature (LCT), extra thermal heat production below LCT (ETH) and heat production at thermal neutrality (H_{th}) were estimated separately for NP, DP and FP from the mean values of H_{tot} per calf during these phases. Estimations of LCT, ETH and H_{th} for these phases were also made from the mean values of H_{cor} per calf. The following model was used to estimate LCT, ETH and H_{th} (using the DUD non-linear regression method of the procedure NLIN; SAS, 1985):

$$H_i = H_{th} + \ln[1 + e^{(ETH \times [LCT - T_{ai}])}] \quad [3]$$

where H_i = heat production (H_{tot} or H_{cor} in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) of calf i ($i = 1, \dots, 23$) during a specific phase of the day; H_{th} = heat production at thermoneutrality (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$); ETH = extra thermal heat production (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$); T_{ai} = ambient temperature (in $^\circ\text{C}$) of calf i ; LCT = lower critical temperature (in $^\circ\text{C}$). This model is based on that of van der Peet et al. (1987). The differences between the model in Equation [3] and the model of van der Peet et al. (1987) are described by Schrama et al. (1993b).

For each of the defined periods within FP, DP and NP, the influence of T_a on H_{tot} and on H_{cor} were quantified by linear regression of H values on T_a . Data at 18°C were excluded from these regression analysis on the assumption that it was at thermoneutrality (Schrama et al., 1993a,b).

Results

Average initial BW of calves were 44.5, 42.2, 42.7, and 45.4 kg (SEM = 1.94; $P > 0.05$) and rates of BW changes during the experimental period were -0.38 , -0.21 , -0.13 , and -0.22 kg/d (SEM = 0.075; $P > 0.05$) at 5, 9, 13, and 18°C , respectively.

Heat Production. In Figure 1, the heat production (H_{tot}) of young calves at the various T_a treatments is shown for the assessment of differences between the night (NP), day (DP) and feeding phase (FP). Within a day, H_{tot} was influenced by phase ($P < 0.001$). Averaged over T_a treatments, H_{tot} was lowest for NP ($466 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) and was higher

by 13 and 127 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ during DP and FP, respectively (Figure 1). Ambient temperature (T_a) affected H_{tot} ($P < 0.001$), but the effect of T_a on H_{tot} was not constant over the total day, indicated by the interaction between T_a and phase on H_{tot} ($P < 0.05$, Figure 1). At 5°C compared with 18°C, H_{tot} was higher by 70, 74 and 118 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for NP, DP and FP, respectively (Figure 1). Thus, thermal requirement characteristics varied between NP, DP and FP. During NP, LCT was lowest (14.1°C; Table 1). Compared with NP, LCT was increased by 1.1°C during DP and by 2.7°C during FP (Table 1). Similar ETH values were observed for NP and DP (Table 1). During FP, ETH was higher by 3.03 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot \text{C}^{-1}$ than during NP (Table 1). Despite the short duration of the FP (in total 3 h), it had a large influence on thermal requirements during the light phase. Without exclusion of the H_{tot} data of FP from the light and dark phases of the day, LCT was 15.7 and 14.1°C, respectively, and ETH was 9.11 and $8.55 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot \text{C}^{-1}$, respectively (data not shown).

TABLE 1. Extra thermal heat production (ETH), lower critical temperature (LCT) and thermoneutral heat production (H_{th}) estimated from total heat production (H_{tot}) at different phases within a day

Phase ^a	ETH, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot \text{C}^{-1}$	LCT, °C	H_{th} , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	RSD ^b	R^2
Feeding	11.55	16.8	529	46.1	0.55
Day	8.28	15.2	442	27.8	0.58
Night	8.48	14.1	433	26.7	0.59

^aThe day was divided into the following phases: feeding phase, the first 1-h periods after the supply of milk and water; day phase, from 0745 to 1945 excluding the first 1-h periods after the supply of milk and water; night phase, from 1945 to 0745.

^bRSD (= residual standard deviation) and R^2 of the model used for estimating ETH, LCT and H_{th} (Equation [3]).

Mean H_{tot} of periods within NP, DP and FP are depicted in Figure 2. At all T_a treatments, a distinct peak in H_{tot} occurred consistently during the 1-h periods after feeding (milk or water). The highest mean H_{tot} value, was found during the 1-h period after the supply of water when rectal temperature was measured. The period with the lowest mean H_{tot} occurred for all T_a at the end of the night phase (from 0500 to 0630). The range of mean H_{tot} values of periods within the day, was wider at low compared with high T_a (Figure 2). The mean H_{tot} values of periods ranged from 463 to 709, from 445 to 671, from 412 to 581, and from 417 to 539 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ at 5, 9, 13, and 18°C, respectively (Figure 2). The influence of T_a on H_{tot} was different between the periods of the day (Figures 2 and 3). Peaks in the linear increase of H_{tot} with decreasing T_a , occurred at periods during and around the moments of feeding.

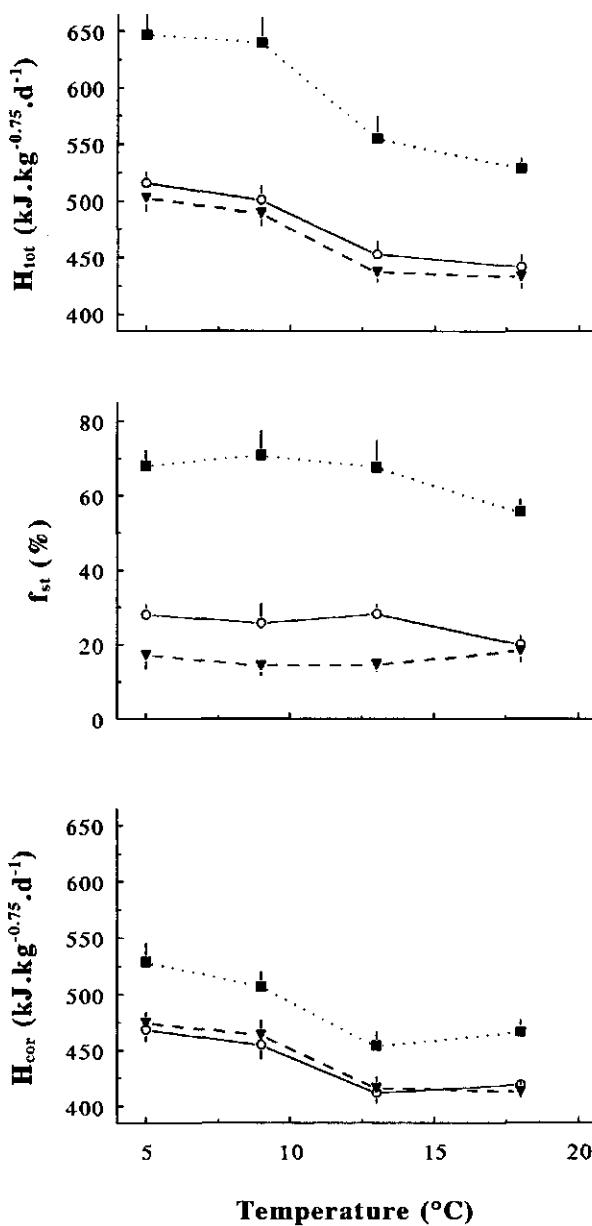


FIGURE 1. Mean heat production (H_{tot}), percentage of time spent standing (f_{st}), and heat production corrected for the energy cost of standing (H_{cor}) of young calves at different ambient temperatures during three phases within the day (....■...., feeding phase; —○—, day phase; ---▼---, night phase). Vertical bars represent SE.

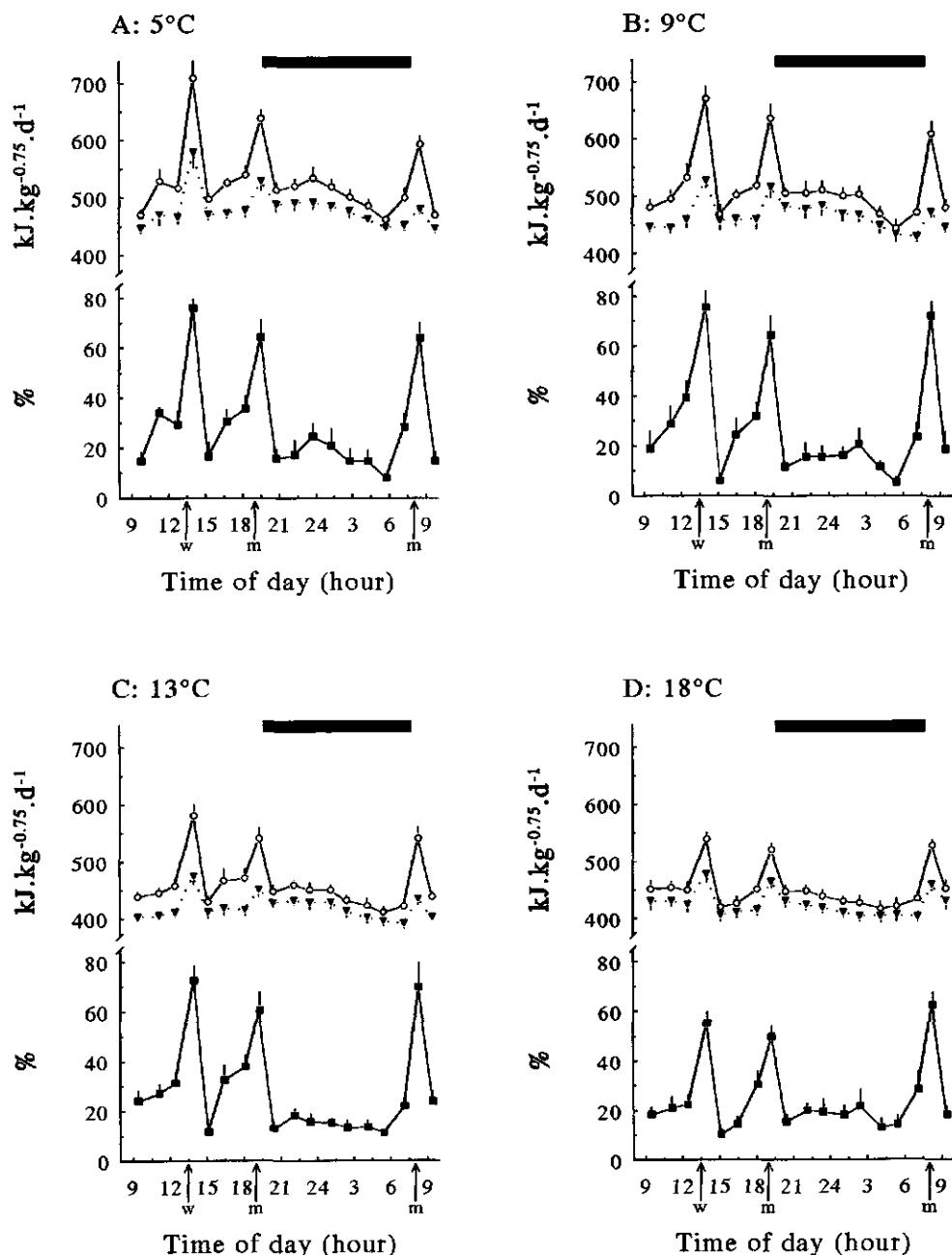


FIGURE 2. Daily pattern in heat production (H_{top} — ○ —), in heat production corrected for the energy cost of standing (H_{cor} ···▽···), and in percentage of time spent standing (f_{st} — ■ —) at different ambient temperatures (part A, 5°C; B, 9°C; C, 13°C; D, 18°C). Vertical bars represent SE. The solid horizontal bars indicate the dark phase of the day and the arrows indicate the time of feeding milk (m) or water (w).

Time Spent Standing. Time spent standing (f_{st}) was different between phases ($P < 0.001$); being 16.1, 25.5, and 65.6% during NP, DP, and FP, respectively (Figure 1). Whereas f_{st} was not affected by T_a ($P > 0.1$), the interaction effect between T_a and phase for f_{st} approached significance ($P < 0.08$). The difference in f_{st} between phases tended to increase with decreasing T_a (Figure 1).

Within NP, DP and FP, f_{st} was not constant (Figure 2). The highest values of f_{st} appeared during the first 1-h after feeding. Following these active periods of drinking milk or water the calves rested, indicated by the lower f_{st} values. Between feeding periods during the light phase of the day, f_{st} increased with time. Toward the end of the night phase, f_{st} decreased to the lowest value of the whole 24-h period (Figure 2). At all T_a treatments, the daily f_{st} pattern conformed with the H_{tot} pattern. High values of f_{st} coincided with high values of H_{tot} . However, increases in H_{tot} related to standing, were larger at low T_a (Figure 2).

Heat Production Corrected for Standing. Similar to H_{tot} , heat production corrected for standing (H_{cor}) was affected by temperature ($P < 0.001$), and by the phase of the day ($P < 0.001$; Figure 1). Averaged over T_a , H_{cor} was 442, 439 and 489 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for NP, DP and FP, respectively. The differences between phases in H_{cor} , were smaller than the differences in H_{tot} (Figure 1): 63% of the $127 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ difference in H_{tot} between FP and NP was caused by the difference in f_{st} . In contrast to H_{tot} , no interaction between T_a and phase effect on H_{cor} was found ($P > 0.1$). At 5°C compared with 18°C, H_{cor} was higher by 62, 50 and 62 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for NP, DP and FP, respectively (Figure 1), indicating that differences between phases in the response in H_{tot} to T_a were caused by differences in f_{st} (Figure 1). The similar response in H_{cor} to T_a was also reflected in the estimation of LCT and ETH from H_{cor} (Table 2). The differences between phases in thermal requirement characteristics (ETH and LCT) estimated from H_{cor} (Table 2) were smaller than those estimated from H_{tot} (Table 1), especially for LCT.

In many respects, the daily pattern in H_{cor} paralleled the pattern in H_{tot} (Figure 2). Heat production corrected for standing was lowest at the end of the night phase and peaked during the 1-h period after feeding, but these peaks in H_{cor} were less distinct than in H_{tot} . Compared with H_{tot} , H_{cor} fluctuated less within the day and the differences between T_a in the range of H_{cor} within the day were also smaller (Figure 2). As an average over T_a , 51% of the variation in mean H_{tot} values between periods was related to the posture of the calves (f_{st}). Within a day (24-h period), the mean H_{cor} values between periods ranged from 447 to 579, from 431 to 528, from 392 to 475, and from 403 to 478 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ at 5, 9, 13, and 18°C, respectively. The range in H_{tot} within a day, was for 46.3, 57.1, 50.9, and 38.5%

related to differences in f_{st} at 5, 9, 13, and 18°C, respectively. The influence of T_a on H_{cor} was different between periods of the day (Figures 2 and 3). The pattern in the linear increase in H_{cor} with decreasing T_a paralleled the pattern in the linear increase in H_{tot} with decreasing T_a (Figure 3). Peaks in the response to T_a occurred at periods during and around the moments of feeding. Between the feeding periods, the response to T_a gradually increased during the light phase, reaching a maximum at the end of the afternoon and the beginning of the evening. Thereafter, it decreased during the second half of the dark phase to the lowest daily level (Figure 3). The differences between periods in the linear increase of H_{cor} with decreasing T_a were smaller than in the linear increase in H_{tot} with decreasing T_a (Figure 3).

TABLE 2. Extra thermal heat production (ETH), lower critical temperature (LCT) and thermoneutral heat production (H_{th}) estimated from heat production corrected for the energy cost of standing (H_{cor}) at different phases within a day

Phase ^a	ETH, kJ.kg ^{-0.75} .d ⁻¹ .°C ⁻¹	LCT, °C	H_{th} , kJ.kg ^{-0.75} .d ⁻¹	RSD ^b	R ²
Feeding	9.06	13.3	463	33.8	0.45
Day	7.26	13.3	417	27.3	0.45
Night	7.55	14.0	413	26.4	0.54

^aThe day was divided into the following phases: feeding phase, the first 1-h periods after the supply of milk and water; day phase, from 0745 to 1945 excluding the first 1-h periods after the supply of milk and water; night phase, from 1945 to 0745.

^bRSD (= residual standard deviation) and R² of the model used for estimating ETH, LCT and H_{th} (Equation [3]).

Discussion

Young calves are less cold-tolerant than adult cattle. Reported studies on the influence of T_a on energy metabolism in young calves (e.g., Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978; Schrama et al., 1992a, 1993b) only provide information for the mean of a whole day. Therefore, the results of the present study on fluctuations in the response of heat production (H_{tot}) to T_a in young calves within a day have been compared with literature data for pigs.

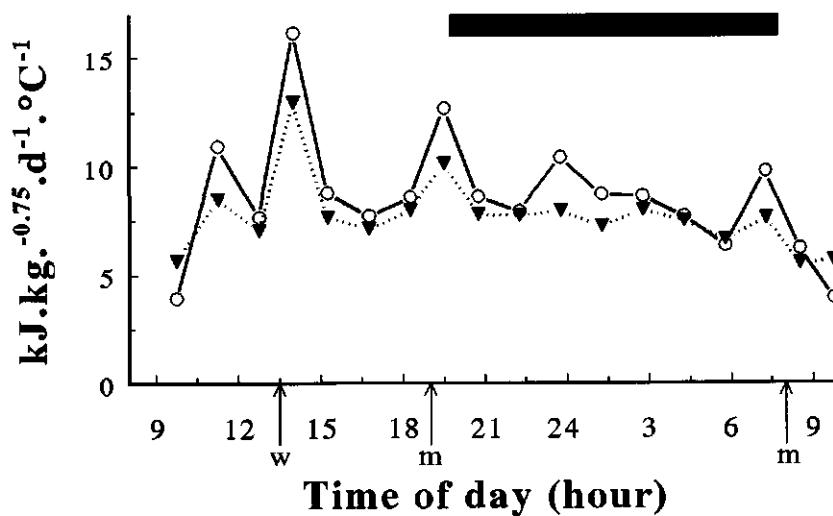


FIGURE 3. Daily pattern of the linear increase in heat production (—○—) and in heat production corrected for the energy cost of standing (···▼···) with decreasing ambient temperatures estimated from the data at 5, 9 and 13°C. The solid horizontal bar indicate the dark phase of the day and the arrows indicate the time of feeding milk (m) or water (w).

The present study demonstrated, that in young calves the relationship between H_{tot} and T_a varied within a day (Figures 1 and 3). The response in H_{tot} to T_a was larger during the light phase (especially during the feeding phase [FP]) than during the dark phase of the day (Figure 1). This was also reflected in differences in thermal requirement characteristics (LCT and ETH) within a day (Table 1). Similar to group housed growing pigs (van der Hel et al., 1984), and individually housed boars (Kemp et al., 1990), LCT of young calves was higher during the light phase of the day (Table 1), but this difference was smaller than for pigs. The within day difference in LCT of young calves also corresponded with the preference by pigs for a higher T_a during the light phase, reported in studies with operant supplementation heating (Balsbaugh and Curtis, 1979; Curtis and Morris, 1982; Verstegen et al., 1987a). During the light phase ETH of calves was higher than during the dark phase (mainly due to the high value at FP; Table 1). This difference in ETH between the dark and light phase, was in agreement with the variance between the active and non-active phase of the day in minimal conductance of mammals (Aschoff, 1981). In pigs, however, ETH was found to be higher during the dark phase of the day (van der Hel et al., 1984; Kemp et al., 1990).

Circadian fluctuations of motor activity, basal metabolic rate, and feeding-induced thermogenesis, as well as other thermoregulatory effectors, are regarded as factors causing daily fluctuations in body temperature (Aschoff, 1970). These factors, among others, can also be considered as causes of daily fluctuations in the response in H_{tot} to T_a . Besides dissimilarities in morphology (e.g., thickness of coat) and in thermoregulatory behaviour (e.g., huddling behaviour of group housed pigs), the differences in daily fluctuations of thermal requirement characteristics between calves and pigs, could be related to differences in age, feeding level, state of adaptation to a new environment, and physical activity. As for feeding level, the calves in the present study were fed below the maintenance requirement. The low feeding level might reduce the daily variation in H_{tot} and thereby may also reduce the daily variation in the influence of T_a on H_{tot} . As for the state of adaptation, calves in the present experiment were not in a steady-state with regard to their energy metabolism (Schrama et al., 1993b). The increased basic metabolic rate in young calves immediately after transportation (Schrama et al., 1992b), may also influence the daily fluctuation in H_{tot} . Furthermore, the physical activity of the calves in the present experiment was restricted due to the small space inside the chambers and because of being tethered. Calves could mainly select their posture (standing or lying). Averaged over T_a , 51% of the variation in H_{tot} within a day, was accounted for by the calf's posture (Figure 2). In group housed pigs, 65 to 70% of the variation in H_{tot} within a day was related to physical activity (van der Hel et al., 1984; Henken et al., 1993). Besides contrasts in the mean activity level, differences in the daily pattern of activity might be a cause of differences in daily variation of the influences of T_a on H_{tot} . An effect of T_a on the activity pattern has been demonstrated in group housed pigs (van der Hel et al., 1986; Verstegen et al., 1986). With decreasing T_a , a shift in activity of the pigs occurred from day to evening. In the present study, the daily pattern of f_{st} in young calves was not altered by T_a (Figure 2).

Other data of the present experiment, previously reported by Schrama et al. (1993a), showed that ETH and LCT were dependent upon the calf's posture. Both these thermal requirement characteristics were higher during standing. Hence, it was hypothesised that differences in mean f_{st} between time-periods as well as in the relation between T_a and f_{st} may lead to differences in the response of H_{tot} to T_a . In agreement with de Wilt (1985), this study showed that calves spent more time standing during the light phase of the day than during the dark phase (Figures 1 and 2), indicating a higher activity level during the light than during the dark phase. The present study (in which motor activity of calves was restricted), demonstrated that fluctuations in posture can be regarded as an additional factor causing daily variation in the influence of T_a on H_{tot} . This was indicated by the reduction in the differences between FP, DP and NP in response in H_{tot} to T_a , when H_{tot} was

corrected for standing (H_{cor} , Figure 1). This was also reflected in the smaller differences between these phases in both ETH and LCT estimated from H_{cor} than in the differences in both ETH and LCT estimated from H_{tot} (Tables 1 and 2).

Similar to restrictively fed pigs (van der Hel et al., 1986; Kemp et al.; 1990), the present study showed that H_{tot} in young calves was strongly increased during feeding (Figure 2). The increased H_{tot} during the 1-h period after drinking milk or water represents the energy cost of eating. Drinking water elicited a similar response in H_{tot} of the calves, as did drinking milk (Figure 2). A comparable phenomenon has been described in pigs (Charlet-Lery, 1975). Webster (1983) suggested that the time spent eating is the main determinant of the energy cost of eating solid food. The observed higher response of H_{tot} during the period of water intake (Figure 2), may be related to the longer duration of drinking. The average amount of liquid intake per meal was approximately 1.0 and 1.9 kg when drinking milk and water, respectively. However, the higher response in H_{tot} during the 1-h period of the supply of water, may also be caused by stress imposed on the calves as a result of the measurement of rectal temperature during this period. Furthermore, the difference in temperature between the milk and water offered, could also have been involved. Holmes (1971) demonstrated in calves that at low T_a the increase in oxygen consumption during the intake of milk was affected by the temperature of the ingested milk. The increased H_{tot} during feeding was primarily accounted for by the calf's posture (Figures 1 and 2); averaged over T_a , 63% of the difference in H_{tot} between FP and NP was related to the contrast in f_{st} . This corresponded with studies on pigs (Charlet-Lery, 1975; van der Hel et al., 1986), which demonstrated that physical activity is a major cause of the increased H_{tot} during feeding. In addition, the present study showed that the energy costs of eating were modified by T_a (Figure 1); the contrast in H_{tot} between FP and both DP and NP increased with decreasing T_a . This was primarily related to the higher level of f_{st} during FP in combination with increased heat loss during standing as previously reported by Schrama et al. (1993a).

Implications

Calves purchased at a young age and fed below maintenance, are particularly prone to cold stress. This study shows that the thermal requirements of young, restrictively fed calves, vary within a day. This indicates that ambient temperature does not need to be kept constant during a day, but may vary within certain limits (at least 3°C) without imposing cold stress. Furthermore, it was shown that variation in posture is a major determinant of

the fluctuation in thermal requirements. Consequently, the daily pattern in thermal requirements can be changed when the pattern of standing is altered (e.g., by changes in feeding frequency).

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General Discussion

GENERAL DISCUSSION

Introduction

Calves to be reared for veal or other meat production are usually transported from the dairy farm to rearing unit during the first 2 weeks of age. Besides exposure to a complex of several stressors during this transportation, calves may be subjected to various changes between the dairy farm and rearing unit such as the housing system, feeding level, dietary composition, and climate. The first 2 to 3 weeks after arrival at the rearing unit are the most critical for the health of calves (Postema, 1985; Webster et al., 1985). In practice, the primary aim is to minimize the incidence of health disorders during this period, rather than to optimize (maximize) growth (production). To reduce the risk of gastrointestinal disorders, calves are fed a particularly low feed allowances during this period. Information concerning energy metabolism is very limited for such young, restrictively fed calves during the critical phase after arrival at the rearing unit. Therefore, in the present study, the energy metabolism as affected by both feeding level and ambient temperature was investigated in young, restrictively fed calves during the period of 1 to 2 weeks after transportation.

The results of the experiments described in this thesis, have clearly demonstrated that young calves are not in a steady-state regarding their energy metabolism. The heat production, and the relationships between heat production and feeding level, and between heat production and ambient temperature change with time (over days) in these calves after arrival (Chapter 1, 2 and 3). For the sake of clarity, the mean effects (feeding level and ambient temperature) over a fixed period after arrival, will be discussed independently of the alterations in energy metabolism with time. In this chapter, the following aspects will be discussed:

- partitioning of energy at thermoneutrality,
- thermal effect on energy metabolism,
- time-related alterations in energy metabolism.

Partitioning of Energy at Thermoneutrality

At thermoneutrality, the energy retention and thus growth rate of a calf, depends on the gross energy intake (GE), the amount of energy losses in the faeces and urine, and the

energy loss through heat production by the calf. Postema (1985) calculated that the amount of feed offered in practice for thermoneutral conditions, for the first 2 to 3 weeks after arrival, is not sufficient to meet the calves' energy requirement for maintenance. During this period, calves are therefore, partially dependent upon the mobilization of body energy reserves to cover the energy requirements, which will be reflected in a low or even negative growth rate. Those calculations of Postema (1985) were made by assuming values for metabolizability of dietary energy and for the maintenance requirement of pre-ruminant calves between 1 to about 10 weeks of age.

The observed metabolizability (ME/GE) of whole milk in pre-ruminant calves, measured between 1 to about 10 weeks of age, ranges from 91 to 96% (Gonzalez-Jimenez and Blaxter, 1962; Johnson and Elliott, 1972a; Holmes and Davey, 1976). Recommended ME/GE values of milk replacer in veal calves range from 90 to 95% (Roy, 1980; Webster, 1984; Toullec, 1989). The present study shows that the energy losses in faeces and urine as a percentage of GE, are much higher in young, milk replacer fed calves for the first week after transportation, than in older veal calves. The ME/GE ratio was affected neither by the feeding level (Chapter 1 and 2) nor the ambient temperature (Chapter 3). The average ME/GE ratios per experiment were 76% (Chapter 1), 79% (Chapter 2) and 81% (Chapter 3). In a later experiment, on young calves transported at 6 d of age, a similar ME/GE value of 80% was found for first week after arrival and furthermore, ME/GE increased to 88% for the second week post arrival (Schrama et al., 1992). According to Webster (1984), 6% and 4% of GE intake is lost by the excretion of faeces and urine, respectively, in 14-wk-old veal calves. The lower ME/GE during the first week after transportation, is related to a higher energy loss both in the faeces (lower apparent digestibility) and urine (higher urea excretion). The absolute increase in energy losses as a percentage of the GE intake, are higher in faeces than in urine. In young calves, the observed losses in faeces and urine as a percentage of the GE intake during the first week after transportation were 13 and 6%, respectively (Chapter 3) and 13 and 7%, respectively (Schrama et al., 1992).

The low apparent digestibility of energy (DE/GE) in young calves one week after transportation may have been related to the dietary composition, and(or) to the capacity of the digestive tract of the animals. Concerning dietary composition, replacement proteins for milk protein are generally less completely digested and can also enhance endogenous protein losses, which may be caused by the presence of anti-nutritional factors and(or) by hypersensitivity reactions in the gastrointestinal tract (Toullec and Guilloteau, 1989). However, most commercial starter milk replacers, such as those used in the present study,

contain protein originating from dairy products. The finding that DE/GE increased from 87% for the first week, to 92% for the second week after transportation (Schrama et al., 1992), suggests that the low apparent digestibility was not due to an inferior dietary composition. Hence, the lower apparent digestibility of energy one week after transportation is mainly related to factors, which determine the capacity of the digestive tract, such as the age of the animal and(or) exposure to stressors during and after transportation. With respect to age, an increase in the apparent digestibility coefficients of dry matter, protein, fat, and energy has previously been described in several studies on pre-ruminant calves (van Es et al., 1969; Neergaard, 1980; Williams et al., 1986). The low DE/GE during the first week after transportation of 6-d-old calves may be related to the incomplete development of the digestive tract after birth. During the first weeks after birth, large adaptations occur in the excretion of enzymes as well as in gut motility (Toullec and Guilloteau, 1989). As for stress, the general responses to stressors include, amongst others, changes in the digestive system (Christopherson and Kennedy, 1983; Makkink, 1993). Of the several stressors occurring during and after transportation, exposure to a change in dietary composition (whole milk vs milk replacer), may specifically result in an adaptation of the digestive tract. Furthermore, exposure to stressors at a very young age may even have a greater negative impact on the digestive capacity of young calves after transport. The designs of the experiments presented in this thesis do not enable us to determine whether the observed low DE/GE (Chapter 3), and consequently low ME/GE (Chapter 1, 2 and 3), relate to the age of the calves and(or) to the exposure to stressors. Further research is needed to separate these factors.

The increased energy losses in urine as a percentage of GE intake in young calves the first week after transportation, is probably associated with the restricted feed allowance after arrival. The digested amino acids are used for protein synthesis (for maintenance or growth) or as an energy source (McDonald et al., 1981). Apart from supplying the maintenance requirement of protein (amino acids), the digested dietary protein in young, restrictively fed calves after transportation, will primarily be used as an energy source. This was indicated by the approximately zero protein gain reported in Chapter 3, and found also in a later experiment (Arieli and Schrama, in preparation). Amino acids utilized as an energy source are deaminated by the liver, leading to the production of urea. This increased production of urea is presumably the cause of the increased energy losses in urine in young, restrictively fed calves after transportation. The inefficient utilization of protein as an energy source, combined with the extra metabolic load on the liver and kidneys, may suggest a lower protein content of the milk replacer for young calves post-transportation, which are fed restrictively. However, a reduction in the protein contents of the milk replacer may have

a negative influence on curd formation in the abomasum and thereby a negative impact on the digestion.

Estimates of the ME requirements for maintenance (ME_m) in young, growing, pre-ruminant calves for the period between 1 to about 10 weeks of age, vary between 390 to 460 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (van Es et al., 1969; Johnson and Elliott, 1972a,b; Holmes and Davey, 1976). The observed ME_m values of 560 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (Chapter 1) and 514 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (Schrama et al., 1992) over the first week post transportation, illustrate that ME_m is elevated by about 17 to 27% for young calves during the first week after arrival at the rearing unit. Additionally, Schrama et al. (1992) demonstrated that ME_m decreased to 440 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ during the second week after arrival. A similar phenomenon of an augmented ME_m , followed by a decrease in ME_m with time, was also demonstrated in 10-wk-old pigs after transportation, regrouping, and exposure to new housing conditions (del Barrio et al., 1993). As for the low ME/GE, possible determinants leading to the increased ME_m of young calves for the first week after transportation, are the age and(or) the exposure to stressors during and after transportation. Young growing animals have a higher ME_m as compared with adult animals, which is thought amongst other factors, to be related to the increased physical activity (van Es, 1972), and higher protein turnover of young animals (Simon, 1989). In a later experiment (Schrama et al., 1992), the ME_m of young, newly purchased calves decreased from 514 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ during the first week after transportation to 440 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ during the second week. This observed decrease in ME_m is, however, relatively large to be completely accounted for by the increasing age of the calves. The effect of chronic stress whereby ME_m is enhanced, has been demonstrated in tethered sows, which exhibited a high frequency of stereotyped behaviour (Cronin, 1985). Furthermore, the high ME_m during the first week after transportation, may be caused by an insufficient (Chapter 1) or even absent adaptation period (Schrama et al., 1992), preceding the experimental period. As reviewed by Turner and Taylor (1983), the estimated relationship between heat production and ME intake, and thereby the estimated ME_m , can be influenced by the previous feeding level when the animals are not fully adapted to the experimental feeding level due to an inadequate adaptation period. Further research is required to determine, which of the above mentioned determinants or combinations of determinants, contribute to the enlarged ME_m in young calves during the first week after arrival at the rearing unit.

TABLE 1. The calculated effect of feeding level and body weight on the metabolizable energy available for growth (in $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) in young calves for three situations (A, B, and C) differing in assumed metabolizability (ME/GE; 80 or 90%) and(or) in assumed maintenance requirements of energy (ME_m ; 440 or 560 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$).

Milk powder ^a intake, g/d		Situation		
		A	B	C
Assumed ME/GE, %	---	90	80	80
Assumed ME_m , $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	---	440	440	560
Body weight, kg:				
40	300	-100	-138	-258
40	400	13	-38	-158
40	500	126	63	-57
45	300	-129	-164	-284
45	400	-26	-72	-192
45	500	78	20	-100
50	300	-153	-185	-305
50	400	-57	-100	-220
50	500	39	-15	-135

^aThe assumed gross energy contents of the milk replacer used in these calculation is 20 kJ/g of powder.

In Dutch practice, the feed allowances of young veal calves during the first 2 weeks after arrival at the rearing unit vary between approximately 300 to 500 g of milk powder per animal per day. The applied feeding schedules increase gradually from approximately 300 g of powder/d shortly after arrival, to about 500 g of powder/d by the end of the second week. Postema (1985), calculated the ME available for growth (ME_p , which is equal to ME intake - ME_m), which was based on the assumption that values of both ME/GE and ME_m of older, growing, pre-ruminant calves are representative for young calves shortly after arrival. These calculations demonstrated that the applied feeding levels were below ME_m (i.e., ME_p was negative) shortly after arrival. The present study shows that in addition to the low feeding levels, the dependency of young calves shortly after arrival upon the mobilization of body energy reserves for covering ME_m is even greater due to the lower ME/GE as well as the higher ME_m . In Table 1, calculations of ME_p are presented for young calves at feeding levels within the range, which occur in practice during the first few weeks after arrival at the rearing unit. These calculations of ME_p were made for three different situations. In situation A, calculations were made using values of ME/GE (90%) and ME_m (440 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) of older, growing veal calves. In situation C, the actual values of ME/GE (80%) and ME_m (560 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) for young calves during the first week after arrival were used. In situation B, which is given to quantify the separate effects of both the

lower ME/GE and higher ME_m value in calves after transportation, calculations were made using only the lower ME/GE value (80%) while ME_m is kept at $440 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. These calculations of ME_p , reveal that young calves are far below their maintenance requirement during the critical phase after arrival at the rearing unit (situation C, Table 1). Consequently, these calves in particular depend upon the mobilization of their body energy reserves for sustaining vital life processes, which is reflected by the negative energy retention, and by the weight loss under thermoneutral conditions (Chapter 1 and 3), during this critical phase. The calculated ME_p demonstrates, furthermore, that the effect of the higher ME_m ($560 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) on energy retention, is much larger than the effect of the lower ME/GE (80%) (Table 1). Moreover, the negative influence of a low ME/GE on energy retention is reduced at the lower feeding levels (300 vs 500 g milk powder/d, Table 1). In practice, the amount of feed offered per calf is normally similar for each calf within the whole group of calves. This implies that within a group, the dependency of the calves upon the mobilization of body energy reserves increases with their weight (Table 1). In summary, newly purchased calves are in a state of energy shortage, because of the restricted feeding levels, the enhanced ME_m , and the lower ME/GE.

Apart from the risk of exhaustion of body energy reserves, which are limited in newborn calves (ARC, 1980; Okamoto et al., 1986), the energy shortage in newly purchased calves may be considered undesirable, since it may be a predisposing factor for health disorders in addition to exposure to several stressors during and after transportation. As reviewed by Kelley (1980), restricted feeding can impair the immune system, just as other stressors do. Results for purchased calves, suggested that mortality was affected by feeding level, being higher at low feeding levels (Williams et al., 1981). The easiest solution for the energy shortage in newly purchased calves would seem to be an increase of the feeding allowances. However, the higher feeding levels combined with the low capacity of the digestive system (DE/GE) will most likely result in high levels of undigested material in the digestive tract, resulting in an increased risk of gastrointestinal disorders in the newly purchased calves. Similar to the hypothesis of Makkink (1993) for young piglets after weaning, a gradual increase in feed intake of young, newly purchased calves could be vital for the optimal adaptation of the digestive tract. An optimal adaptation of the digestive tract may be essential with regard to the occurrence of gastrointestinal disorders. From the energetic point of view, further research is required to delineate the factors causing the enhanced ME_m of newly purchased calves. With respect to gastrointestinal disorders, it is also important to delineate the causes of the low DE/GE and the factors involved in the adaptation of the digestive system.

Thermal Effect on Energy Metabolism

Whole Day Thermal Requirements

Young, newly purchased calves are highly dependent upon their body energy reserves during the first 2 to 3 weeks after arrival at the rearing unit. The provision of optimal climatic conditions for newly purchased calves during this critical period is important in order to prevent an enhancement of the strain of the energy shortage imposed upon them. The negative impact of cold conditions on the energy retention of homeothermic animals is related to an enhanced energy requirement for maintenance, due to the energy costs to sustain constant body temperature. Furthermore, the energy retention may be reduced by a decrease in the availability of nutrients from the diet. The enhanced maintenance requirement is a major cause of the negative impact of cold environmental conditions (Close, 1987).

In ruminants, the digestibility of roughages is decreased by exposure of the animals to low ambient temperatures (Christopherson and Kennedy, 1983). Data are conflicting concerning the effect of ambient temperature in young, pre-ruminant, milk replacer fed calves. The present study (Chapter 3), and a later experiment (Arieli and Schrama, in preparation), show that energy and nitrogen apparent digestibility of milk replacer is not affected by ambient temperature in young, newly purchased calves. This is in agreement with the findings of Williams and Innes (1982) on the dry matter, nitrogen, and fat apparent digestibility of milk replacer in pre-ruminant calves between 24 to 38 d of age, kept at different ambient temperatures (3 vs 18°C). Similarly, findings of Cockram and Rowan (1989b) showed that abomasal digestion and apparent ileal digestibility of milk replacer did not differ between ambient temperatures of 5°C and 25°C in young calves between 5 to 27 d of age. However, in contrast with the other studies, Cockram and Rowan (1989a) observed an effect of ambient temperature on the dry matter, nitrogen, fat and energy apparent digestibility of milk replacer. Furthermore, they demonstrated that an increased air velocity (< 0.2 vs > 3 m/s) resulted in lower apparent digestibilities of dry matter, fat and energy. Moreover, the effect of air velocity was enhanced at a low ambient temperature (10 vs 25°C). The difference between studies on the effect of exposure to cold conditions on digestion in young, pre-ruminant calves is possibly related to the differences in feeding level between studies. Cockram and Rowan (1989a) observed that the negative influence of air velocity was enhanced with increasing feeding level. Furthermore, variation between studies may involve the magnitude of the exposure to cold stress. The impact of a lower

digestibility caused by cold stress will only have a minor effect on the energy shortage, which is imposed on newly purchased calves 1 to 2 weeks after transportation, because of the low feed allowances during this period as shown in Table 1. However, the possible interaction between feeding level and exposure to cold stress may need to be assessed further in order to provide information for the creation of optimal environmental conditions to increase feed allowances in newly purchased calves without increasing the risk of gastrointestinal disorders.

Knowledge concerning the lower critical temperature (LCT) of young newly purchased calves is important, because exposure to ambient temperature below the LCT will lead to an increase in the energy requirement for maintenance, and thereby to a more negative energy retention. Reported values of LCT vary between 8 to 11°C in young (between 2 d to about 8 weeks of age), growing, pre-ruminant calves at feeding levels ranging between 730 to 950 kJ of ME.kg^{-0.75.d-1} (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978). Despite the very low feeding levels (below ME_m) in young, newly purchased calves, the present study shows that the mean LCT values over the period of about 1 week after transportation is only slightly higher than the reported values for young growing calves fed above ME_m. In Chapter 3, the mean LCT for the first 5 d after transportation was 14.5°C for young, newly purchased calves with an ME intake of 300 kJ.kg^{-0.75.d-1}. The results in Chapter 2 showed that the LCT of young, newly purchased calves was not affected by feeding level (ME intake of 290 versus 460 kJ.kg^{-0.75.d-1}). Averaged over both feeding levels, the observed mean LCT over the period between 4 to 12 d after transportation was 12.5°C. As discussed in Chapter 2, the method of estimating LCT from the minimum of whole-body conductance and thermoneutral heat production appears to give lower estimates for LCT than the estimations of LCT from the relationship between heat production (or heat loss) and ambient temperature (see Table 6, Chapter 2). If one considers the influence of estimation procedure, the difference in LCT between the present study and the literature becomes even smaller, despite the contrasts in feeding level. The absence of an effect of feeding level on LCT in young calves as observed in the comparison between different studies, and as observed in Chapter 2, is in disagreement with the theory that LCT declines with increasing feeding levels. According to that theory, the LCT is lowered by an increase in thermoneutral heat production when the feeding level is increased (see Figure 2, general introduction). This phenomenon has been demonstrated in sheep (Graham et al., 1959) and in pigs (Close, 1970; Verstegen et al., 1973). The relatively low LCT values observed in the present study of young, newly purchased calves may be caused by their relatively high thermoneutral heat

production despite the low feeding level. The high thermoneutral heat production is apparently related to the high value of ME_m in these calves as observed in Chapter 1. This effect of an enhanced thermoneutral heat production on the LCT agrees with the finding in Chapter 3 of an increase in LCT with time after arrival, as a consequence of the greater decrease of heat production with time at thermoneutrality, than at temperatures below the LCT. As for the high ME_m value, possible causes of the relatively low LCT values in relation to the low feeding level for these calves are the young age and(or) the exposure to stressors during and after transportation. In addition, there may also be a carry-over effect of the feeding level (metabolic rate) before arrival at the rearing unit on the LCT of the calves at the rearing unit.

In homeotherms, the generally applied theory on the effect of feeding intake on heat production in relation to ambient temperature, assumes that at thermoneutrality heat production (as depicted in Figure 2, general introduction) is dependent on feed intake. Below the LCT on the other hand, heat production is not affected by feed intake but is fully dependent on the climatic conditions (Holmes and Close, 1977; Robertshaw, 1981; Curtis, 1983). This implies that theoretically, below the LCT the efficiency of ME utilization is equal to unity, which has been demonstrated in sheep (Graham et al., 1959) and pigs (Verstegen et al., 1973). In addition to the absence (or small) effect of ME intake on LCT, data from the present study (Chapter 2), reveal that heat production in young, newly purchased calves is affected by the ambient temperature below LCT, indicating that the efficiency of ME utilization is smaller than unity. The presence of an effect of ME intake on heat production below LCT was also observed in other experiments with young calves during the first week after arrival (Schrama et al., 1991; Arieli and Schrama, in preparation). These conflicting results for young, newly purchased calves may be related to their unadapted state. However, data from a later experiment (Arieli and Schrama, in preparation) showed that the effect of ME intake on heat production remained similar over the whole experimental period of 2 weeks after transportation. Furthermore, a similar phenomenon of an efficiency of ME utilization smaller than unity below LCT has been demonstrated in rats (Jeszka et al., 1991) and in pigs (Close, 1978). These results on rats and on pigs, together with the results observed in young, newly purchased calves, suggest that there is a need to reevaluate the current theory for homeotherms on the effect of feed intake on heat production in relation to ambient temperature.

Furthermore, data in Chapter 2 showed that the rectal temperature of young, newly purchased calves declined with decreasing ambient temperature. This decline in rectal

temperature was not related to having reached its summit metabolism, because heat production increased further with decreasing ambient temperatures (Chapter 2). The effect of ambient temperature on heat production was larger at the low compared with the high feeding level (290 versus 460 $\text{kJ ME} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$; Chapter 2). This is in agreement with the findings of Scibilia et al (1987) for young calves between 7 to 28 d of age. The greater decline in rectal temperature at the low feeding level may be an indication of a depletion of body energy reserves at the low feeding level, due to the low ambient temperature. However, in a subsequent experiment (Chapter 3), ambient temperature did not affect the rectal temperature of calves with a ME intake of $300 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. Also, the lower decrease in heat production with time at low compared with high ambient temperature (Chapter 2 and 3), suggests that body energy reserves were not exhausted. This is supported by the absence of an ambient temperature effect on protein retention (Chapter 3). Rectal temperature patterns of calves exhibit a circadian rhythm, which is affected by ambient temperature (Schmoldt, 1985). It was shown that the difference in rectal temperature between ambient temperatures (5 vs 20°C), was largest at the beginning of the morning and smallest around noon (Schmoldt, 1985). The differences in the response of rectal temperature to ambient temperature between experiments of the present study (Chapter 2 vs 3) could be related to the moment of measurement during the day. However, the question remains whether this possible effect of ambient temperature on circadian rhythm in rectal temperature, is a reflection of an effect of ambient temperature on circadian rhythm in deep body temperature. It can also be an indication of an effect of ambient temperature on a rhythm in temperature gradient between body core and body surface, being a reflection of a circadian rhythm in whole-body insulation. The observed, within day, variation of the influence of ambient temperature on heat production below LCT in Chapter 5, indicates the existence of such a rhythm in whole-body insulation of young calves. However, the observed ambient temperature effect on rectal temperature, together with the fact that the partial efficiency is below unity, may also be an indication that thermoregulation in these calves is not fully developed at this age. Further research on within day changes in rectal temperature, whole-body insulation, and heat production, is needed to test these hypotheses.

The increase in heat production with decreasing ambient temperature below LCT is equivalent to the increase in ME_m for sustaining constancy of body temperature. Data from Chapter 2 reveal that the extra thermoregulatory heat production (ETH) was not affected by the feeding level. The observed ETH values in the present study were 8.4 (Chapter 2), and $9.5 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$ (Chapter 3), for young, newly purchased calves over the first week after transportation. Expressed as a percentage of the ME_m for young, newly

purchased calves during the first week after transport (514 to 560 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$), this is an increase of 1.6 to 1.8% in ME_m per $^{\circ}\text{C}$ fall in ambient temperature below LCT. The impact of ambient temperatures of 5 and 10°C below LCT, respectively, on the energy retention, and the resulting extra milk powder requirement is shown in Table 2 for young calves.

TABLE 2. The calculated effect of an exposure to an ambient temperature of 5 and 10°C below the lower critical temperature (LCT) on the energy retention (ER) and the extra milk powder allowance due to the increased maintenance requirement in young, newly purchased calves at different body weights^a.

Body weight, kg	5°C below LCT		10°C below LCT	
	Effect on ER, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	Extra milk powder ^b , g/d	Effect on ER, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	Extra milk powder ^b , g/d
40	-45	45	-90	89
45	-45	49	-90	98
50	-45	53	-90	106

^aCalculations are based on an extra thermoregulatory heat production value of $9.0 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot {}^{\circ}\text{C}^{-1}$.

^bContaining 20 kJ gross energy per gram powder with a metabolizability of 80%.

Young, newly purchased calves are particularly dependent on body energy reserves to meet their energy requirements during the first 2 to 3 weeks after transportation. This is a critical phase due to the limited feed allowances, the low ME/GE and the enhanced ME_m . Exposure of those calves during this critical period to cold climatic conditions will enhance the energy shortage, which is even imposed on them under thermoneutral conditions. The increase in ME_m caused by cold exposure, cannot be compensated for by increasing the feeding level, because this will increase the risk of gastrointestinal disorders. Therefore, provision of optimal climatic conditions is the only available option to prevent an increased catabolism of body energy reserves by exposure to cold. Apart from the risk of exhaustion of body energy reserves, exposure to low ambient temperature (cold stress) can be considered as a predisposing factor for health disorders. The negative impact of exposure to cold on health can be attributed by a direct effect on the immune system (Kelley, 1980; Webster, 1981). For these young, newly purchased calves the increased energy shortage (negative energy retention) provoked by the cold exposure, might be an additional factor affecting the health status of these calves.

Behaviour and Thermal Requirements

In general, behavioral, autonomic, and neuroendocrine responses are the three general types of biological responses, which an animal utilizes in its attempts to cope with exposure to stressful conditions (Moberg, 1985). These responses allow homeothermic animals to maintain a constant body temperature during exposure to adverse climatic conditions. By thermoregulatory behaviour, the animal specifically influences its heat loss by avoidance of the adverse climatic conditions and(or) by conservation of body heat (Young et al., 1989; Figure 1). By avoidance behaviour the animal can actively select the most optimal micro-climate available, as has been demonstrated in e.g., rats (Gordon, et al., 1991), and in experiments with operant supplementation heating in pigs (Baldwin, 1979; Balsbaugh and Curtis, 1979; Verstegen et al., 1987) and sheep (Baldwin, 1979). Conservation of body heat (i.e., increase in whole-body insulation) in response to cold stress, can partially be realised by animals through shifts in behaviour such as huddling (Boon, 1981; Gerkema, 1991; Brown and Foster, 1992) and reduction of floor contact area during lying (Mount, 1967). Because of the impact on heat exchange, the occurrence of thermoregulatory behaviour is dependent upon the climatic conditions (e.g., ambient temperature).

Besides thermoregulatory behaviour, other types of behaviour such as locomotor activity (movement and(or) exercise), posture (standing or lying), and eating, can affect the thermal requirement characteristics (LCT and ETH) of animals. This is because the non-thermoregulatory behaviour may affect heat loss (i.e., whole-body insulation) and(or) heat production (thermoneutral heat production) (Figure 1). In rodents (Hart and Janský, 1963; Mount and Willmott, 1967; Arnold et al., 1986) and birds (Zerba and Walsberg, 1992), it has been demonstrated that thermogenesis induced by locomotor activity can substitute for cold-induced thermogenesis. These results suggest that during locomotor activity LCT may be lowered because of the increased heat production (at thermoneutrality). Results of the present study demonstrated that the thermal requirements of young calves are dependent upon their posture (standing vs lying; Chapter 4). During standing, the thermoneutral heat production is increased but the conservation of body heat is decreased. The latter effect is indicated by the higher ETH during standing than during lying of the calves. In comparison with lying, LCT was higher by 3.5°C during standing. This indicates that the enhancement effect of the higher ETH on LCT was greater than the reduction effect of the higher thermoneutral heat production. With regard to feeding, the present study shows that both ETH and LCT were higher during the periods of the day when the calves were drinking (milk or water) than for the rest of the day. The major cause of the higher ETH and LCT

values during the feeding periods is the increased percentage of time spent standing during these period (Chapter 5).

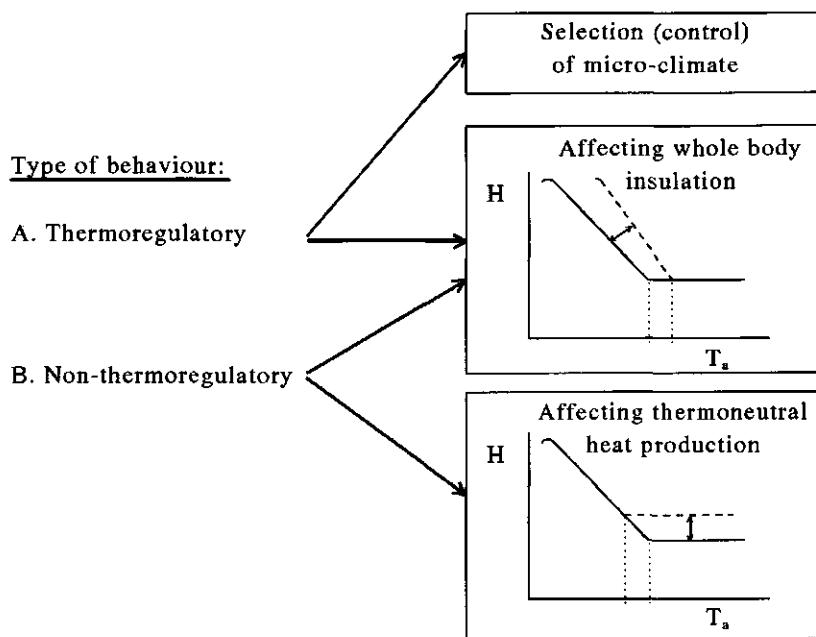


FIGURE 1. Effects of type of behaviour on the thermal requirements of animals under conditions of cold. The graphs show the possible alterations in the relationship between heat production (H) and ambient temperature (T_a) induced by behaviour.

The effect of some types of non-thermoregulatory behaviour on the thermal requirement characteristics poses the question as to whether shifts in such types of behaviour are (or can be) utilized by animals as a resource for coping with cold environmental conditions. With regard to energy expenditure, changes in behaviour, which affect only the thermoneutral heat production (e.g., such as locomotor activity), are probably inappropriate as a response for coping with cold stress. This is due to the fact that the total energy expenditure of an animal will not be altered if cold-induced thermogenesis is completely substituted by another type of thermogenesis. However, shifts in types of behaviour, which modify the whole-body insulation (i.e., alter ETH), can be utilized by animals as a mechanism for reducing energy expenditure during exposure to cold stress. For instance, a decline in the time spent standing at low ambient temperatures could reduce the increase in heat production below LCT, and thus also reduce the increase in ME_m caused by cold exposure (see Figure 3, Chapter 4). However, the results of Chapter 4 do not

exhibit such an effect. The time spent standing by the calves even tended to increase at low ambient temperatures. This suggests that in young calves, the benefit of decreasing the time spent standing under conditions of cold stress does not prevail over factors inducing the need to stand. Such a strong urge to stand by these young calves may be related to the very low feed allowances which thereby, evoke hunger. It may also be related to the calf's need to satisfy their suckling behaviour. Young calves especially have a strong desire to suck (Broom, 1991). Although the time spent standing during a day in young calves was observed not to be affected by ambient temperature, the number of intervals of standing in combination with the duration of these intervals can be altered by ambient temperature. Toutain et al. (1977) demonstrated that the heat production during standing in sheep was highest directly after the alteration in posture and decreased with time within a standing interval. If the decrease in heat production within a standing interval can be influenced by ambient temperature, shifts in both the number and duration of standing intervals without alteration of the total time spent standing may also be a way, whereby calves can minimize their total energy expenditure at lower ambient temperatures. Furthermore, it can be hypothesised that an increased standing interval may be present at low ambient temperature because of an increased reluctance to lie down on a cold floor. Differences in the LCT of animals caused by the type of floor (bedding) as observed in pigs (Verstegen and van der Hel, 1974), may also be related to shifts in non-thermoregulatory behaviour, in addition to the differences in conductive heat loss to the floor.

Additional knowledge concerning the impact of non-thermoregulatory behaviour on thermal requirements will improve the comparison of results from different studies of the effects of ambient temperature on energy metabolism. Furthermore, it may lead to improved recommendations for optimal climatic condition for practical animal husbandry. Future alterations in husbandry systems such as individual vs group-housed calves may affect thermoregulatory as well as non-thermoregulatory behaviour and thereby the calves' thermal requirement characteristics. Thus when housing conditions are altered, research may be required to assess its impact on thermoregulation of animals. With advances in the technology of climate control systems for animal husbandry, the application of varying ambient temperatures within a day becomes feasible for practical animal husbandry. Variation of ambient temperature within a day may be a way of reducing the use of fossil energy sources. Within day variation of the thermal requirements of farm animals needs further assessment in relation to delineate factors (e.g., feeding level) influencing and factors (e.g., behaviour) causing this variation. Furthermore, there is a need to study the impact of variation in ambient temperatures within a day on the health and welfare of animals.

Time-related Alterations in Energy Metabolism

The present study was designed to assess the effects of feeding level and ambient temperature on the energy metabolism of young, newly purchased calves during the critical period after arrival at the rearing unit. Until now, feeding level and ambient temperature have been discussed with respect to their mean effects on energy metabolism, which were observed over the total experimental periods. The results in Chapter 1, 2 and 3 show clearly that young, newly purchased calves are not in a steady-state with regard to their energy metabolism. Despite constant feeding levels (GE intake), heat production of the calves decreased between days during the experimental period. Similar findings of alterations in heat production with time have been observed in young pigs after transportation, regrouping and exposure to new housing conditions (Verhagen, 1987; del Barrio et al., 1993). The decrease in heat production was affected by feeding level (Chapters 1 and 2) and by ambient temperature (Chapters 2 and 3). A generalization of the impact of feeding level as well as of ambient temperature on the decline in heat production with time is depicted in Figure 2.

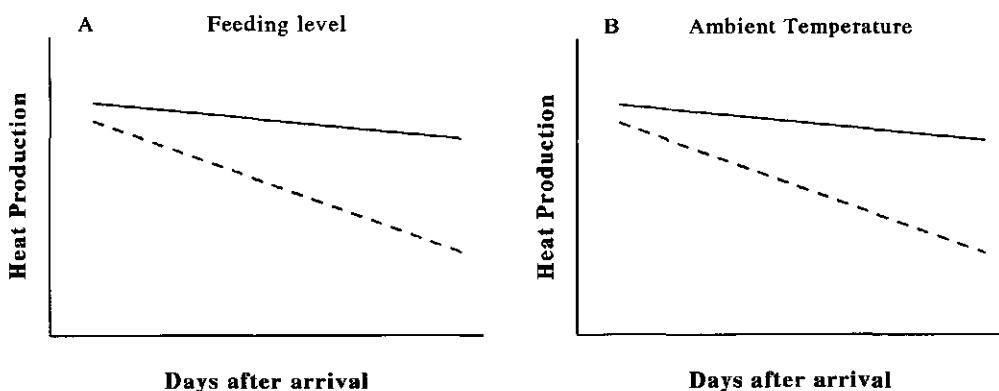


FIGURE 2. The alteration of heat production with time in young, newly purchased calves as affected by feeding level (Part A: ----, low feeding level; —, high feeding level) and as affected by ambient temperature (Part B: ----, high ambient temperature; —, low ambient temperature).

As for feeding level, it was observed that the decline in heat production with time was larger for the lower than for the higher feeding level (Chapters 1 and 2). Similar findings of an effect of feeding level on the alterations in heat production with time were observed in a experiment on 10-wk-old pigs after transportation, regrouping and exposure to new housing conditions (del Barrio et al., 1993). The influence of feeding level on the alteration of heat production with time, indicates that the relationship between heat production and ME intake alters with time in young calves after arrival. In the experiment described in Chapter 1, the changing relationship with time was such, that the efficiency of utilization of ME and the extrapolated heat production at zero ME intake decreased, whereas ME_m remained similar. In contrast with the results of Chapter 1, it was observed in a later experiment on young, newly purchased calves (Schrama et al., 1992) that ME_m also decreased with time. Such a decline in ME_m was also observed in 10-wk-old pigs after transportation, regrouping, and exposure to new housing conditions (del Barrio et al., 1993).

As in the case of ambient temperature, the results of Chapter 2 and 3 demonstrated that the decline in heat production was larger for high rather than for low ambient temperatures. Thus, the relationship between heat production and ambient temperature was altered in young calves with time after transportation. From the results presented in Chapter 2, it was hypothesised that this changing relationship should lead to time-related changes in the thermal requirement characteristics (ETH and LCT). In Chapter 3 it was shown that in young, newly purchased calves, LCT increased with time by $0.9^{\circ}\text{C}/\text{d}$, whereas ETH remained similar over time. Despite the low feeding level, the LCT value of 13°C for the first day post-arrival was similar to values of LCT observed in young calves fed above ME_m (Gonzalez-Jimenez and Blaxter, 1962; Holmes and McLean, 1975; Webster et al., 1978). However, with the passage of time (days) after arrival, the LCT of these newly purchased calves fed below ME_m increased, and thus an effect of feeding level on LCT occurred in contrast with the studies of young calves fed above ME_m .

Part of the total energy expenditure of animals relates to their physical activity (Blaxter, 1989; Richard and Rivest, 1989; Shetty, 1990). Consequently, differences in physical activity between animals are a source of variation in energy expenditure as has been demonstrated in laying hens (Luiting, 1991). In young pigs after transportation, regrouping, and exposure to new housing conditions, it was shown that the alterations in heat production with time were partly related to changes in physical activity with time (Schrama et al., 1993). Furthermore, it was noted in those pigs, that the changes in physical activity were affected by feeding level. The changes were largest at the high levels of feed intake. In young, newly purchased calves, which are individually housed, physical activity

is limited only to their choice of posture (standing vs lying). The observed decline in the heat production of young, newly purchased calves, may thus be partly related to a decrease in the time spent standing between days. However, unpublished data of the experiment presented in Chapter 3 show that the time spent standing increased with time during the experimental period. Hence, the decrease in heat production with time will be larger if corrected for the time spent standing. The increase in time spent standing after transportation could possibly be related to the age of the calves and(or) to exhaustion induced by the transportation. Data on beef heifers showed that the time spent standing is much lower at 2 days of age than above the age of 3 months (Baker et al., 1991). The finding that a higher percentage of time spent resting and sleeping (lying) immediately after transportation in 15-d-old calves by Atkinson (1992), was suggested to relate to exhaustion as a result of transport. In addition to the alteration in time spent standing, the observed alteration in heat production in the present study may also be partly accounted for, by an alteration in the energy cost of standing with time. Blaxter (1974) demonstrated in sheep that the energy cost of standing declined with time as a consequence of a process of training the animals to the experimental procedures. However, the observed decline in heat production of young, newly purchased calves as well as the difference in decline between treatments (feeding level or ambient temperature) can only be partly related to physical activity. This means that parts of the alterations in heat production with time are caused by changes in the energy expenditure, which does not relate to physical activity. Alterations in the sympathetic nervous system activity, as well as the neuroendocrine activity of thermogenic hormones (such as thyroid hormone) play an important role in the regulation of the metabolic rate of animals, which does not relate to physical activity (Shetty, 1990). Further research on the non steady-state of young, newly purchased calves with regard to their energy metabolism should focus on the role of behaviour (physical activity), and on the neural and hormonal regulation.

In the present investigation, it was observed that in young, newly purchased calves the effect of both feeding level and ambient temperature on heat production, altered with time. The effect of feeding level (Chapters 1 and 2), and the effect of ambient temperature (Chapters 2 and 3) were relatively small shortly after arrival, but both of these effects increased on successive days after arrival of the calves (Figure 2). This suggests that shortly after arrival the level of heat production of these calves was determined by factors other than feeding level and ambient temperature. Possible factors, which may have overruled the effects of both feeding level and ambient temperature, were: 1) a carry-over effect of the previous feeding level combined with the extremely low feed allowances (below ME_m) after

arrival, 2) the young age, and 3) exposure to the complex of stressors during and after transportation.

After an alteration in feeding level, the heat production of animals gradually changes with time to a new steady-state level (Turner and Taylor, 1983). Thus, before energy metabolism has reached a new steady-state, both the heat production and the alterations in heat production depend on the preceding feeding level. Young, newly purchased calves are fed very low feed allowances after arrival at the rearing unit. Depending on the feeding strategy applied at the dairy farm, it can be expected that young, newly purchased calves are exposed to a large reduction in feeding level after arrival at the rearing unit. Shetty (1990) distinguished two mechanisms involved in the reduction of resting metabolic rate during energy restriction; a short term (< 2 weeks) reaction by decreasing the metabolic activity of body tissues, and a longer term (> 2 weeks) reaction by reducing the size of active body tissue. Therefore, apart from the carry-over effect of the previous feeding level, the observed alterations in heat production of young calves after arrival may also be a reflection of a decrease in metabolic activity of body tissues due to the restrictive feeding level itself.

Calves to be reared for veal or other types of meat production are normally transported to the rearing unit during the first 2 weeks of age. Under thermoneutral conditions, the metabolic rate of young mammals is high shortly after birth, and declines with age (Poczopko, 1981). In young calves, it has been demonstrated that the fasting heat production decreased with time (age) during the first 3 weeks of age (Roy et al., 1957; Settemire et al., 1964). It could be hypothesised that the young age of the calves overruled the effects of feeding level and ambient temperature on heat production, as was observed in the present study (Chapters 1, 2, and 3). This hypothesis is supported by the findings of Okamoto et al. (1986) that the feeding of colostrum does not affect the resting and summit metabolism of 1-d-old calves. Figure 3 depicts how age may overrule the effect of feeding level as well as that of ambient temperature. An hypothesised relationship between heat production and age of the calves is shown in Figure 3A. The alteration in heat production with time after arrival is shown in Figure 3B in the case of age at transportation equals T . If the steady-state levels of heat production determined by either feeding level or ambient temperature are below the heat production at the age T , it can be expected that heat production will decline with time. Figure 3B also shows that the decline in heat production will be larger when the steady-state level of heat production is lower ($H1$ vs $H2$). This hypothetical overruling effect of age as described in Figure 3, is in agreement with the findings in the present study of a greater decline in heat production at low feeding levels (Chapter 1 and 2) as well as at high ambient temperatures (Chapters 2 and 3).

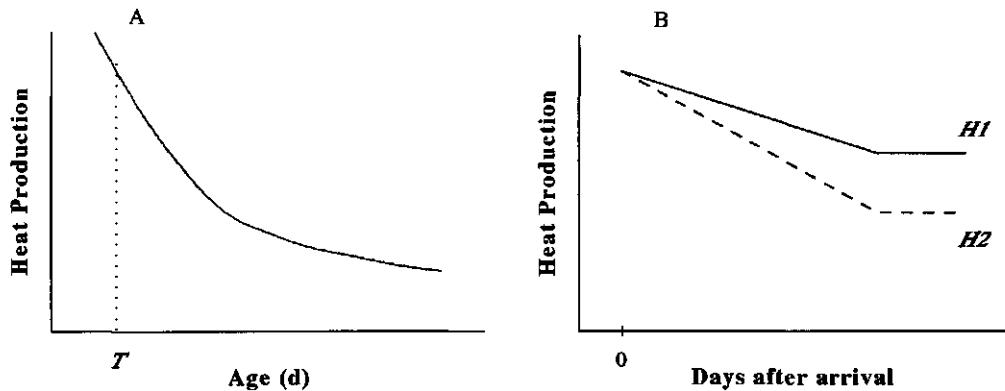


FIGURE 3. The underlying mechanism by which age may overrule the effects of feeding level and(or) ambient temperature on heat production (H). In part A, the relation between H and age is given. In part B, the alterations in H with time after transportation are given at two different steady-state levels of H ($H1$ and $H2$), when the age of the calf is T at the moment of transportation ($d = 0$).

Stress in animals results in a wide range of physiological changes in order to maintain their homeostasis (Moberg, 1985). The response to stressors comprises the activation of the sympathetic-adrenomedullary system, which involves the immediate release of catecholamines, or the hypothalamic-pituitary-adrenocortical system, which involves the more gradual release of glucocorticoids (Dantzer and Mormède, 1983; Moberg, 1985; Oliverio, 1987). In general, the release of catecholamines and glucocorticoids in a stressed animal are directed to the rapid mobilization of energy reserves for metabolic processes (Dantzer and Mormède, 1983). Calves are exposed to several stressors during and after transportation to the rearing unit. The observed alterations in heat production with time after arrival of young calves (Chapters 1, 2, and 3) may be an indication of recovery from the acute stress of transportation and(or) an adaptive response to the more chronic stress imposed on the calves after arrival. Shortly after arrival, the effects of feeding level and ambient temperature on the heat production of calves may have been overruled by the exposure to stressors during and after transportation. This hypothesis of the overruling effect of exposure to stressors is shown in Figure 4. In Figure 4A, three different models

are depicted, which may describe the relation between the magnitude of stress and heat production in animals: 1) a model of a linear relationship (*R1*); 2) a threshold model in which below the threshold, heat production is not affected by stress, and above the threshold, a linear relationship exists (*R2*); and 3) a threshold model in which there is a fixed response of heat production above the threshold (*R3*). The alteration in heat production with time after arrival is shown in Figure 4B for the situation that the magnitude of stress at arrival is S . If the heat production at a stress level S is higher than the steady-state levels of heat production determined by either feeding level or ambient temperature, it can be expected that heat production will decline with time. In this situation the decrease in heat production will be larger when the steady-state level of heat production is lower (*H1* vs *H2*). Such a hypothetical overruling effect of stress is shown in Figure 4, and is in agreement with the results of the present study of a higher decrease in heat production at low feeding levels (Chapters 1 and 2) as well as at high ambient temperatures (Chapters 2 and 3).

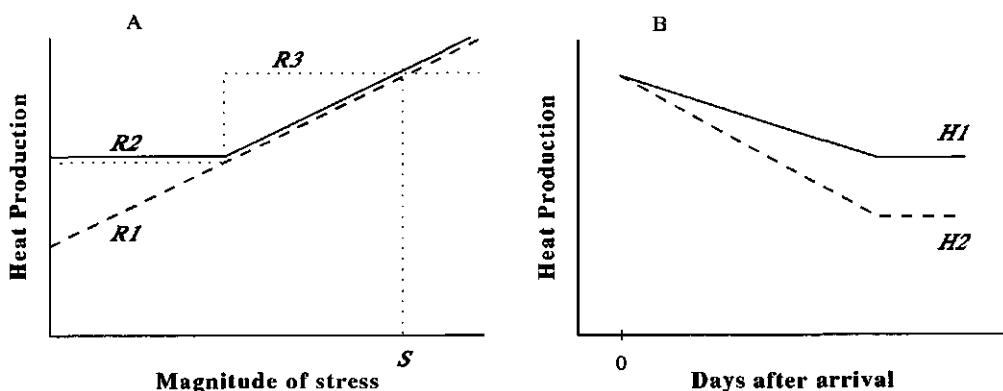


FIGURE 4. The underlying mechanism by which stress may overrule the effects of feeding level and(or) ambient temperature on heat production (H). In part A, three different types of relationships between H and magnitude of stress are given (*R1*, *R2*, and *R3*). In part B, the alterations in H with time after transportation are given at two different steady-state levels of H (*H1* and *H2*), when calves are exposed to a stress level of S at the moment of transportation ($d = 0$).

From the results of the experiments presented in this thesis (Chapters 1, 2, and 3), it is impossible to distinguish whether the alterations in energy metabolism in young, newly purchased calves are due to age, or are the results of a mechanism of adaptation to the restricted feeding regime or to exposure to stress. Further research is needed to determine, which of these factors cause the non steady-state in young, newly purchased calves with regard to their energy metabolism. The presence of interaction effects between these factors should not be ruled out, especially that between age and exposure to stress. As reviewed by Trunkfield and Broom (1990), studies on transportation stress demonstrate that the response in serum cortisol levels increases with the age of the calves, which suggests that young calves are less affected by stress. However, cortisol may be an inappropriate indicator of stress when comparing calves of different ages, because basal cortisol levels decrease substantially during the first month of life (Mormède et al., 1982). Brown adipose tissue is present in the newborn calf (Alexander et al., 1975; ter Meulen and Molnar, 1975). The presence of brown adipose tissue may result in a strong thermogenic reaction as a response to stress-exposure by the release of catecholamines due to activation of sympathetic-adrenomedullary system. This may imply that young calves are even more susceptible to stressors. Additional research on the relation between exposure to stressors and energy metabolism (heat production) in animals is required, since heat production may be a good indicator for measuring stress responses in addition to hormonal alterations. Furthermore, information concerning the effects of ambient temperature and feeding level on the energy metabolism of farm animals, which are not in a steady-state, is also of practical importance, since under practical conditions of husbandry, animals will inevitably be exposed to external stimuli, which challenge their homeostasis.

Concluding Remarks

The investigations described in this thesis deal with the energy metabolism of young, restrictively fed calves during the period of 1 to 2 weeks after transport. The results show that:

- In addition to the low feed allowance during this period, the energy shortage imposed on these calves is enhanced by the low metabolizability of dietary energy from the milk replacer, and by the high energy requirements for maintenance. During this period, the metabolizability can be as low as 80%, and the energy requirement for maintenance as high as $560 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$.
- Averaged over this period, the lower critical temperature (LCT) of such calves

ranges from 12 to 15°C. The extra thermoregulatory heat production (ETH) below LCT (i.e., the increase in energy requirements for maintenance) is $9.0 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$.

– The current concept of thermoregulation for homeotherms is not totally applicable for these very young calves. Averaged over this period, the LCT of such calves is not affected by feeding level. Below LCT, heat production is influenced by the feeding level (i.e., the efficiency of utilization of metabolizable energy is below unity). Furthermore, there are indications that rectal temperature decreases with declining ambient temperatures, despite the fact that the heat production of these calves has not yet reached their summit metabolism.

– Non-thermoregulatory behaviour, such as posture (standing vs lying) affects the thermoregulation of animals. During standing, LCT as well as ETH of calves is higher than during lying. Time spent standing by the calves is not decreased at ambient temperatures below LCT, despite the fact that calves require an increased cold-induced thermogenesis when standing.

– The influence of ambient temperature on heat production of calves varies within a day. The circadian fluctuation in the relationship between ambient temperature and heat production is partly related to the within day variation in time spent standing.

– These calves are not in a steady-state with regard to their energy metabolism. Heat production declines with time (over days) during this period, for as yet unknown reasons.

– Both the relationship between heat production and feeding level, and between heat production and ambient temperature, alter with time after arrival. The decline in heat production is greater at 'low' compared with 'high' feeding levels. At high ambient temperatures, the decrease in heat production is larger than at low ambient temperatures. Both the effect of feeding level and ambient temperature on heat production are overruled by other, still unknown factors. The changing relationship between heat production and ambient temperature is reflected in an increase with time in LCT of calves after transportation ($0.9^\circ\text{C}/\text{d}$), but is not reflected in an alteration of ETH over time.

The research presented in this thesis clearly demonstrates that in practice, young, newly purchased calves are particularly dependent on the body energy reserves to meet their energy requirements, not only because of the low feeding level but also due to the low metabolizability and high maintenance requirements for energy. Possibilities to reduce this energy shortage by increasing the feeding levels are limited due to the increased risk of gastrointestinal disorders. Therefore, further research on factors, which cause the low metabolizability (digestibility) and high maintenance requirement, is needed to provide information for the practical husbandry of young, newly purchased calves so as to improve

their energy retention.

Concerning the high maintenance requirement, the unadapted state of these calves with regard to their energy metabolism particularly requires further assessment. As suggested in this thesis, possible factors, which may cause the unadapted state of these calves are their age, the restricted feeding level (carry-over effects of feeding levels), and(or) exposure to stressors during and after transportation. Depending on the outcome, future research on these factors (such as optimal age of transportation, and ways of reducing the stress imposed on them during and after transportation) may provide information for practical animal husbandry to improve the health and welfare of these calves during the critical phase after transportation.

In this thesis, it has been demonstrated that providing optimal climatic conditions to young, newly purchased calves after transportation, is important in order to prevent extra mobilization of energy reserves. Immediately after arrival ambient temperature should not be less than 14°C. As a consequence of the unadapted state of the calves, LCT increases with time during the first week after arrival. Adjustment of the ambient temperature with time (over days) may be needed depending on the applied feeding level (increasing with time).

Finally, it should be emphasised again that large changes in energy metabolism of unadapted calves occur with time. Even under the most ideal husbandry conditions, farm animals will inevitably be exposed to external stimuli, which threaten their homeostasis. Therefore, information about energy metabolism as affected by feeding level and by ambient temperature (i.e., energy requirements and thermal requirements) in unadapted (or adapting) farm animals is essential for practical animal husbandry.

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Summary

SUMMARY

In The Netherlands, calves to be reared for veal or other meat production are transported from the dairy farm to the rearing unit at about 1 to 2 weeks of age. In addition to the stress of transportation itself, these calves are subjected to various other changes such as housing system, feeding level, dietary composition, and climate. The first 2 to 3 weeks at the rearing unit represent a critical phase in veal production in relation to the health of the calves. To reduce the risk of gastrointestinal disorders in practice, calves are fed at very low feeding level during this period. The feeding levels applied in practice during this period, are insufficient to cover the calves' energy requirements for maintenance. So, during this critical period, the calves depend partially upon their body energy reserves. Research on the energy metabolism of pre-ruminant calves has been done mainly at feeding levels above maintenance and between the age of 1 to about 10 weeks. In this thesis, the energy metabolism of young, newly purchased calves, as affected by both feeding level and ambient temperature, was studied during the first 1 to 2 weeks after transport. The applied feeding levels in the experiments presented in this thesis, are representative for feeding levels used in practice.

For the first 1 to 2 weeks after transport, calves are exposed to an energy shortage because of the restricted feeding levels applied during this period. In addition to restrictive feeding, the energy requirement for maintenance of these young, newly purchased calves ($560 \text{ kJ.kg}^{-0.75} \cdot \text{d}^{-1}$ for the first week after transport) appeared to be higher than the values reported in the literature for older milk-fed calves (Chapter 1). Furthermore, it was observed that the metabolizability of the dietary energy of the milk replacer was lower for these calves compared with reported values in literature. The mean metabolizability during the first week after arrival was about 80% (Chapter 1, 2 and 3). Thus after arrival, young, newly purchased calves are highly dependent upon body energy reserves to meet their energy requirements due to restrictive feeding, higher maintenance requirements and lower metabolizability.

After transport, young calves should not be exposed to ambient temperatures below the lower critical temperature (LCT), because this will lead to an increase in the mobilization of body energy reserves due to the increased heat production. Because of the restricted feeding levels during this period, it can be expected that these calves have a relatively high LCT. Therefore, the thermal requirements of young calves after transport were studied (Chapters 2 and 3). Averaged over the period of 1 to 2 weeks after

transportation, LCT of young calves ranged between 12 and 15°C. During this period, the extra thermoregulatory heat production (ETH) was $9 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$.

The averaged LCT over this period was not affected by the feeding level (Chapter 2). The influence of feeding level on LCT was also absent when the observed LCT values were compared with literature data. Despite the large difference in feeding level, the average LCT values as observed in Chapter 2 and 3 were similar to those reported in the literature. This indicated that during the period of 1 to 2 weeks after arrival, the response of young calves to ambient temperature was inconsistent with the current concept of thermoregulation for homeotherms. Also in contrast with the current concept of thermoregulation, the heat production of young, newly purchased calves was influenced by the feeding level at ambient temperatures below LCT (Chapter 2). Furthermore, there were indications that rectal temperature was influenced by ambient temperature before these calves had reached their summit metabolism (Chapter 2).

The physical activity of veal calves, which are commonly housed individually, is restricted mainly to the selection of their posture (standing vs lying). In Chapter 4, the thermal requirements of young calves were studied in relation to posture (standing vs lying). The effect of ambient temperature on heat production was higher during standing than during lying. This was reflected in the high energy cost of standing at low compared with high ambient temperatures. During standing, the ETH was 50% higher than during lying. Despite the fact that calves required an increased cold-induced thermogenesis when standing, the time spent standing by the calves was not decreased at ambient temperatures below LCT. The lower critical temperature was 3.5°C higher during standing than during lying. These results show that non-thermoregulatory behaviour, such as posture (standing vs lying) can affect the thermoregulatory mechanisms of animals.

Like many other physiological traits, heat production, heat loss and body temperature of homeothermic animals, exhibit circadian rhythms. Circadian fluctuations in the effect of ambient temperature on heat production and its relation to posture were investigated, and are reported in Chapter 5. The effect of ambient temperature on heat production was not constant within a day. Both LCT and ETH varied within a day. Averaged over ambient temperatures, 51% of the within day variation in heat production was accounted for by the calves' posture. The variation in both ETH and LCT was reduced when heat production was corrected for the time spent standing. Thus part of the within day variation in thermal requirements of calves was related to posture.

This thesis concerns the energy metabolism of young calves during the first 1 to 2 weeks after transportation. The results presented in Chapter 1, 2 and 3, clearly demonstrated that young calves are not in a steady-state with regard to their energy metabolism during the first 1 to 2 weeks after transportation. Heat production decreases with time (over days) during this period. The decline in heat production with time is affected both by feeding level and by ambient temperature. Thus both the relationship between heat production and feeding level as well as between heat production and ambient temperature, alters with time after arrival of the calves. Due to the effect of feeding level on the decline in heat production with time, the basic metabolic rate and the efficiency of the utilization of metabolizable energy for maintenance decrease with time (Chapter 1). However, the energy requirements for maintenance remained virtually unchanged during this period (Chapter 1). The change in relationship between heat production and ambient temperature is reflected in an increase in LCT with time of young calves after transportation ($0.9^{\circ}\text{C}/\text{d}$), but is not reflected in an alteration of ETH over time (Chapter 3).

Young, newly purchased calves can be considered as unadapted to their new environment, during the period of 1 to 2 weeks after arrival. Apart from the alterations in heat production with time, the low metabolizability of dietary energy, and the high maintenance requirement observed in those calves, as well as the noted deviations from the current concept of thermoregulation in homeotherms, are indications for the unadapted state of these calves. From the results of the experiments presented in this thesis, it is impossible to determine whether the unadapted state of these young, newly purchased calves is due to age, or is the result of a mechanism of adaptation to the restricted feeding level or to exposure to stressors. Further research is required to delineate, which of these factors cause the unadapted state and how long this unadapted state may persist.

Samenvatting

SAMENVATTING

In Nederland worden kalveren, voor de kalfsvleesproductie of voor andere soorten van vleesproductie, op een leeftijd van 1 tot 2 weken getransporteerd vanaf het melkveebedrijf naar de kalvermesterij. Naast de stress ten gevolge van het transport op zich, worden deze kalveren ook blootgesteld aan andere veranderingen, zoals in huisvestingssysteem, voerniveau, voersamenstelling en klimaat. Met betrekking tot de gezondheid van de kalveren vormen de eerste 2 tot 3 weken na aankomst op het mesterijbedrijf een kritieke fase in de kalfsvleesproductie. Om het risico van maagdarmstoornissen te beperken worden kalveren gedurende deze periode op een zeer laag voerniveau gehouden. De voerniveaus die gedurende deze periode in de praktijk worden toegepast, zijn ontoereikend om in de energetische onderhoudsbehoefte van deze kalveren te voorzien. Dit betekent dat gedurende deze kritieke periode de kalveren gedeeltelijk afhankelijk zijn van de energiereserves in hun lichaam. Onderzoek naar de energiestofwisseling van niet-herkauwende kalveren is hoofdzakelijk uitgevoerd bij voerniveaus boven onderhoud en bij een leeftijd van 1 tot ongeveer 10 weken. In dit proefschrift is de invloed onderzocht van zowel voerniveau als omgevingstemperatuur op de energiestofwisseling van jonge, pas aangekochte kalveren, en dit gedurende de eerste 1 tot 2 weken na transport. De toegepaste voerniveaus in de beschreven experimenten zijn representatief voor de voerniveaus zoals die in de praktijk gehanteerd worden.

Kalveren worden gedurende de eerste 1 tot 2 weken na transport blootgesteld aan een energie-tekort vanwege de beperkte voerniveaus die gedurende deze periode worden toegepast. Naast het beperkt voeren, bleek dat de energiebehoefte voor onderhoud van deze jonge, pas aangekochte kalveren ($560 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ gedurende de eerste week na transport) hoger te zijn dan de waarden die in de literatuur gerapporteerd zijn voor oudere, melk-gevoerde kalveren (Hoofstuk 1). Verder werd waargenomen dat de metaboliseerbaarheid van de energie van het kunstmelkvoeder lager was voor deze kalveren dan de waarden die in de literatuur vermeld worden. De metaboliseerbaarheid tijdens de eerste week na aankomst varieerde rond 80% (Hoofdstukken 1, 2 en 3). Na aankomst zijn jonge, pas aangekochte kalveren dus sterk afhankelijk van de energiereserves in hun lichaam vanwege de beperkte voergift, de hogere onderhoudsbehoefte en de lagere metaboliseerbaarheid.

Jonge kalveren mogen na transport niet blootgesteld worden aan omgevingstemperaturen beneden de onderste kritieke temperatuur (LCT). Dit zal immers leiden tot een verhoogde warmteproductie met als consequentie een verhoogde mobilisatie van energie-

reserves in het lichaam. Vanwege de beperkte voerniveaus gedurende deze periode is het te verwachten dat deze kalveren een relatief hoge LCT hebben. Dit is de reden waarom de temperatuursbehoefte van jonge kalveren na transport werd onderzocht (Hoofdstukken 2 en 3). Gemiddeld over de periode van 1 tot 2 weken na transport lag de LCT van jonge kalveren tussen de 12 en 15°C. De extra thermoregulatoire warmteproduktie (ETH) was 9 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1} \cdot ^\circ\text{C}^{-1}$ gedurende deze periode.

De gemiddelde LCT over deze periode werd niet beïnvloed door het voerniveau (Hoofdstuk 2). De afwezigheid van een effect van voerniveau op LCT werd ook gesuggereerd bij de vergelijking van de waargenomen LCT waarden met waarden vermeld in de literatuur. Ondanks het grote verschil in voerniveau waren de waargenomen LCT waarden in de Hoofdstukken 2 en 3 vergelijkbaar met de waarden, vermeld in de literatuur. Dit geeft aan dat gedurende de periode van 1 tot 2 weken na transport de reactie van jonge kalveren op omgevingstemperatuur niet in overeenstemming is met het huidige concept van thermoregulatie bij homeotherme dieren. Verder bleek dat de warmteproduktie van jonge, pas aangekochte kalveren ook afhankelijk was van het voerniveau bij temperaturen beneden LCT (Hoofdstuk 2). Ook dit is in tegenspraak met het huidige concept van thermoregulatie. Bovendien waren er aanwijzingen dat de rectaaltemperatuur beïnvloed werd door de omgevingstemperatuur, zelfs voordat deze kalveren hun maximale metabolisme bereikt hadden (Hoofdstuk 2).

De activiteit van vleeskalveren, die gewoonlijk individueel gehuisvest worden, is in hoofdzaak beperkt tot de keuze van hun lichaamshouding (staan versus liggen). In Hoofdstuk 4 werd de temperatuursbehoefte van jonge kalveren bestudeerd in relatie tot lichaamshouding (staan versus liggen). Tijdens het staan was het effect van omgevingstemperatuur op de warmteproduktie groter dan tijdens liggen. Dit uitte zich in de hogere energiekosten van staan bij lage omgevingstemperaturen in vergelijking met hoge omgevingstemperaturen. Tijdens staan was de ETH 50% hoger dan tijdens liggen. De tijd die door de kalveren staande werd doorgebracht, werd niet verlaagd bij omgevingstemperaturen beneden LCT, ondanks het feit dat kalveren een verhoogde, koude-geïnduceerde warmteproduktie nodig hebben tijdens het staan. De onderste kritieke temperatuur is 3.5°C hoger tijdens staan dan tijdens liggen. Deze resultaten tonen aan dat niet specifiek thermoregulatoire gedrag zoals houding (staan versus liggen) toch de thermoregulatoire mechanismen van dieren kan beïnvloeden.

Zoals vele andere fysiologische kenmerken vertonen warmteproduktie, warmteafgifte en lichaamstemperatuur dagelijkse ritmes. Dagelijkse fluctuaties in de invloed van

omgevingstemperatuur op de warmteproduktie zijn onderzocht in relatie tot houding (Hoofdstuk 5). Het effect van omgevingstemperatuur op warmteproduktie was niet constant binnen een dag. Zowel LCT als ETH varieerden binnen een dag. Bij de bestudeerde omgevingstemperaturen werd 51% van de variatie in warmteproduktie binnen een dag veroorzaakt door de houding van de kalveren. De variatie in zowel ETH als in LCT werd gereduceerd wanneer de warmteproduktie werd gecorrigeerd voor de tijd die staande werd doorgebracht. Dus een gedeelte van de variatie in de temperatuursbehoefte binnen een dag was gerelateerd aan de houding van de kalveren.

Dit proefschrift behandelt de energiestofwisseling van jonge kalveren gedurende de eerste 1 tot 2 weken na transport. De resultaten die gepresenteerd zijn in de Hoofdstukken 1, 2 en 3, tonen duidelijk aan dat gedurende de eerste 1 tot 2 weken na transport jonge kalveren zich niet in een evenwichtssituatie bevinden ten aanzien van hun energiestofwisseling. Gedurende deze periode daalt de warmteproduktie in de tijd (over dagen). De daling in warmteproduktie met tijd wordt zowel beïnvloed door voerniveau als door omgevingstemperatuur. Dus de relatie tussen warmteproduktie en voerniveau enerzijds en tussen warmteproduktie en omgevingstemperatuur anderzijds verandert na aankomst van de kalveren in de tijd. Het basaal stofwisselingsniveau en de efficiëntie van de benutting van metaboliseerbare energie voor onderhoud dalen in de tijd door het effect van voerniveau op de daling in warmteproduktie in de tijd (Hoofdstuk 1). De energiebehoefte voor onderhoud bleef echter nagenoeg onveranderd gedurende deze periode (Hoofdstuk 1). De verandering in de relatie tussen warmteproduktie en omgevingstemperatuur in de tijd kwam tot uitdrukking in een stijgende LCT van jonge kalveren na transport ($0.9\text{ }^{\circ}\text{C/d}$) als functie van de tijd, maar niet in een verandering in ETH in de tijd (Hoofdstuk 3).

Gedurende 1 tot 2 weken na aankomst op het mestbedrijf zijn kalveren niet aangepast aan hun nieuwe omgeving. Deze vaststelling steunt op de volgende argumenten: de warmteproduktie wijzigt in de tijd, de metaboliseerbaarheid van energie in het rantsoen is laag, de kalveren hebben een hoge onderhoudsbehoefte, en hun warmtehuishouding wijkt af van het huidige concept van thermoregulatie in homeotherme dieren. Op basis van de experimenten die in dit proefschrift zijn gepresenteerd kan geen uitsluitsel gegeven worden over de achtergrond van deze gebrekkige aanpassing. Met name een mogelijk effect van leeftijd kan niet worden onderscheiden van de mogelijke gevolgen van een aanpassing aan het verlaagde voerniveau enerzijds, en de aanpassing volgend op een blootstelling aan stress anderzijds. Verder onderzoek is nodig om te bepalen hoe deze gebrekkige aanpassing verklaard kan worden, en hoelang deze toestand voortduurt.

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CURRICULUM VITAE

Johannes Wilhelmus Schrama werd geboren op 3 augustus 1965 te Amsterdam. In 1983 behaalde hij het VWO diploma aan het Sint Nicolaas Lyceum in Amsterdam. In datzelfde jaar begon hij met de studie Zoötechniek aan de toenmalige Landbouw Hogeschool in Wageningen. Na het behalen van de propaedeuse onderbrak hij voor een jaar zijn studie. Gedurende dit jaar verbleef hij in Nieuw Zeeland. In augustus 1989 studeerde hij met lof af aan de Landbouwuniversiteit Wageningen met als hoofdvak Veevoeding en als bijvakken Statistiek en Pluimveeteelt. Vanaf september 1989 is hij voor 20 uur per week aangesteld als universitair docent bij de sectie Gezondheidsleer en Reproductie van de vakgroep Veehouderij. Voor de overige 20 uur is hij verbonden als wetenschappelijk medewerker bij de vakgroepen Veehouderij en Veevoeding voor gezamenlijk onderzoek op het gebied van energiestofwisseling bij landbouwhuisdieren. Het onderzoek dat hij in de afgelopen vier jaar uitvoerde bij jonge kalveren staat beschreven in dit proefschrift.