

finalreport

Feedlots

Project code: FLOT.314
Prepared by: PM Kennedy
PB Cronjé¹
CSIRO Livestock Industries
JM Rendel Laboratory
Box 5545 Rockhampton 4702

¹Current address 103 Todd
Ave, Yeppoon, QLD 4703

Date published: June 2005
ISBN: 9781 7419 1 5709

PUBLISHED BY
Meat & Livestock Australia
Locked Bag 991
NORTH SYDNEY NSW 2059

Dietary strategies for amelioration of heat load in feedlot cattle

Abstract

The proposition was examined that feeding management and ration formulation can lead to amelioration of body heat load in feedlot cattle exposed to high environmental heat load. From the available literature, it was concluded that changes in diet formulation by itself, for instance by inclusion of rumen-inert lipid or slowly-digesting grain, were less likely to lead to significant heat load amelioration than a strategy which combined dietary changes with changes in feeding time. This would allow a match between the period of peak heat production and the cooler night period.

Knowledge required for assessment and implementation of this strategy was identified. A key component of the assessment would be investigation of the utility to predict heat production from cattle, using an existing Australian database of rates of grain fermentation. The anticipated outcome would be to provide a tool to reduce mortalities and production losses in the feedlot industry during heat waves.

Executive Summary

(i) Project Objectives

As a consequence of the report of Sparke et al. (2001), Meat and Livestock Australia Ltd funded this study to produce a review with the aim (i) to evaluate the potential of nutritional and feeding strategies that could reduce effective heat load from feedlot diets and (ii) to make recommendations of research and development appropriate to amelioration of environmental heat load (EHL) in cattle. In particular, the broad objectives of the present study were to (i) produce a well-researched literature review that evaluates the potential of dietary modifications and nutritional management and (ii) provide a clear recommendation on whether heat load mitigation strategies can be developed on current knowledge or whether new generation knowledge is required and/or warranted (iii) if new knowledge is required, provide a clear definition of the gaps in existing knowledge/information that are of crucial importance to the formulation of strategies for reduction of heat load in feedlot cattle (iv) outline a recommended R & D program to generate the new knowledge/information required, including an appraisal of research techniques and concepts that could be employed to enable strategic ration formulation and testing.

(ii) Main results and conclusions

Heat increment (HI) results from acquisition and processing costs of feeding, inefficiencies in metabolism of nutrients in ruminal microbes and in host tissues, and the need to maintain metabolic machinery and homeostasis. Heat from metabolism in the ruminant arises partly from fermentation in the rumen consequent to anaerobic microbial fermentation, but the majority arises from aerobic intermediary metabolism in the splanchnic bed (including liver and gut tissues) and peripheral tissues. Nutrient classes (carbohydrates, fat and protein) are metabolised with different efficiencies depending on the purpose for which nutrients are used by the animal, and associative effects can occur between nutrients that result in changes in efficiency.

Efficiency of utilisation of starch depends on site of digestion; fermentation to volatile fatty acids (VFAs) in the rumen leads to a HI of about 0.36 (i.e. 36% of metabolisable energy intake appeared as heat), while the HI of hydrolysis and absorption of starch from the small intestine is considered to be about 0.28. Fats and oils have minimal theoretical HI above maintenance energy requirements of 0.1, with values of 0.25 to 0.45 being used by NRC (1996). Accordingly, inclusion of lipids into diets of ruminants has been suggested as a means to lower metabolic heat load. Results of trials to test this proposition have not been conclusive, perhaps because of variability in the degree of lipid inertness in the rumen. It appears that some research on the use of pure hydrogenated fatty acids to lower HI would be worthwhile. Dietary protein in excess of requirements leads to increased metabolic heat production through increased urea synthesis, but there are a number of postulated factors involved.

The Variable Net Energy System was used to illustrate that HI varied with diet energy density and level of feeding.

Few experiments have described variation of HI with time post feeding in ruminants, yet this information is crucial in tactical feeding to increase the opportunity for heat loss from the body during the cool night period. The heat of fermentation in the rumen can be assumed to be contemporaneous with digestion of dietary components, but definition of the time-course and quantitative contribution of the more significant source of heat from metabolism in the gut, liver and

peripheral tissues, is needed for different grains and processing methods. In addition, it is known that exposure of cattle to EHL is likely to slow down rate of digesta passage from the rumen, with resultant increases in the amount of ruminal digestion of slowly-fermentable dietary starch and increase in HI.

Using the AUSBEEF mechanistic ruminant model, simulations were performed to illustrate the effects of inclusion of 10% molasses, 5% fat or 10% soluble protein in a feedlot diet, on the evolution of HI after feeding. Inclusion of fat had a marked effect on heat production. By feeding during late afternoon instead of mid-morning, simulations predicted that an additional 13 % (57% vs 44%) of HI was generated during the 10 night-time hours. Because AUSBEEF was not developed with the aim of accurate prediction of the time-course of HI, this result is indicative only. It therefore appears that there is potential to manipulate the time of peak HI to more closely coincide with the night-time period and to increase heat loss from cattle during periods of EHL. Whether conventional assessments of rates of passage and of ruminal microbial fermentation of nutrients, especially of starch, are sufficiently accurate to predict the time course of HI evolution, remains to be established.

Proactive measures that might be employed to increase tolerance to hyperthermia were also reviewed. A key consideration is maintenance of the integrity of the gut lining, in order to reduce the incidence of endotoxic shock and promote resilience of the rumen through feeding of compounds such as betaine or probiotics.

(iii) Recommendations

Data are needed which define the physiological responses of cattle to increasing duration of hyperthermia. In respect to optimising the formulation of low-heat diets, and of time of feeding to maximise daily heat loss from the animal, appropriate experimentation is required to assess:

- The value of hydrolysed fatty acids (rumen inert lipid) in reducing HI.
- The degree to which HI from dietary metabolism can be reduced by appropriate selection of dietary components or by changes in grain processing method.
- The contributions of heat from ruminal fermentation and from heat of metabolism to total HI, and their respective profiles with time.
- The adequacy of methods to predict the time course of total HI from fermentation HI, using available Australian data on rates of digestion of dietary components and assumptions about passage rates from the rumen during EHL exposure.
- Interactions of meal quantity and timing in maximising night-time heat dissipation, and the importance of heat stress and differences in day/night temperatures.
- The role of adaptation to EHL on the HI response.
- Whether the available models of cattle digestion can satisfactorily predict HI patterns.
- Whether telemetric devices to monitor core temperature of sentinel cattle can accurately predict hyperthermia.

In respect to development of feed additives designed to increase the resilience of cattle to hyperthermia, it is suggested that research be conducted on the roles of protected fats in changing membrane lipid content and of probiotics and betaine added to feedlot diets.

It is also suggested that research is warranted on use of commercially available telemetric systems for monitoring body temperatures for use as an aid in tactical decision making in the advent of climatically adverse conditions.

Contents

	Page
Executive summary.....	2
1 Background.....	7
1.1 Introduction	7
1.2 Options for nutritional management of environmental heat load	8
1.3 Circadian patterns of body temperature	9
1.4 Heat increment: concept and components	12
1.4.1 Origin of HI	12
1.4.2 Contribution to HI from gut and microbes	14
1.5 Time course of production of HI	14
2 Relationship of HI with diet composition.....	16
2.1 Heat Increment of carbohydrates	16
2.2 Heat Increment of lipids.....	19
2.3 Heat Increment of sources of protein.....	20
2.4 Integrated effects of ration components on heat increment	22
2.5 Conclusions.....	27
3 Time course of thermogenesis	28
3.1 Dietary-related thermogenesis.....	28
3.2 Simulation of effects of diet composition on HI	30
3.3 Feeding time management to increase heat amelioration.....	32
3.4 Does rate of ruminal fermentation affect HI?	35
3.5 Conclusions.....	36
4 Continuous monitoring of heat load during EHL ...	38
4.1 Data loggers.....	38
4.2 Conclusions.....	38
5 Increasing tolerance to hyperthermia	38
5.1 The pathophysiology of hyperthermia	39
5.2 Acidosis	40
5.3 Probiotics.....	41
5.4 Betaine	41
5.5 Fatty acids	42
5.6 Heat Shock Proteins	42
5.7 Conclusions.....	43
6 Summary of findings and R&D opportunities	43
6.1 Gaps in current scientific knowledge.....	43

6.2 Refinement of a risk assessment model for heat load in cattle44
6.3 Discrimination of components of HI & effect of feeding times44
6.4 Potential of feed additives for hyperthermic cattle46
6.5 Evaluation of management aids.....46
7 Recommended research and development plan....46
8 References49

1 Background

1.1 Introduction

As a consequence of the report of Sparke et al. (2001), Meat and Livestock Australia Limited (MLA) commissioned this study to produce a review with the aims (i) to evaluate the potential of nutritional and feeding strategies that could reduce effective heat load from feedlot diets and (ii) to make recommendations of research and development appropriate to amelioration of environmental heat load (EHL) in cattle. In particular, the broad objectives of the present study were to (i) produce a well-researched literature review that evaluates the potential of dietary modifications and nutritional management and (ii) provide a clear recommendation on whether heat load mitigation strategies can be developed on current knowledge or whether new generation knowledge is required and/or warranted (iii) if new knowledge is required, provide a clear definition of the gaps in existing knowledge/information that are of crucial importance to the formulation of strategies for reduction of heat load in feedlot cattle (iv) outline a recommended R & D program to generate the new knowledge/information required, including an appraisal of research techniques and concepts that could be employed to enable strategic ration formulation and testing.

Factors contributing to heat stress in domestic livestock have been extensively researched over the last 50 years, and these findings have been collated in several reviews (Collier et al. 1982; Sanchez et al. 1994). Other reviews have assessed the extent of production losses associated with chronic heat exposure for animals in extensive grazing situations (Turner 1984; Finch 1986). Despite this knowledge, heat stress mortalities still occur with sufficient regularity in feedlots to be unacceptable, with generation of negative publicity as well as financial loss.

Applied studies have investigated animal responses to changes in environmental heat load (EHL)¹, usually over relatively short periods. The practical application of such data has been formulation of heat load indices by which assessments can be made of animals' accumulated heat load over time. Indices derived from weighted estimates of environmental variables that can be easily measured, such as wet- and dry- bulb temperatures, relative humidity, and wind speed. While there is no doubt that the index approach is of value, it is necessary to acknowledge that the precision of such indices is limited, because the response of individual animals to EHL is affected by variations in feedlot microclimate, in addition to variations of susceptibility between animals to heat stress.

Maust et al. (1972) compared the temperature-humidity discomfort index and the temperature humidity combination index to measurements of air temperature, relative humidity and wind velocity for predicting the effects of weather on lactating Holstein cows. Rectal temperature was highly correlated to single measurements of weather conditions (maximum and minimum temperature), and these correlations were as high as those based on multiple measurements or indices combining temperature and humidity. Milk yield, however, showed little relationship to any of these variables on the same day, but was correlated with conditions 2-4 days previously. This emphasises the temporal and cumulative dimensions of heat load, and indicates that a 3-4 day lag time is required for cattle to balance heat dissipation capabilities with reduced metabolic heat production (i.e. reduced feed intake). The deaths of 4000 feedlot cattle in a heat wave event in the USA can also be explained on this basis: in this case, the rate of increase in thermal load over several successive days exceeded the 3-4 day lag time required to induce thermoregulatory responses (Hahn 1999). In another

¹ EHL as used in Sparke et al. (2001) occurs when a combination of local environmental conditions and animal factors, leads to an increase in body heat content beyond the normal physiological range, and the animal's ability to cope.

instance where 100 feedlot cattle died, a depression in feed intake in response to two successive heat waves was actually the cause of mortalities in a third heat episode (Hahn 1999). Cool days between the first and second heat waves induced animals to increase feed intake far in excess of normal levels to compensate for the heat-induced reduction in intake. Unfortunately the resultant dietary heat load coincided with a third heat wave, and the combination of the high residual endogenous heat load and the external heat load resulted in the death of many animals (Hahn 1999). St-Pierre et al. (2003) estimate that for Texan feedlots the opportunity costs, in the absence of heat abatement, are in growth rate (17 kg/head/yr) and mortalities (5 per 1000 head).

Strategies that increase heat dissipation or decrease the generation of body heat represent potential solutions to these problems. While much research effort has been directed at reducing solar radiation load or increasing heat dissipation (e.g. design of feedlots, provision of shade, installation of mist sprayers), less effort has been directed at reducing heat generation in the body. Nutritional approaches that have been advocated to reduce generation of heat by the animal range from changing diet composition to management of feed intake amount or time of feeding (Beede and Collier 1986; West 1999). Thus the focus of the present review is to examine the extent of current scientific knowledge on the potential of dietary modification and feeding strategy to reduce heat load in feedlot cattle. To accomplish this, there will be focus on the contributions of the thermogenic effects of different nutrients in metabolic processes in the animal, and the time course of heat generated from metabolism.

1.2 Options for nutritional management of environmental heat load

When climatic conditions prevent the ready dissipation of excess heat for cattle fed *ad libitum*, feed intake declines in order to maintain thermal homeostasis. This represents a problem for operators of feedlot systems because economic efficiency peaks at high levels of feed intake. In addition to this, prior consumption of high levels of feed increases the amount of metabolisable energy (ME) required for maintenance (support) metabolic processes, and thereby renders these animals particularly vulnerable to hyperthermia during sporadic heat waves. Accordingly, the feedlot operator may need several nutritional tools to manage high average EHL in summer months by strategic changes in animal type and diet formulation, and reserve additional tactics for heat wave events that may be forecast several days in advance, for which emergency management and dietary changes may be appropriate. Thus a distinction must be made between the effects of sustained exposure to environmental heat, to which acclimation of animals can occur, versus the effects of short-term exposure to acute EHL events.

Under conditions where a heat wave is anticipated, some feedlot operators will decrease the amount of ration offered a few days before the EHL event. This tactic has been investigated by Mader et al. (2002) and Davis et al. (2003) and shown to decrease the core temperature of feedlot cattle by 0.5°C. Growth rates are, of course, decreased. In addition to the potentially catastrophic consequences of an unexpected repeated occurrence of EHL following resumption of feeding illustrated in the example discussed above, engorgement following feed restriction will increase the incidence of deaths related to acidosis and bloat. Disruption of feeding patterns during inclement weather has been implicated as a cause of acidosis, and prevention of over-consumption by restriction of intake following weather changes has been recommended to reduce its incidence (Owens et al. 1998).

An alternative tactic that has been recommended is to increase the roughage content of feedlot diets (Sparke et al. 2001). An increase in the proportion of dietary forage or silage will slow the rate of

fermentation and consequently reduce total heat increment (HI) in cattle from all internal metabolism. However this practice will also result in reduced total energy intake and production losses. Colgan and Mader (2005) reported that feeding a diet comprising 96% hay and silage significantly reduced body temperature compared to a low roughage diet, but will be again accompanied by depression of growth rate. Prevention of over-consumption following replacement of tactical diets with normal high-grain content diets is essential.

Although not a focus of the present review, it is worth noting that water and mineral intake may affect ability of feedlot cattle to cope with EHL. Water intake is usually related to feed intake, and usually increases markedly in response to EHL (NRC 1981) but this relationship may be dependent on temperature of the water (Lofgreen et al. 1975). Accordingly, provision of clean, cool, fresh water is recommended when cattle are heat stressed. Studies with *B. taurus* cattle showed that cooled water resulted in higher growth rates than with non-cooled water, but water temperature did not affect growth rates of *B. indicus* or cross-bred cattle, even under severe EHL (Blackshaw and Blackshaw 1994). Milk production by cows in Texas was increased with offering chilled water (West 2003). Poor drinking water quality, especially water containing high concentrations of sulphate and possibly chloride ions may be deleterious for lactating cows in hot weather, but other interactions with feed intake of divalent cations were detected by Sanchez et al. (1994). Cattle drinking water with significant amounts of dissolved minerals will have a double requirement of energy to satisfy thermoregulatory processes plus that required to excrete the osmotic load.

Owing to the losses of K^+ in sweat, and of Na^+ in urine of heat-stressed cattle, there is depletion of these minerals in rumen fluid and altered blood acid-base chemistry as a result of EHL (West 2003). Often respiratory alkalosis, a result of loss of carbon dioxide during pulmonary hyperventilation, may compromise buffering ability needed with high-grain rations if rumen acidosis is to be avoided. Supplementation of cations (Na^+ , K^+) may increase feed intake of dairy cow (West 2003), but Sanchez et al. (1994) stated that experimental results were not conclusive for dietary mineral buffers to correct potential subclinical chronic ruminal lactic acidosis. For heat-stressed cattle, two different diets fed in sequence to alleviate respiratory alkalosis in the hot part of the day followed by another supplement in the cool part of the day to treat compensated metabolic acidosis, may be worth consideration (Sanchez et al. 1994).

1.3 Circadian patterns of body temperature

Body temperature in mammals is often thought of as a constant. In fact, body temperature follows a circadian rhythm (Piccione et al. 2002; Wakamura and Tokura 2002), reaching a peak during the early hours of the evening and a nadir early in the morning. In cattle the amplitude of this diurnal rhythm is typically between 0.5 and 1.2 °C (Hahn 1999), but may reach as much as 3 °C in cattle subject to heat stress (Finch 1984). Because the thermal gradient between animal and surroundings is more favourable for heat loss at night, this rhythm represents an opportunity to dissipate heat that was accumulated during the day. The problem of maintaining heat balance in cattle therefore should be defined in terms that take the dynamic nature of thermal balance into account.

Considerations of 24-hr heat fluxes led to the conclusion that about 75% of heat load in feedlot cattle heat was from animal metabolism (Sparke et al. 2001). However, at the time of day with highest EHL, the heat gain from the environment may exceed that from metabolism.

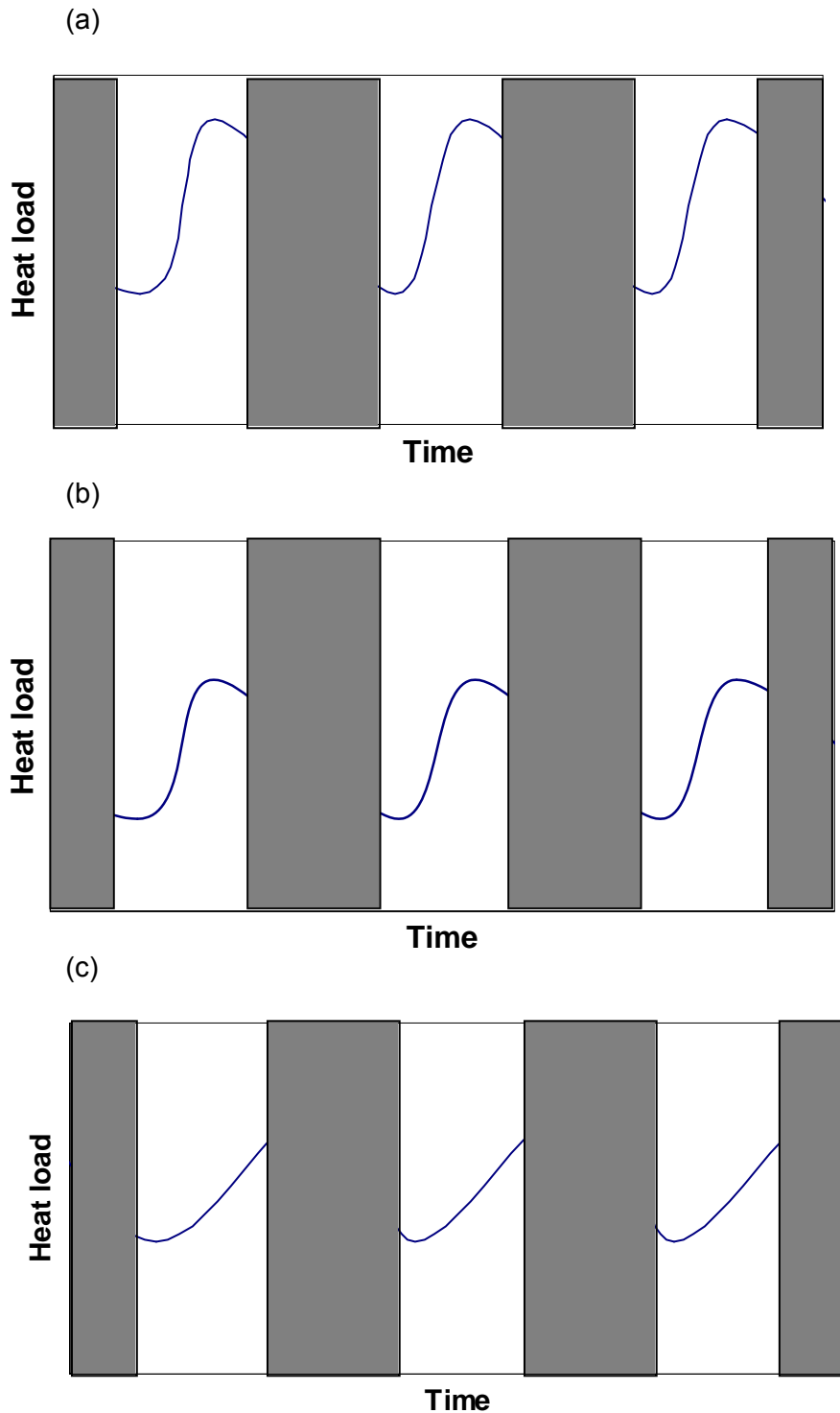


Figure 1. The typical circadian pattern of heat load (from HI and EHL) in the body of a feedlot steer in a hot environment during daylight (light bars) and the cooler night hours (shaded bars). Figure 1(a) standard situation (b) possible nutritional manipulation to reduce energy production in animal (c) rescheduling the time of feeding or absorption of nutrients.

The temporal dimension of heat load on an animal from HI and EHL is illustrated schematically in Figure 1a. The typical circadian pattern of heat load in the body of a feedlot steer in a hot environment is characterised by a peak two to three hours after the highest EHL during daytime (light bars) followed by a decline during the cooler night hours (shaded bars). Potential ways in which this heat load could be altered by nutritional means are by reducing total load by changing dietary formulation (Figure 1b), or by scheduling peak HI to coincide with the coolest ambient temperature (Figure 1c). Options by which the latter could be achieved include manipulating the time of feeding and/or the pattern of absorption of nutrients. The amount of time lag between feeding and heat production is crucial to this strategy, and is illustrated by results of Arieli et al. (2004), who found that 60% of feed was eaten over 11 daylight hours, but 49% of heat was produced in that time.

While the benefits of altering feeding schedules have been advocated in the popular press, evidence for the efficacy of this strategy, in the form of statistically significant results, is scarce. A clear advantage was demonstrated for Holstein steers (mean weight 154 kg), limit-fed a medium-energy corn-based diet at 2.3% of body weight for 2 months in a Kansas summer (mean max. temp, 31°C, mean RH, 73%) when they gained significantly more (0.90 kg/d) when given the entire ration at 20:00, vs. 0.75 kg/d when fed at 08:00 (Reinhardt and Brandt 1994). Other results are equivocal. Brosh et al. (1998a) fed Hereford steers in southeast Queensland at either 08:00 or 16:30 during summer, and reported that feeding of the high concentrate feed at 16:30 resulted in higher body temperatures at night than feeding at 08:00. Similarly, Davis and Mader (2002) and Davis et al. (2001) observed that although feeding time affected body temperature in cattle under feedlot conditions, this did not improve intake, growth rate or carcass characteristics. Recently, Davis et al. (2003) reported that core (tympanic) temperature of feedlot steers fed at 16:00 was lower than that of steers fed at 08:00, although it may require 3-4 days of acclimation to hot conditions before the influence of feeding regime on body temperature is apparent (Holt et al. 2004). Ominski et al. (2002) fed lactating dairy cows at either 08:30 or 20:30 under conditions in which ambient temperatures were programmed in a climate-controlled facility, to increase to 32 °C from 07:00 and fall to 20 °C from 18:00. Although the body temperatures of animals fed at night decreased more quickly between 18:00 and 02:00, milk fat percentage was not improved and indeed was depressed. The timing of the afternoon feeding may be important. Davis et al. (2003) suggested that the benefit of feeding after 15:00 may be accentuated if the bunks had been empty for several hours before feeding. Bunk management of feed may shift the time of peak metabolic heat load away from the peak EHL, but at the risk of reduced intake (5% in the study of Holt et al. 2004).

B. indicus cattle can maintain intake in the face of EHL better than *B. taurus* (Beatty et al. 2004), in agreement with the lower energy requirements for maintenance of *B. indicus* cattle (SCA 1990). Therefore differing bunk management strategies may be appropriate, depending on breed. The stimulation of feeding behaviour that occurs on filling the feed bunk assists in achieving a significant intake within a few hours, but it is possible that if feeding occurs in late afternoon, there may be some reluctance to feed by cattle that had experienced a high EHL. In addition, the strategy may not be successful in the face of limited night-time cooling (Gaughan et al. 1996). Other considerations include animal differences in feeding behaviour associated with breed and conversion efficiency (Robinson and Oddy 2004).

When animals are exposed to heat loads, they eat more frequent meals of smaller size, and eating activity tends to be concentrated in the ascending portion of the body temperature circadian rhythm (Nienaber and Hahn 1991). The cyclical nature of body and ambient temperatures suggests that

there could be advantages to scheduling the time of feeding so that peak in diet-induced thermogenesis coincides with cooler evening hours.

1.4 Heat increment: concept and components

1.4.1 Origin of HI

The capacity for internal heat generation and homeostasis in mammals is thought to have arisen from the evolution of 'leaky membranes', which facilitate the conversion of food energy to heat by intracellular ion pump activity (Else and Hulbert 1987). As a result, heat production from metabolism of nutrients in the rumen and body tissues is added to heat from homeostatic processes to form the HI. The capacity of the body to limit debilitating increases of deep body temperature in the face of EHL is dependent on the ease by which heat is dissipated to the environment. Accelerated panting during EHL may increase maintenance requirements for energy by 7 to 25% (NRC 1981). During the course of a meal (Webster 1980), total heat production may increase by as much as 80% depending on the type of nutrient ingested. About 50% of the amount of ME used for gain is converted to heat in cattle fed balanced feedlot diets showing high rates of gain (Ferrell and Jenkins 1998).

The fate of the gross energy contained in feeds is shown in Figure 2. The amount of energy available for animal body maintenance and production is defined as metabolisable energy (ME). ME intake is the energy available after subtraction of the energy lost in faeces, urine and methane from the intake of gross energy in feed. The HI of a feedstuff, as usually defined, represents the proportion of ME that is lost as heat in the process of converting food energy into a form that is available to the animal for useful purposes, i.e. in the formation of net energy (NE). For example, if an animal retains 6 MJ of NE after consuming food containing 10 MJ of ME, the efficiency of utilisation of ME (k) is 0.6 and the HI is 0.4. HI can thus be defined as the complement ($1-k$) of the efficiency of utilisation of ME. When defining HI, some authors (e.g. Williams and Jenkins 2003a) exclude the basal (fasting) heat production, but we have not followed that practice.

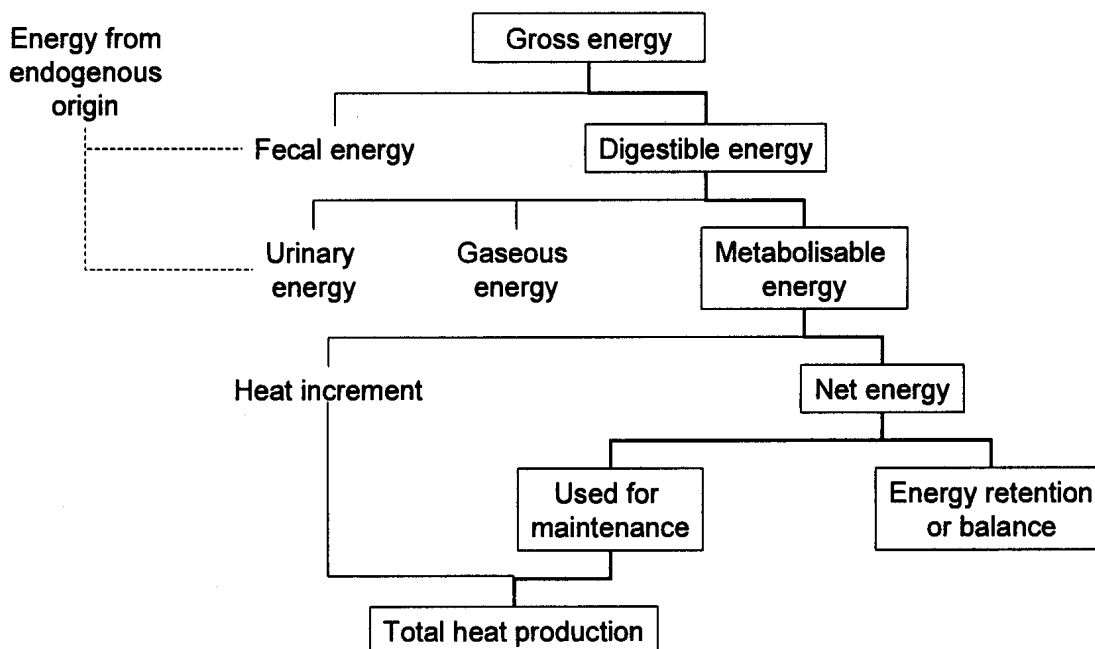


Figure 2. The partition of food energy in the ruminant, as traditionally presented (Blaxter 1989).

Partitioning of heat energy into meaningful components is somewhat problematical (Williams and Jenkins 2003a). For our purpose, HI includes fasting heat production, heat associated with digestion, absorption, assimilation, microbial fermentation, waste formation and excretion, product formation, voluntary activity, rumination and eating and also with thermal regulation. Heat is evolved by transport of nutrients, intermediary storage of nutrients, cellular ion pumps, protein synthesis, substitution of endogenous energy sources by nutrients, and conversion of absorbed nutrients to adenosine triphosphate (ATP) being the 'internal energy currency' of cells.

Obligatory heat can be defined as that arising from eating and rumination, together with that associated with storage of glucose as glycogen, fatty acids as triglycerol and the catabolism of amino acids. Further aerobic metabolic activity gives rise to facultative heat, produced in addition to that expected from the obligatory processes and postulated to be under hormonal control (Warwick and Baines 2000). All NE used for maintenance of support metabolism, including locomotion, appears as heat, and is identified as HI_m (essentially related to energy required for weight stasis) while the residue of NE is used for productive purposes, and for the growing animal is described as HI_g . The notional maintenance energy requirements for a growing animal and therefore HI_m , are not fixed, but vary with level of feed intake (Williams and Jenkins 2003a). For the purposes of discussion in this review, a simplified concept of maintenance is applied. It is relevant to calculations of HI, that *Bos indicus* have lower requirements for ME at weight stasis than *B. taurus* cattle (SCA 1990). HI in the fed ruminant can be three times that produced in the fasting animal.

Microbial metabolism in the gastrointestinal tract gives rise to products that provide nutrients to the host, as well as products that are not nutrients, especially methane and heat of fermentation. The latter products are differentially treated in the ME system as depicted in Figure 2. ME includes fermentation heat but excludes methane energy.

Current understanding of the relative energy costs of digestion and metabolism in the gut in comparison with non-gut tissues is summarised in Table 1. Values are for ruminants with intakes of energy that are below and above maintenance energy requirements.

Table 1 illustrates several important concepts:

- the relative contribution of the components of HI differs between feedstuffs.
- within a feedstuff the relative contribution of the components of HI differs according to the amount fed.
- the major contributor to HI is the cost of metabolic transactions associated with tissues other than the gut.
- the rumen fermentation component of HI declines as feed intake increases.

Table 1. Percentage contribution of processes to the total heat increment of various feedstuffs in the ruminant, when animals are receiving dietary energy that is below or above their energy requirements for maintenance (adapted from Webster 1980).

	Chopped hay		Fresh Herbage		Barley pellets	
	Below Maint. req.	Above maint. req.	Below maint. req.	Above maint. req.	Below maint. req.	Above maint. req.
Eating	7	4	8	5	1	1
Rumination	2	1	3	2	0	0
Rumen fermentation	24	14	23	13	12	6
Metabolic activity of gut	9	26	9	25	11	30
Total gut	42	45	43	45	24	37
Metabolic activity of tissues other than gut	58	55	57	55	76	63

1.4.2 Contribution to HI from gut and microbes

In ruminants feeding on most diets, the majority of dietary nutrients are catabolised and transformed by rumen microbes before being made available to ruminant tissues. Within rumen microbes, as in the host animal, heat is generated by energy expended during maintenance and production of microbial tissue. Stoichiometry of Czerkawski (1986) indicates that fermentation heat is relatively constant at 6-8% of the ruminally-digested energy across a wide range of requirements for cell maintenance, volatile fatty acid (VFA) patterns and digesta turnover rates in the rumen, and is relatively unaffected by type of substrate (starch, sugars or plant cell wall carbohydrate). ATP production from microbes is approximately 30% more efficient for production of butyrate and lactate than for acetate and propionate (Kohn and Boston 2000), but across diets this does not usually lead to significant variation in efficiency of ATP production, because butyrate and lactate account for a small proportion of end-products. Inspection of the values presented by Webster (1980) for barley pellets fed above maintenance requirements for energy, suggests that the heat production arising from fermentation of feedlot diets containing high concentrations of grains would be small (6.5%) compared to the total HI. The fermentation heat would be further lowered by feed processing that facilitated escape of starch from the rumen in favour of intestinal digestion.

1.5 Time course of production of HI

The time course of HI is principally determined by the amount and rate of heat production sequentially arising from the cascade of heat-producing events, principally digestion and absorption, followed by metabolism in tissues, as depicted hypothetically in Figure 3 for a discrete feeding event of a rapidly fermentable feed.

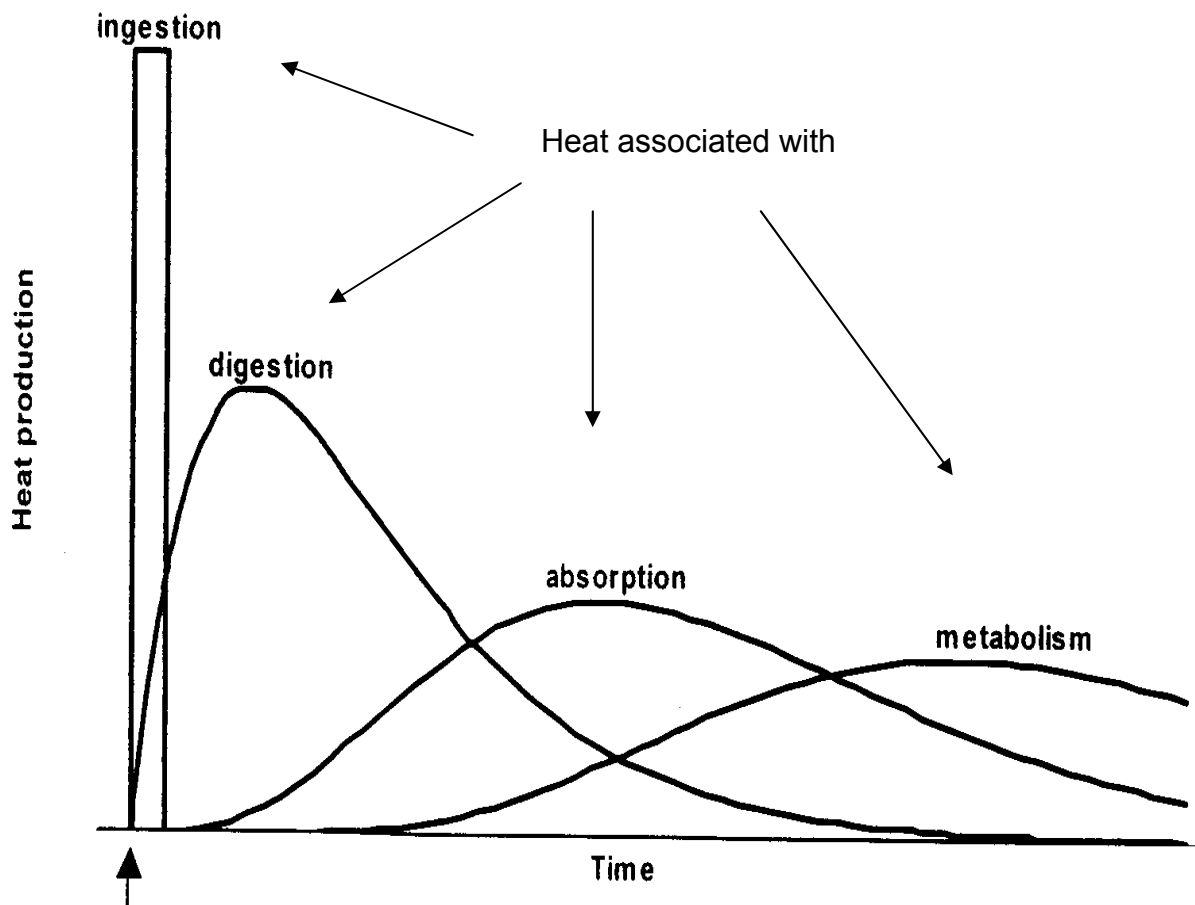


Figure 3. Depiction of cascade of heat generated from various sources after a discrete, rapidly-digested meal ingested at ↑ (From Milgen et al. 2001).

Nutritional change, and individual feeding events can lead to very rapid responses in heat production from tissues, perhaps indicative of an involvement of the central nervous system in splanchnic bed metabolism (Derno et al. 2001); this effect is labelled in Figure 3 as “ingestion”. The study of Derno et al. (2001) also showed that feeding caused a rapid rise in respiratory quotient, indicating a shift from oxidation substrate from fat to carbohydrate. Huntington (1999) reported that portal-drained viscera (gastro-intestinal tract, spleen, pancreas, associated connective tissue and adipose tissue) uses about 21% of total oxygen (O_2) consumption by cattle and sheep, quantitatively equivalent to O_2 use by the liver; these estimates apply with good precision across a wide range of conditions, from fasted animals to those at 2.6 times maintenance. Accordingly, opportunity to control the extent of oxidative metabolism by visceral tissues and liver could reduce HI in cattle. It may be noted here that at low intake, increased concentrate proportion in the diet may result in a shift in energy expenditure and associated heat production from splanchnic to peripheral tissues (Sole et al. 2004).

It is important, for effective amelioration of heat load, that the pattern of heat production be defined, but relevant information from the literature is sparse. This topic will be further discussed below, following the discussion of HI of components of diets.

2 Relationship of HI with diet composition

2.1 Heat Increment of carbohydrates

It is accepted that changes in ration composition may reduce HI. HI for some carbohydrates, as components of a nutritionally balanced diet, is shown in Table 2. These values include heat evolved from the eating and rumination components that contribute to HI, and do not represent the theoretical biochemical efficiency of utilisation or deposition of nutrients.

Table 2. Heat increment and efficiency of utilization of dietary ME for fattening in ruminants (adapted from McDonald et al. 1981 and Blaxter 1989).

Food constituent	Efficiency of utilization of ME above maintenance	HI above maintenance (HI _g)
Carbohydrate	0.54	0.46
Glucose	0.54	0.46
Sucrose	0.58	0.42
Starch	0.64	0.36
Cellulose	0.61	0.39

It is important to appreciate that HI values such as those shown in Table 1 are not constants as determined by chemical composition, but vary according to the purpose for which nutrients are used by the animal, and may be affected by deficiencies in other nutrients. For instance, for typical cattle with energy intake below that required for maintenance, the HI associated with a typical diet is 60% lower than for those cattle with above maintenance intakes (Blaxter 1989). The total HI resulting from a feed is thus a compound function of the proportion of energy used for maintenance and that used for growth; this in turn, is a function of the energy content of the diet. This concept is illustrated in Table 3, which include HI due to the eating and rumination. Representation in Table 3 of HI for maintenance and gain was derived by assuming linear responses to increments of ME intake, differentiated below maintenance and above maintenance energy requirements. It has been recognised that this is a simplification of a smooth (shallow) exponential curve from below to above maintenance (Ferrell and Jenkins 1998). The ratio of protein:fat in the net gain of body tissue is relevant, as it is well recognised that efficiencies of fat and protein deposition differ. Fat is deposited with an efficiency of 0.73, while protein efficiency is 0.21 (Williams and Jenkins 2003b).

FLOT.314 - Dietary strategies for amelioration of heat load in feedlot cattle

Table 3. Heat increments for diets of various ME concentrations and ratios of roughage:concentrate for animals in a thermoneutral environment, when used for maintenance or gain in beef cattle (adapted from NRC 1996).

ME concentration (MJ/kg)	Roughage: concentrate ratio	Heat Increment	
		Maintenance (HI _m)	Gain (HI _g)
8.4	100:0	0.42	0.70
9.2	83:17	0.39	0.65
10.0	67:33	0.37	0.62
10.9	50:50	0.35	0.59
11.7	33:67	0.33	0.56
12.6	17:83	0.32	0.54
13.4	0:100	0.31	0.52

Although this approach allows a convenient comparison of HI values of diets, by summation of HI attributed to individual dietary components, it does not account for the associative effects that can occur between such components. For instance, it was shown in the 1930's that if maize was added to a ration of oat straw, maize meal and molasses, a lower HI for maize was measured than when it was added to a ration of lucerne hay, linseed meal and bran (Blaxter 1962). Thus, the HI of maize varied from 0.26 to 0.42 depending on the nature of the basal ration to which it was added (McDonald et al. 1981). These associative effects in ruminants are a result of the modification by rumen micro-organisms of chemical components of feeds prior to their absorption by the host animal. For example, the products of rumen fermentation available for use as an energy source by the host animal can vary from 74:17:7 molar percent of acetate:propionate:butyrate with a roughage diet to 34:46:6 with a concentrate diet. In general terms, the proportion of acetate increases in relation to the roughage content of the diet, and the proportion of propionate increases in relation to the grain content. Butyrate increases most notably in relation to the fermentable sugar or molasses content of the diet.

Associative effects may result from changes in the balance of nutrients available to the rumen microbes or to animal tissues. The balance of nutrients can be affected by selection of grain type or processing changes that affect the rate of starch fermentation to VFAs in the rumen and thus the proportion of starch absorbed in the small intestine. Protein to energy ratios of absorbed nutrients will be partially determined by Intestinal absorption of microbial protein synthesised as a result of ruminal starch fermentation Efficiency of utilisation of starch absorbed as glucose from the small intestine will be higher than if the starch is modified into VFAs in the rumen (72% vs 64%, McDonald et al. 1981). McLeod et al. (2001) found that shifting the site of soluble starch infusion from the rumen to abomasum decreased methane, and resulted in a 33% increase in energetic efficiency. HI is therefore decreased if the balance is shifted towards intestinal absorption.

An important implication of associative effects is that tabulation of values of efficiency of ME utilisation as summation of values for individual feed components, is of restricted utility in the presence of significant associative effects. This criticism can be applied to both the ME and to the NE (NRC 1996) systems.

The importance of associative effects can be illustrated from the research literature, using as an example the efficiency of use of VFAs absorbed from the rumen, which appeared to offer a simple explanation for the observed differences in HI of dietary components. Armstrong and Blaxter (1984) measured HI in animals that were alternately fed a diet that provided energy sufficient for maintenance or that diet plus intra-ruminal infusions of various VFAs (Blaxter 1962). Their results showed that the HI of acetate (0.67) was much higher than that of propionate (0.44) or butyrate (0.38). However, when infused together with propionate, the HI of acetate was substantially decreased, and it was suggested that the synergistic effect of the higher ratio of propionate to acetate absorbed from the grain diet (1.35:1 vs. 0.35:1) was responsible for the discrepancy. Several years later, Ørskov's group developed a technique for sustaining ruminants entirely by intragastric infusion of VFA and casein (Ørskov and McDonald 1979) that enabled them to eliminate the confounding effect of the basal diet in Blaxter's experiments while infusing acetate, and obtained what they believed to be a more accurate measure of the HI of acetate. In contrast to Blaxter's findings, they observed no difference between the HI in lambs sustained entirely by infusion of nutrients containing a wide range of ratios of acetate, propionate and butyrate acids (Ørskov et al. 1979). However, use of Ørskov's technique entailed infusion of casein, which would supply glucogenic amino acids which may have allowed high efficiency of acetate utilisation (Annison and Bryden 1999). These findings unleashed a debate that was to endure for many years.

Leng (1990) proposed that the high HI of acetate in the absence of sufficient propionate was a consequence of the diversion of acetate used for fat synthesis to a substrate for heat-generating futile cycles. Leng's group showed that the rate of disappearance of acetate from the blood was increased by the addition of propionate to the diet (Cronjé et al. 1991), suggestive of a synergistic effect of propionate on the HI of acetate due to the provision of biochemical "reducing equivalents" necessary for the efficient metabolism of acetate.

More recently, Jessop (2000) reviewed the evidence supporting this theory and suggested that the ability of acetic acid to generate heat by increased ion transport is due to its ability to cross cell membranes. They proposed that acetic acid acts as a proton ionophore by dissociating in the intracellular fluid and activating the Na^+/H^+ antiporter, resulting in stimulation of Na^+,K^+ -ATPase activity and generation of heat. According to this paradigm the rate of diffusion of acetate into the cell, and hence HI, would depend on the extracellular concentration of acetate relative to the cell's ability to metabolise it.

The balance of evidence suggests that the HI of acetate used in tissues will increase if the supply of glucose is low. Certainly, diets that could be expected to result in a high HI are those that contain large quantities of roughage in combination with little grain or protein to provide gluconeogenic precursors to allow glucose synthesis in the liver. While the high HI of acetate is of considerable importance for subsistence farming systems in developing countries where ruminants are typically sustained by low quality fibrous roughages alone, it is unlikely to have any practical significance for feedlot diets. The HI of acetate is likely to be at a minimum and will vary little across a range of typical feedlot diets, since these diets usually give rise to a high ratio of propionate to acetate, and provide high levels of additional glucose precursors such as amino acids. Recent findings by Taniguchi et al. (2004), that absorption of acetic acid from the gastro-intestinal tract was almost

doubled in sheep exposed to 35°C compared to 20°C, would indicate that extracellular concentration of acetate is likely to be increased by EHL.

The early results of Armstrong and Blaxter (1984) showed that butyrate had a low HI. In theory, the inclusion of molasses could reduce the HI of feedlot diets, as rumen fermentation of molasses typically results in an increase in the ratio of butyrate to acetate and propionate. Lofgreen and Otagaki (1960) used the comparative slaughter technique to evaluate the net energy value of molasses for fattening steers. They reported that molasses was used as efficiently as grain when included at a level of 10% of the diet, but molasses inclusion at levels greater than 10% resulted in a substantial decrease in efficiency of utilization. Although this implies that HI was increased at levels in excess of 10%, they did not measure HI directly and were unable to explain their results. Research from the CSIRO Rendel Laboratory in Rockhampton indicates that poor efficiency of utilisation of molasses was not observed for a molasses content of up to 50% of the dietary dry matter.

2.2 Heat Increment of lipids

The HI of dietary fats and oils is lower than that of carbohydrate. HI can be as low as 0.1 when absorbed lipid is converted to body fat (Baldwin et al. 1980). Theoretically, if rumen fermentation of lipid is minimised by feeding ruminally inert fat, observed HI values may approach 0.1 (see Table 4). This will be increased if some of the lipid is not inert in the rumen. For sheep fed tallow or soya-acid oil (unsaturated) or a mixture of the two at 5% of the ration, the ME of all lipid sources were used at about 0.81 for production and 0.61 for maintenance (Wainman and Dewey 1987). The realised efficiency of use of ME in lipid is dependent on whether the fatty acids absorbed from the gut are directly incorporated into body lipid as can occur during growth, or are catabolized to acetyl-CoA and ATP. The degree of similarity of fatty acid composition of dietary lipid to that of adipose tissue will largely determine the efficiency of use of dietary lipids in the growing animal.

The ME value of lipid inclusion at 6% in compound rations was measured by Thomas et al. (1988) using a range of oils and fats (including rumen-inert lipid), and the ME content of the compound diet could be readily predicted from knowledge of the oil and cellulase digestible organic matter following extraction with neutral detergent. This topic has been further discussed by Sparke et al. (1998).

Table 4. Heat increment and efficiency of utilisation of ME of lipid sources in ruminants (NRC 1996).

Food constituent	Efficiency of utilisation of ME above maintenance	HI above maintenance (HI _g)
Fat, theoretical value	>0.90	<0.10
Fat, hydrolysed animal	0.75	0.25
Vegetable oil	0.55	0.45

Although the potential utility of dietary lipids for the reduction of heat load in dairy cows has been reviewed by several authors (Beede and Collier 1986; Huber et al. 1994; West 1999), evidence that added fat decreased HI is inconclusive (see also Knapp and Grummer 1991; White et al. 1992). Drackley et al. (2003) found that dairy cows had lower respiration rates at 07:00 when fed a diet containing choice white grease compared to an iso-energetic starch-based diet. Paradoxical results were reported by O'Kelly (1987). When cattle were fed a lucerne diet containing 18% whole

cottonseed, rectal temperatures were reduced by 0.2-0.4°C at both thermoneutral and hyperthermic temperatures, but evaporative water loss was also increased, indicative of enhanced heat dissipation which would not be expected if the feed had a low HI. Sheep data are also inconclusive. For example, inclusion of whole cottonseed in diets supplying double the requirement for maintenance energy, reduced heat production by 7% at 24°C, but had no effect on heat production at 34°C (Arieli 1994), thus raising the question whether metabolism of lipid in heat-stressed ruminants differs from that of animals in thermo-neutrality. Interpretation of experiments may be confounded by reductions in intake associated with the inhibitory effect on rumen microbes of lipids, and the effect of the extra protein when lipid is supplied in material such as whole cottonseed.

Interpretation of the benefits of feeding fats needs to be made in the light of reports that calcium soaps of fatty acids are subject to dissociation in the rumen at pH levels seen in the rumen of cattle fed feedlot diets (Sukhija and Palmquist 1990). These products may therefore not be as ruminally inert as previously thought. The third generation of rumen inert lipid products, containing pre-hydrolysed and mostly hydrogenated pure fatty acids, are better candidates for use as components of low-heat rations as they have no negative effects on rumen digestion (Loften and Cornelius 2004), but there appears to be little pertinent information about their potential to significantly reduce HI. The availability of these products represents an opportunity to reduce heat load in feedlot cattle, and research needs to be conducted to determine the magnitude of the reduction.

West (1999) suggested for a general guideline that no more than 30- 40% of total dietary fat should come from oil seeds, and 15-39% from ruminally inert lipids, reflecting limits in the amount of fat that can be fed to ruminants and the reduction in post-ruminal digestibility with high lipid levels (Palmquist 1994; Zinn 1994). A limit of 5% of inert lipid to replace carbohydrate in a feedlot diet could potentially reduce total HI by a maximum of about 4 to 5%.

2.3 Heat Increment of sources of protein

The HI associated with dietary protein is higher than that of dietary carbohydrate or lipid (Table 5).

Table 5. Heat increment and efficiency of utilization of ME from protein for fattening in ruminants (adapted from McDonald et al. 1981 and Blaxter 1989).

Food constituent	Efficiency of utilization of ME above maintenance	Heat increment (HI _g)
Protein	0.45	0.55
Mixed proteins	0.51	0.49
Casein	0.50	0.50
Fishmeal protein	0.53	0.47

The biochemical efficiency of amino acid incorporation into protein is relatively high (75%), and the apparent low efficiency of protein (30 – 50%) may be attributable to protein turnover (Johnson et al. 2003). The process of protein synthesis and turnover makes a significant contribution to thermogenesis, and accounts for 20-30% of whole body heat production (Kelly and McBride 1990; Lobley 1991); whether this cost is best attributed to protein deposition or to maintenance requirements can be argued (Johnson et al. 2003). The gut accounts for 40% of whole body protein

synthesis, and skeletal muscle for 14-33%. The contribution of protein breakdown to thermogenesis is not known (Kelly and McBride 1990), but is likely to be small (Lobley 1991). Because protein synthesis is increased by amino acid absorption, the consumption of diets that contain crude protein in excess of requirements is likely to add to the heat load of feedlot cattle. Blaxter (1962) also suggested that protein turnover may increase with heat stress. Additionally, urea synthesis from excess amino acids confers an energy cost of 31 KJ /g urea-N synthesised; thus an increase in HI associated with urea synthesis would also result from diets that contain excess rumen degradable protein (Tyrrell et al. 1970; Huber et al. 1994). The conclusion from U.S. studies is that feeding a low-degradable protein improves milk production during exposure of dairy cows to summer temperatures, providing that the protein is of good quality (Taylor et al. 1991). The underlying mechanism appears to relate to maintaining adequate supplies of protein in the small intestine in the face of a reduction in passage rate of digesta from the rumen.

White et al. (1992) found that steers fed grass:concentrate (20:80) with either fishmeal or soybean meal while being exposed at long-term high (33°C) ambient temperatures, showed increased plasma urea levels. The authors suggested diets of heat-stressed cattle should be formulated to contain increased ruminal escape protein. Whether this change should accompany a reduction of protein level in the diet will depend on the effect of EHL on feed intake (Beede and Collier 1986). Ames et al. (1980) established that the efficiency of protein utilization is decreased by EHL and proposed that the total cost of urea synthesis associated with protein breakdown would increase. The accompanying lowered growth rates could be supported by a lower dietary protein content without further detriment to growth rates. Ames et al. (1980) proposed that less energy will be available for protein synthesis because of increased energy expenditure on heat dissipation. It was these findings that lead NRC (1981) to propose that, in formulation of rations for thermally-stressed sheep, that protein and energy needs required separate consideration.

Protein turnover rates are commonly manipulated in feedlot cattle through the use of hormonal growth promotants. The effect of growth promoting agents in alleviation of HI in heat-stressed cattle has received little attention. β_2 -agonists increase protein accretion by stimulating protein synthesis and inhibiting protein degradation (Hocquette et al. 1998) and could be expected to increase thermogenesis. β_2 -agonists are not available in Australia, but widespread use is made of trenbolone acetate and estradiol-17 β . *A priori*, it would be expected that growth promotants with oestrogenic activity would increase thyroid gland activity and feed intake, which might counter benefits of reduced protein breakdown rate, with an uncertain effect on HI. On the other hand, androgens promote a lower voluntary feed intake and lower rate of protein breakdown (Hunter et al. 1993) and could thus be expected to contribute to a slight reduction in HI. In one study reported by Kreikemeier (2003), use of an oestrogen implant increased rectal temperature by approximately 0.5°C when compared to an androgen or oestrogen/androgen implant. Use of the combination implant resulted in the lowest heat production per unit feed intake when animals were exposed to EHL, but all implanting regimes appeared to increase HI compared to the pre-implant period (Kreikemeier 2003). A lack of improvement in weight gain was reported when feedlot steers were implanted with a range of growth promotants during a very hot summer (Ray et al. 1969).

2.4 Integrated effects of ration components on heat increment

The preceding discussion of the multitude of factors that influence HI shows that estimation of the total HI of a diet is a complex task. The question of how best to accommodate variable efficiency caused by diet and feeding level, into calculations designed to provide a practical way of estimating the extent to which ruminant diets meet the requirements of livestock, has occupied the minds of scientists for many years. Disagreement on whether to take this energy loss into account by increasing estimates of animal requirements or by decreasing estimates of the nutritive value of feedstuffs was the main factor that led to the evolution of the different feeding systems in use today. In reality, these systems differ more in terms of application than in the underlying principles.

For the purposes of this discussion, the Variable Net Energy System (MAFF 1975) was used. The two main factors influencing the HI of a diet are its energy density (Figure 4), and the level of production at which it is fed (Figure 5). Translated into practical terms, these figures show that although an energy dense feedlot diet will give rise to relatively less heat per unit feed, the proportion of heat generated will increase as the amount fed is increased. An integration of the effects of these two factors is shown in Figure 6.

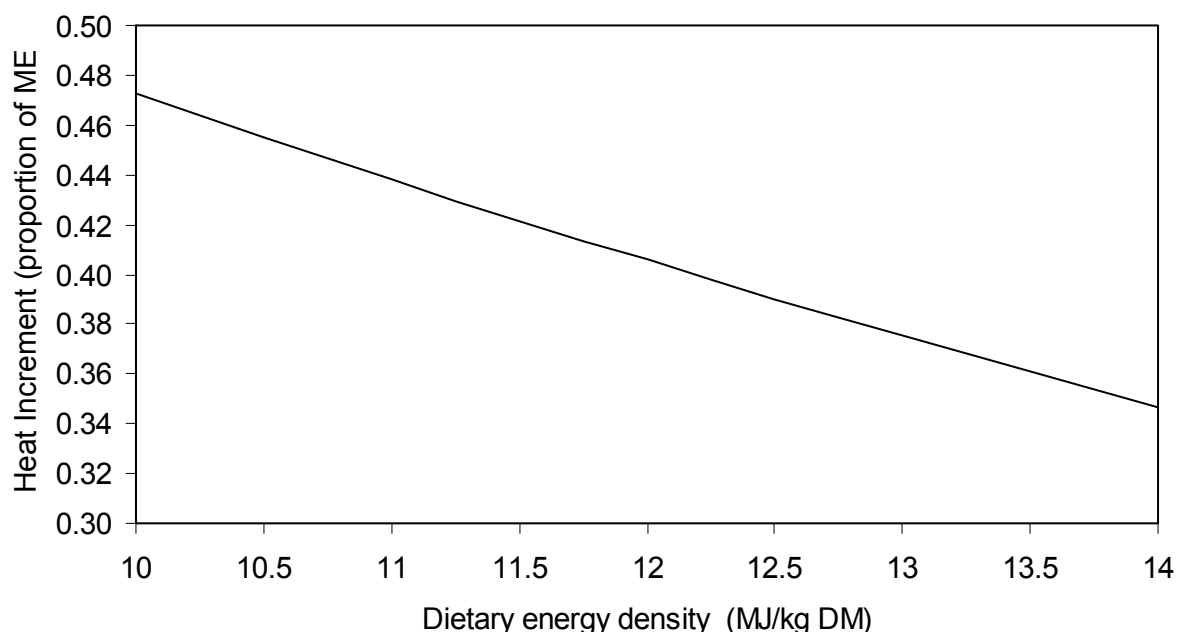


Figure 4. Effect of dietary energy density on heat increment of a 400 kg steer

Figure 6 shows that the relative effect of the amount fed (i.e. animal production level) on HI varies according to the energy density of the diet. In practical terms, if a diet containing 12 MJ ME/kg DM and an animal production level of 2.25 x maintenance NE requirements (equivalent to that required by a 400 kg steer gaining at 1.5 kg/d) is assumed to be broadly representative of that likely to be encountered in a feedlot, a greater reduction in HI will be achieved by increasing the energy density by 10% than by decreasing the amount fed by 10%.

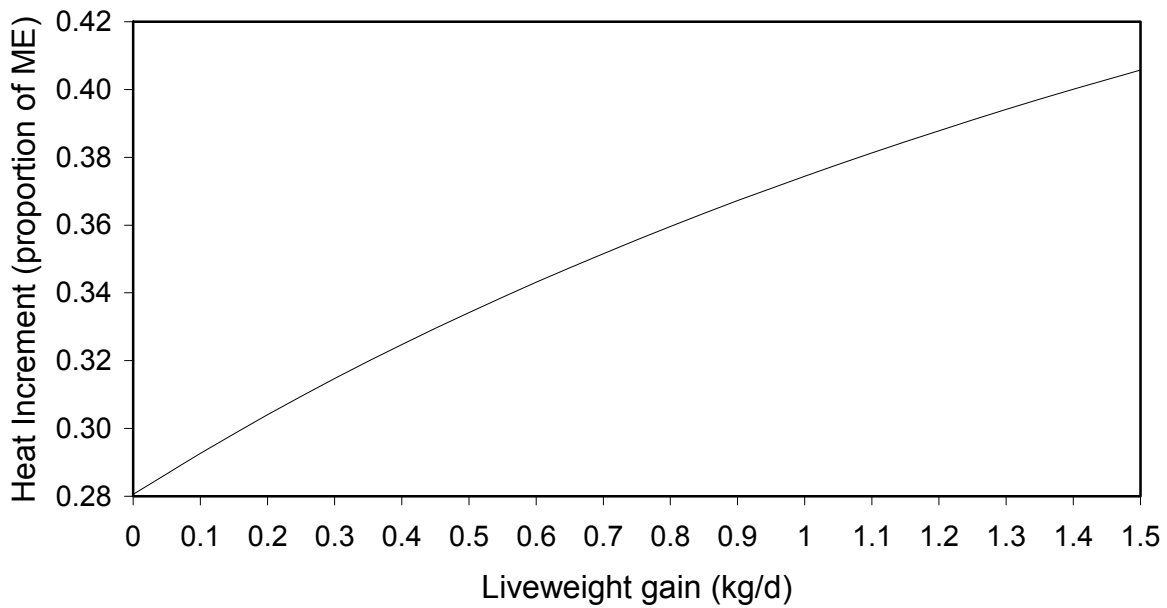


Figure 5. Effect of level of production of a 400 kg steer on HI of a diet containing 12 MJ ME/kg DM

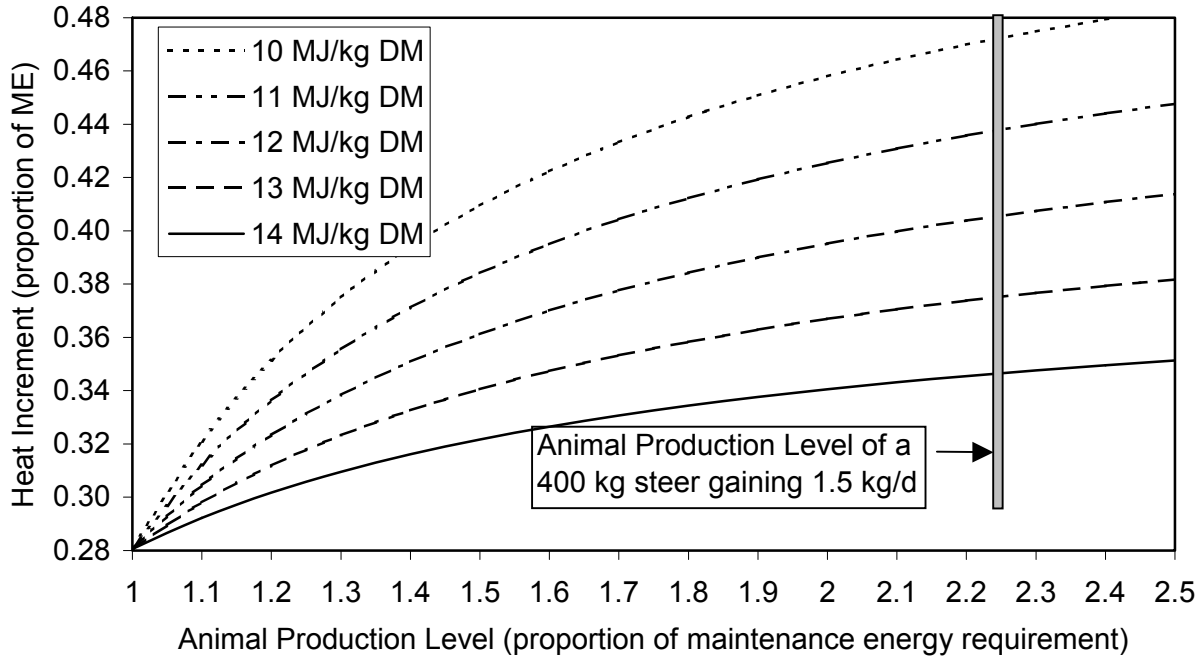


Figure 6. Effect of animal production level and dietary energy density on heat increment.

Examples of the relative substitution effects of some feedstuffs in a feedlot diet are given in table 6.

FLOT.314 - Dietary strategies for amelioration of heat load in feedlot cattle

Table 6. Effect of diet composition on energy density.

Ingredient	ME (MJ/kg DM)	Diet A		Diet B		Diet C		Diet D	
		%	MJ ME	%	MJ ME	%	MJ ME	%	MJ ME
Wheat	13.3	36	4.79	33.5	4.4555	67	8.91	13	1.73
Sorghum	12	36	4.32	33.5	4.02			36	4.32
Molasses	11	3.5	0.39	3.5	0.39	3.5	0.39	3.5	0.39
Tallow	37			5	1.85	5	1.85		
Whole cottonseed	14.5	8	1.16	8	1.16	8	1.16	8	1.16
Sorghum silage	9.1	10	0.91	10	0.91	10	0.91	10	0.91
Wheat straw	7	2	0.14	2	0.14	2	0.14	25	1.75
Minerals & Vitamin Premix	0	4.5	0	4.5	0	4.5	0	4.5	0
		100	11.7	100	12.9	100	13.4	100	10.3

The energy density of diet A is 11.7 MJ ME/kg DM. The energy density of this diet is increased to 12.9 MJ ME/kg by replacing 5 percentage units of the grain component with tallow (diet B); the energy density of diet B was further increased to 13.4 MJ ME/kg DM by replacing the sorghum component with wheat (diet C). Diet D, in which the roughage component (wheat straw) was increased to 25% at the expense of wheat grain, was included for the purposes of this exercise because this practice has been suggested as a tactic during heat waves (Sparke et al. 2001).

In order to calculate the HI of the various diets for animals in themoneutral conditions, using equations of MAFF (1975), it is first necessary to estimate the desired animal production level (APL). APL is expressed in terms of multiples of maintenance requirements, in order to account for the difference in HI above and below maintenance. Thus:

$$APL = 1 + ((LWG (6.28 + 0.0188 W)) / ((1 - 0.3 LWG)(5.67 + 0.061 W)))$$

where LWG = liveweight gain (kg/d) and W = liveweight (kg)

For a 400 kg steer gaining at a rate of 1.5 kg/d, the APL will be 2.25. Then, HI for maintenance and production can now be calculated using the energy density of the diet (MD) as follows:

$$HI = 1 - ((MD \times APL) / ((1.39 \times MD) + (23 (APL - 1))))$$

where MD = MJ ME/kg DM and HI is expressed as the proportion of ME lost as heat

Using the energy density values from Table 6 and this equation, a HI of 0.42 for diet A can be calculated (Table 7). Substitution of grain with tallow resulted in a decrease of HI to 0.38 (diet B). Substitution of grain with tallow and of sorghum with wheat decreased HI to 0.36 (diet C). Substitution of grain with straw, on the other hand increased the HI to 0.46 (diet D).

FLOT.314 - Dietary strategies for amelioration of heat load in feedlot cattle

The NE required for maintenance and gain (NE_{mp}) can be calculated from MAFF (1975) as:

$$NE_{mp} = 1.05 (5.67 + 0.061 W) + (1.05 LWG (6.28 + 0.0188 W)) / (1 - 0.3 LWG)$$

The NE_{mp} required for a 400 kg steer gaining at 1.5 kg/d is 71.1 MJ/d. The relative amounts of heat coincident with the intake of sufficient DM to satisfy this NE requirement can be calculated as a basis for estimating the relative substitution effects of different feedstuffs (Table 7).

Table 7. Relative daily heat increments of various diets at an animal production level of 2.25.

Diet	MD	HI (proportion of ME)	HI (MJ/kg DM)	NE_{mp} (MJ/kg DM)	Intake (kg)	HI (MJ/d)	NE (MJ/d)	HI (relative to diet A)
A	11.70	0.42	4.86	6.84	10.4	50.5	71.1	1.00
B	12.92	0.38	4.88	8.04	8.84	43.1	71.1	0.85
C	13.36	0.36	4.87	8.48	8.38	40.9	71.1	0.81
D	10.25	0.46	4.75	5.50	12.9	61.4	71.1	1.22

In this diet, substitution of grain with tallow decreased daily HI by 15%; substitution of grain with tallow and of sorghum with wheat decreased the daily HI by 19%. Substitution of grain with straw, however, gave rise to a relative increase in heat production of 22%. While the theoretical intake used in the case of diet D will not be attained in practice, the procedure used above does afford a means of comparing relative values of feed ingredients. In reality, the inclusion of 25% relatively indigestible forage would induce a decrease in feed intake that would compensate for the higher fractional HI. The practice of increasing the roughage content of the diet as a precaution against heat load has been recommended by Sparke et al. (2001).

It is stressed that the values shown in Table 7 are only valid for an animal production level of 2.25, equivalent to the NE required to sustain a 400 kg steer gaining liveweight at a rate of 1.5 kg/d. If the same 400 kg steer were fed to grow at 1 kg/d (APL 1.66), not only would the total HI change, but the relative HI would differ from those given above, as shown in Table 8.

Table 8. Relative daily HI of various diets at an animal production level of 1.66.

Diet	MD	HI (proportion of ME)	HI (MJ/kg DM)	NE_{mp} (MJ/kg DM)	Intake (kg)	HI (MJ/d)	NE_{mp} (MJ/d)	HI relative to diet A)
A	11.70	0.38	4.47	7.23	7.23	32.3	52.3	1.00
B	12.92	0.35	4.55	8.37	6.25	28.5	52.3	0.88
C	13.36	0.34	4.58	8.78	5.96	27.3	52.3	0.84
D	10.25	0.42	4.32	5.93	8.81	38.1	52.3	1.18

FLOT.314 - Dietary strategies for amelioration of heat load in feedlot cattle

The examples above serve to illustrate that the relative HI of a component of a diet cannot be estimated without consideration of the diet in which it is contained and the rate of growth of the animal, and must be computed anew for each diet. Relative HI of several typical feedlot diets are compared in Tables 9 and 10.

Table 9. Composition and energy density of typical feedlot diets.

	ME (MJ/kg DM)	Diet E		Diet F		Diet G		Diet H		Diet I		Diet J	
		%	MJ ME	%	MJ ME	%	MJ ME	%	MJ ME	%	MJ ME	%	MJ ME
Wheat	13.3	27	3.59			21	2.79	24.3	3.23	35	4.655		
Barley	13	19	2.47	72	9.36	47	6.11	20	2.6				
Sorghum	12	20	2.4					15	1.8	35	4.2	68	8.16
Molasses	11	3	0.33	3	0.33	3	0.33	3	0.33	3.5	0.39	4.5	0.50
Tallow	37									2	0.74	2	0.74
Cottonseed meal	11.7	13	1.52	6.5	0.76	10	1.17	9	1.05				
Canola meal	10.4			4.5	0.47								
Whole cottonseed	14.5							10	1.45	8	1.16	9	1.31
Maize silage	10.8	15	1.62										
Sorghum silage	9.1									10	0.91	10	0.91
Wheat straw	7									2	0.14	2	0.14
Cereal hay	8.5			10	0.85	15	1.28	15	1.28	4.5	0.38		
Minerals, Vitamins, Buffers	0	3	0	4	0	4	0	3.7	0		0	4.5	0
Total		100	11.9	100	11.8	100	11.7	1000	11.7	100	12.6	100	11.8

FLOT.314 - Dietary strategies for amelioration of heat load in feedlot cattle

Table 10. Relative daily heat increments of the various diets shown in table 9 at an APL of 2.25.

Diet	MD	HI (proportion of ME)	HI (MJ/kg DM)	NEmp (MJ/kg DM)	Intake (kg)	HI (MJ/d)	NEmp (MJ/d)	HI (relative to diet E)
E	11.9	0.41	4.87	7.03	10.11	49.2	71.1	1.00
F	11.8	0.41	4.86	6.94	10.25	49.8	71.1	1.01
G	11.7	0.42	4.86	6.84	10.39	50.5	71.1	1.03
H	11.7	0.42	4.86	6.84	10.39	50.5	71.1	1.03
I	12.6	0.39	4.88	7.72	9.21	44.9	71.1	0.91
J	11.8	0.41	4.86	6.94	10.25	49.8	71.1	1.01

2.5 Conclusions

The HI of various substrates, subject to the reservations expressed concerning the consequences of associative effects should they exist, can be summarised as in Table 11.

Table 11. Heat increment of dietary components above energy maintenance requirements.

Food constituent	Heat increment (H_{i_g})
Roughage	0.70
Protein	0.47-0.55
Grains: rapid digestion (barley, flaked maize)	0.46
Sugars	0.42-0.46
Grains: slowly digested (e.g. maize)	0.26-0.42
Rumen lipid of varying 'inertness'	0.1-0.25

It is evident that HI of feedlot diets could be decreased by increasing the energy density. Details of alternative energy dense feedstuffs for the cattle feedlot industry are to be found in Sparke et al. (1997) and in the review of Owens et al. (1997) on the effect of grain processing. Most feedlot diets, however, are formulated to contain a high density of energy, and the use of alternative high-energy grain sources is unlikely to have a further substantial impact on HI through increased energy density.

Inclusion of lipid into the diet can make a substantial impact on HI if significant inclusion rates can be achieved without effects on ruminal microbial activity. The report of MLA project FLOT.106 (Sparke et al. 1998) gives an excellent overview of the use of commodity fats and oils and other energy

dense feedstuffs in the Australian cattle feedlot industry and also contains useful tables of energy density values.

The availability of products in which pure fatty acids are effectively protected from rumen fermentation represents an opportunity to reduce heat load in feedlot cattle, and research aimed at defining the relative economic value of these products for tropical feedlot systems would be desirable.

Formulation of rations according to the requirements of various classes of animals for total protein and the ratio of rumen degradable to rumen undegradable protein will reduce heat load in feedlot cattle. Where appropriate, the use of trenbolone acetate and estradiol-17 β will also reduce heat load.

3 Time course of thermogenesis

3.1 Dietary-related thermogenesis

In humans, thermogenesis typically increases by 10-17% within 30 minutes of a meal (Westerterp 2004). The time course of this transient change in thermogenesis is dependent on the type of nutrient absorbed and also on the physical form of the meal (Blaak and Saris 1995; Peracchi et al. 2000). In contrast, despite the considerable amount of literature on the HI of feeds in farm animals, short-term post ingestive effects have virtually been ignored. In contrast to the approach followed by human nutritionists, where diet-induced thermogenesis is measured following a meal, estimates of HI in ruminants have traditionally been derived by comparing two intake levels where each measurement is made over a minimum of 24 hours and after a period of adaptation to the diet (Moe 1992). A similar preponderance of 'average data is apparent in the literature on ruminant fermentation and digestion (Illius and Jessop 1996).

For cattle, heat production can be measured from gas exchange (O₂ consumption, methane and carbon dioxide output) during indirect calorimetry; allowance for carbon dioxide from fermentation can be made by assuming that the ratio of carbon dioxide:methane remains constant. Data available in the literature are few, but those available show that metabolism almost immediately responds to changes in nutrient inputs. For example, in sheep it appears that increases in HI (as indicated by O₂ consumption) occur within 15 minutes of feeding, effectively coincident with increased fermentation as indicated by methane output (Figure 7). In fact the changes are sufficiently rapid that they indicate that central nervous responses are involved as well as increased fluxes of absorbed nutrients (Derno et al. 2001), which adds a new level of complexity to consideration of HI following nutrient absorption as depicted in Figure 2. The other feature of note in Figure 2 is the divergence of O₂ consumption from methane output 4 hours after lucerne was offered to sheep. This was consistent with increased evolution of metabolic heat at that time.

Brosh et al. (1998b) proposed that an indirect estimate of energy expenditure could be obtained from heart rate after calibration of heart rate with gas exchange measurements for individual animals. The authors used heart rate measurements to conclude that heat production closely followed feeding, but the components of HI could not be distinguished.

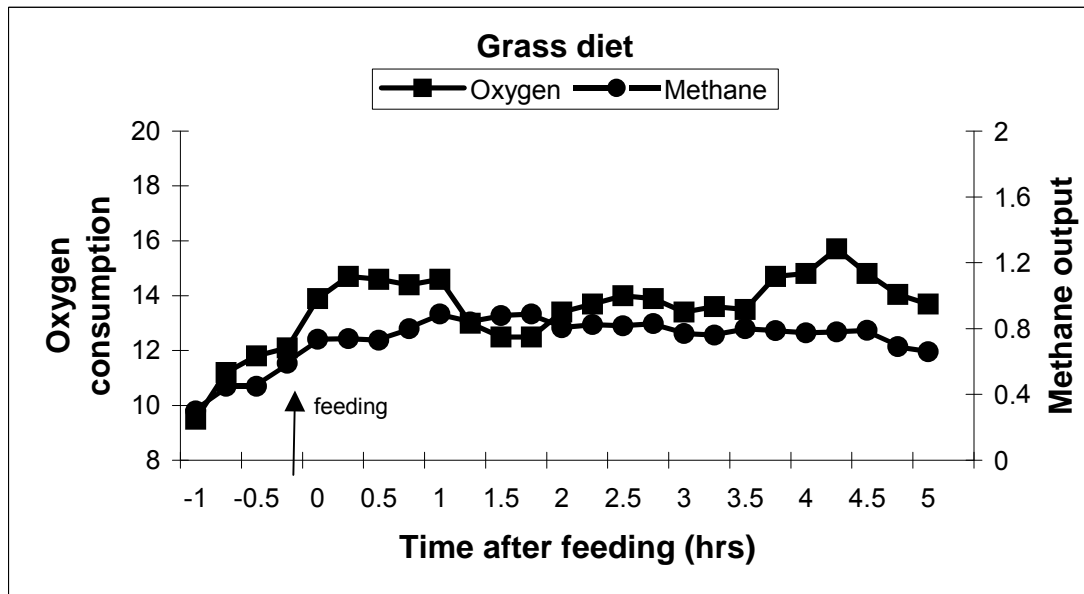
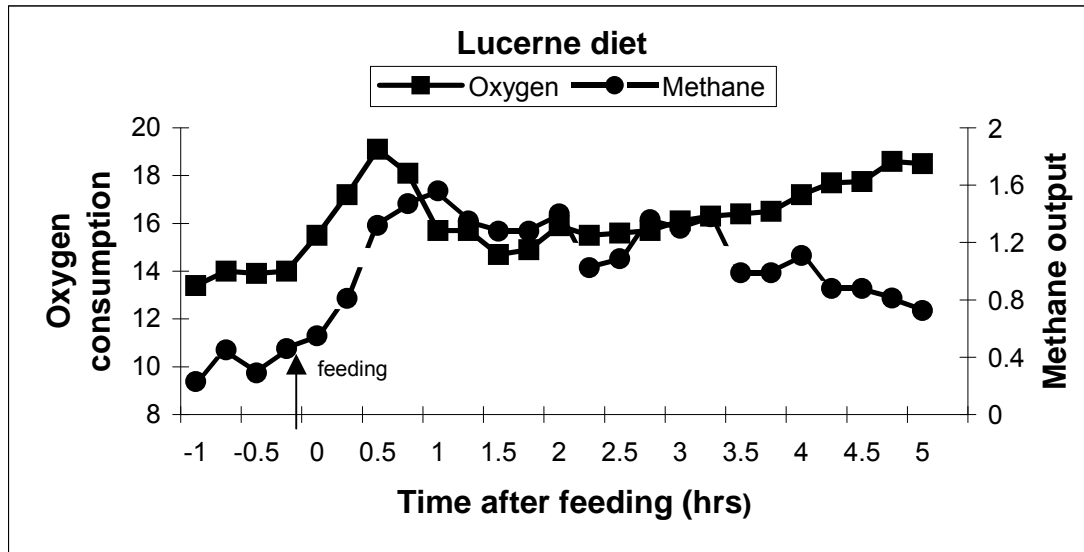


Figure 7. Time course of oxygen consumption and methane evolution (ml/min/kg^{0.75}) after feeding of two diets to sheep (redrawn from Takahashi et al. 1999).

Ilius and Jessop (1996) have postulated that the protein to energy ratio of absorbed nutrients in ruminants varies substantially within several hours after a meal. According to their hypothesis, the postprandial influx of water from the blood to the rumen increases the fluid phase outflow from the rumen, and hence the outflow of VFA to the abomasum where, because of the low pH, absorption is more rapid than from the rumen. Because microbial protein is associated with the flow of particulate matter, which lags behind the water phase, a transient postprandial decrease in the ratio of protein to VFA is predicted. Since there is evidence to suggest that the HI of acetate is related to the supply

of dietary protein (Cronjé et al. 1991), a low postprandial ratio of protein to VFA could increase thermogenesis.

Although many authors have shown that a synchronous supply of energy and nitrogen can increase the efficiency of microbial protein synthesis in the ruminant (see Beever 1993), the importance of degree of synchronicity on HI in the host animal is unclear but generally the effects of uncoupled fermentation of carbohydrates in the rumen are considered to be minor for cattle fed feedlot diets.

In addition to the direct effect of the pattern of nutrient absorption on heat production, the osmolality of digesta has a substantial effect on thermogenesis in rats that is mediated through intestinal osmoreceptors (Osaka et al. 2001) that appear to be distributed throughout the gastrointestinal tract (Schoorlemmer and Evered 2002). The thermogenic effect in rats was associated with increases in osmolality of gut contents of up to 2.4 times that of blood. Other findings suggest that diet-induced thermogenesis in the rat also has a component that is mediated by an increase in plasma osmolality which results from circulating nutrients after the ingestion of a meal (Kobayashi et al. 2001). In cattle, ingestion of concentrate-based diets can double the osmolality of rumen digesta (Nagaraja et al. 1979), with the greatest contribution to osmotic pressure of rumen contents under acidotic conditions due to acetate (Owens et al. 1998), but whether this leads to a thermogenic effect has not been investigated in cattle. Blood osmolality is elevated as a consequence of overt acidosis in feedlot cattle fed concentrate diets, and it has been suggested that the short-term feed intake depressions seen with sub-clinical acidosis may reflect fluctuating osmolality (Owens et al. 1998).

3.2 Simulation of effects of diet composition on HI

Because there are few data available on the temporal pattern of HI in ruminants, the current version of the CSIRO ruminant model, AUSBEEF, was used to examine the potential effects on HI of addition of sources of rapidly fermented carbohydrate, fat and protein to a feedlot diet. AUSBEEF is the only available ruminant growth model capable of providing time profiles of HI, because heat production in other models is calculated using empirical equations and only mean daily values are estimated. The AUSBEEF model was developed with support from the Premium Grains for Livestock Program funded principally by the Grain Research and Development Corporation and Meat and Livestock Australia Ltd. In these simulations, the appearance of heat after feeding is based on kinetics of digestion in the rumen (using a database for Australian feed grains) and also on a less precise estimate of the time course of metabolic heat based on mechanistic estimations of oxidative metabolism from biochemical pathways for individual metabolites as described by Baldwin et al. (1987) (Nagorcka, personal communication). Therefore the HI patterns from AUSBEEF presented below are indicative only, until validated with experimental data.

The simulated effects on HI of the inclusion of 10% molasses, 5% fat or 10% soluble protein in a feedlot diet are shown in Figures 8, 9 and 10 respectively. When molasses replaced grain in the diet, there was a simulated increase of HI in the first two hours after meal consumption (Figure 8), which is consistent with the known rapid rate of rumen fermentation of molasses. The HI of molasses then fell below that of grain from the sixth hour after consumption of the meal, and diverged from that of grain until 21 hours after feeding. Overall, the simulation indicated that molasses is efficiently metabolised and results in a comparatively low daily HI. This is consistent with the findings of Lofgreen and Otagaki (1960).

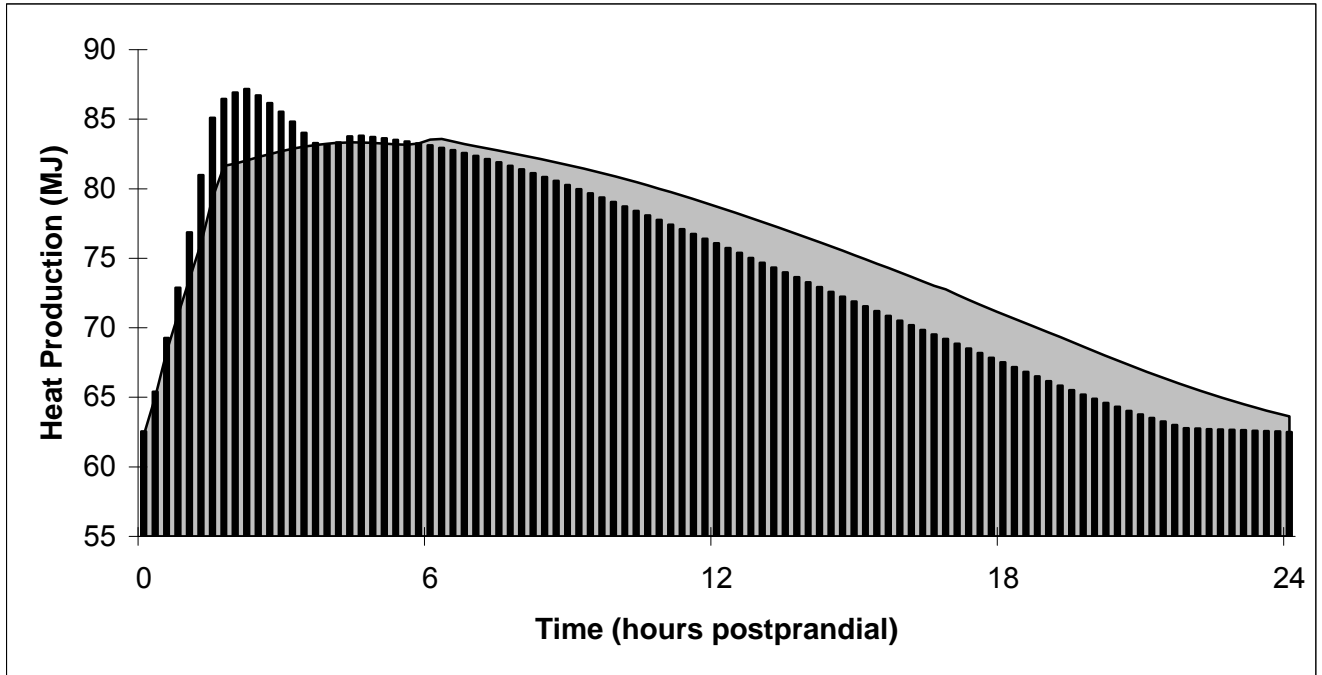


Figure 8. Simulated HI following a single meal of a diet containing 70% grain and 30% roughage (shaded area) and the effect of substitution of 10 percentage units of grain with molasses (bars).

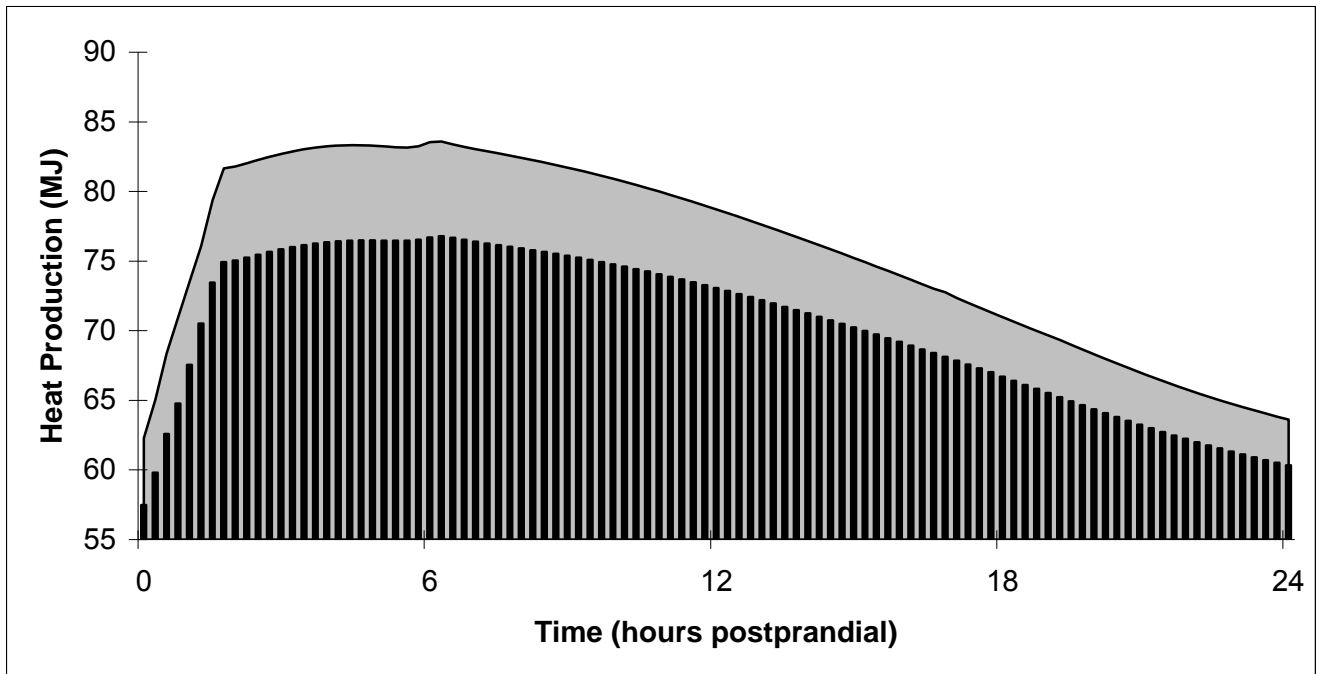


Figure 9. Simulated HI following a single meal of a diet containing 70% grain and 30% roughage (shaded area) and the effect of substitution of 5 percentage units of grain with fat (bars).

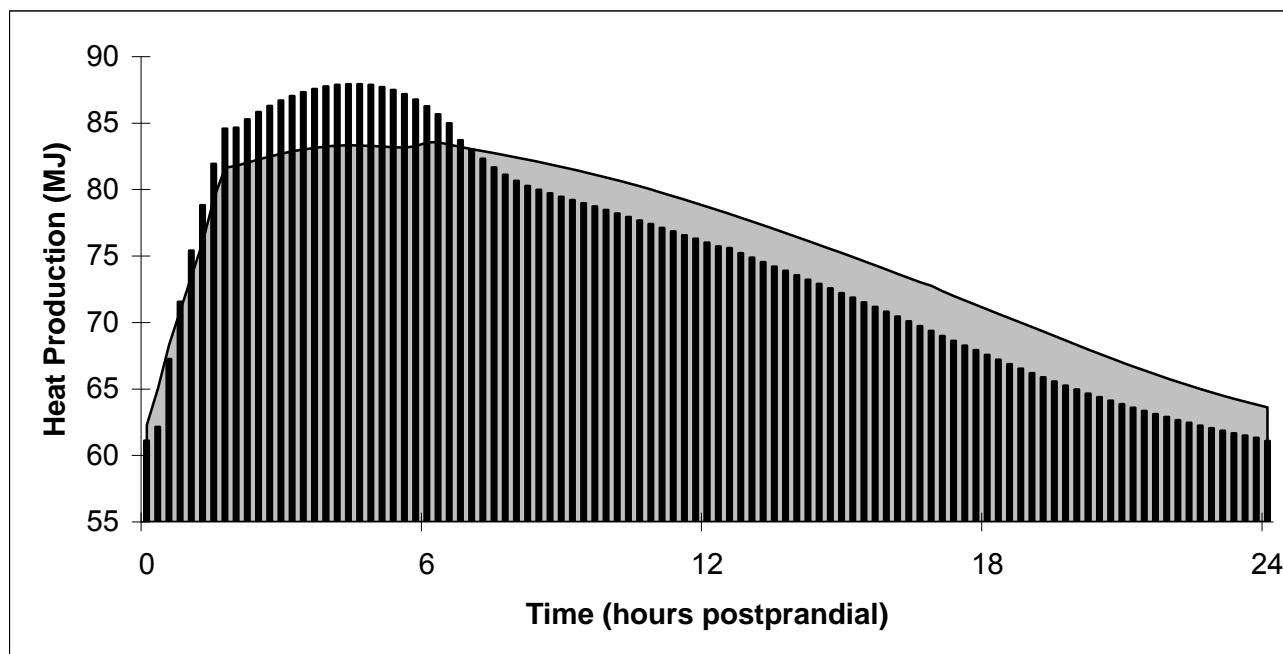


Figure 10. Simulated HI following a single meal of a diet containing 70% grain and 30% roughage (shaded area) and the effect of substitution of 10 percentage units of grain with soluble protein (bars).

The pattern of the simulated time profile after fat inclusion did not differ markedly from that of the diet as a whole (Figure 9) but gave rise to a lower HI, as would be expected from the previous discussion. The simulated effect of inclusion of 10% soluble protein (Figure 10) was somewhat similar to that of Figure 8. For addition of both soluble substrates, heat production rapidly increased to a peak at 3-5 hours after feed ingestion, when it was 12% higher than for the control diet. Thereafter heat production decreased, and by 8-9 hours after feeding was substantially less than that of the control diet. In addition, the simulation shows that the integrated post feeding increase in heat production above the 60 MJ baseline prior to feeding, comprises about 20% of total heat produced over 24 h. These simulations with AUSBEEF require validation by appropriately designed experiments, and it would be desirable to modify the model output to identify the partition of the heat sources from rumen fermentation, and tissue metabolism components.

3.3 Feeding time management to increase heat amelioration

An integral part of a successful strategy would be knowledge of how diet composition affects the magnitude and timing of the HI relative to the cooler evening hours, without necessarily compromising energy intake. The simulated effect of time of feeding on heat production is illustrated in Figure 11. By feeding during late afternoon instead of mid-morning, an additional 13 % (57% vs 44%) of HI was generated during the 10 night-time hours.

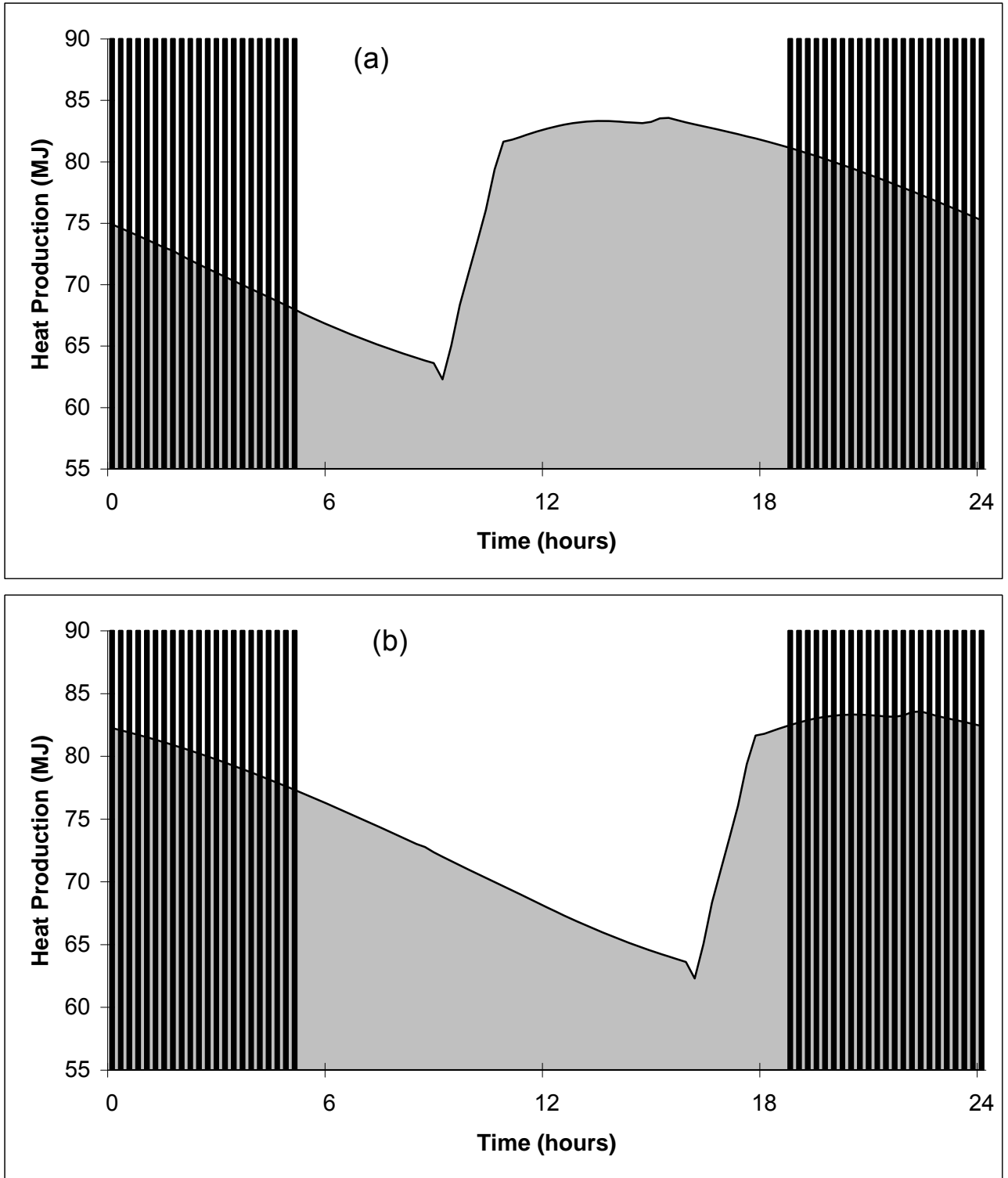


Figure 11. Simulated eat production following a single meal of a feedlot diet containing 70% grain and 30% roughage at 09:00 (a) or 16:00 (b). Bars indicate hours between sunset and sunrise at Rockhampton on 22 December.

The predicted impacts of the addition of rapidly fermentable energy, soluble protein, rumen degradable protein and lipid to a feedlot-type diet, simulated using the AUSBEEF model, and the predicted effects were found to be qualitatively consistent with what would be expected from published experimental data collected under thermoneutral ambient temperatures. At this stage of development, the model does not include subroutines to enable the effects of elevated ambient temperatures on body temperature, feed intake, feeding frequency or growth rate to be predicted.

No data sets could be identified that were sufficiently comprehensive for validation of the predictions from the AUSBEEF model of time course of HI. The paucity of data on short term dynamics of critical metabolic transactions has also been noted by other modellers: Illius and Jessop (1996) commented that “nearly all experimental work has attempted to maintain steady state by constant, low level feeding over the 24-hour period when large fluctuations in ruminal dynamics are unlikely”.

It is evident that the generation of data sets describing the temporal dynamics of thermogenesis from various feedstuffs and feeding strategies at different EHL is necessary before the AUSBEEF model can be validated or implemented to describe HI. Such studies should include measurements of body temperature, heat production, respiration rate and blood metabolite concentrations at frequent intervals over a 24-hour period.

Whether AUSBEEF can be modified to better describe the time course of HI from tissue metabolism requires further investigation. A first approach could be simply to measure how close is the relationship between HI in animals given feedlot diets (measured by whole-animal O₂ consumption), and the calculated pattern of HI from fermentation. If the relationship is close, then the implication is that the lag between absorption and metabolism of nutrients in tissues is negligible. In experiments of Kim et al. (1998), nutrient delivery to tissues was variable and not clearly related to O₂ consumption and there was considerable variability between animals. Other work with sheep fed forage diets is consistent with the concept that rapid absorption of nutrients (from alfalfa) is associated with rapid rise in liver O₂ consumption (Park et al. 1997). Accordingly, clarification is needed concerning the relationship between nutrient absorption and HI arising in the splanchnic bed and peripheral tissues. Remond et al. (2003) concluded that the liver faced a constant flux of amino acids while VFA and ammonia net fluxes varied in response to timing of meals. For cattle fed feedlot diets of different fermentation characteristics, we might expect diets that give rise to rapid nutrient absorption to be reflected in a contemporaneous increase in HI, but this requires examination. Brosh et al. (1998a) fed Hereford steers in southeast Queensland at either 08:00 or 16:30 during summer, and reported that morning feeding increased O₂ consumption and heart rate during the hottest part of the day, when compared to afternoon feeding. One puzzling feature in this experiment was that O₂ consumption and heart rate of morning-fed animals was similar whether animals were exposed or protected from solar radiation. The authors speculated that exposed animals may have reduced the metabolic contribution to HI, perhaps by reduction of splanchnic bed activity.

There is little evidence that the degree of synchrony of use of nutrients in peripheral tissues affects heat production. In pigs fed at maintenance, when feeding of protein was separated from that of the energy components, thermogenesis was not affected (Kirchgessner and Miller 1998). As mentioned previously, synchrony of nutrient release in the rumen appears to be of little import for heat production in feedlot cattle.

3.4 Does rate of ruminal fermentation affect HI?

Rates of fermentation of ration components and their rates of passage from the rumen will determine the quantity and time course of absorption of nutrients. Rates of starch disappearance by solubilisation and fermentation can vary quite widely, especially for starchy materials, as depicted in Figure 12. In respect of the non-soluble but potentially-degradable starch fraction, the fractional disappearance rate from nylon bags was about 5 and 48%/h for maize and barley grains respectively (Tothi et al. 2003).

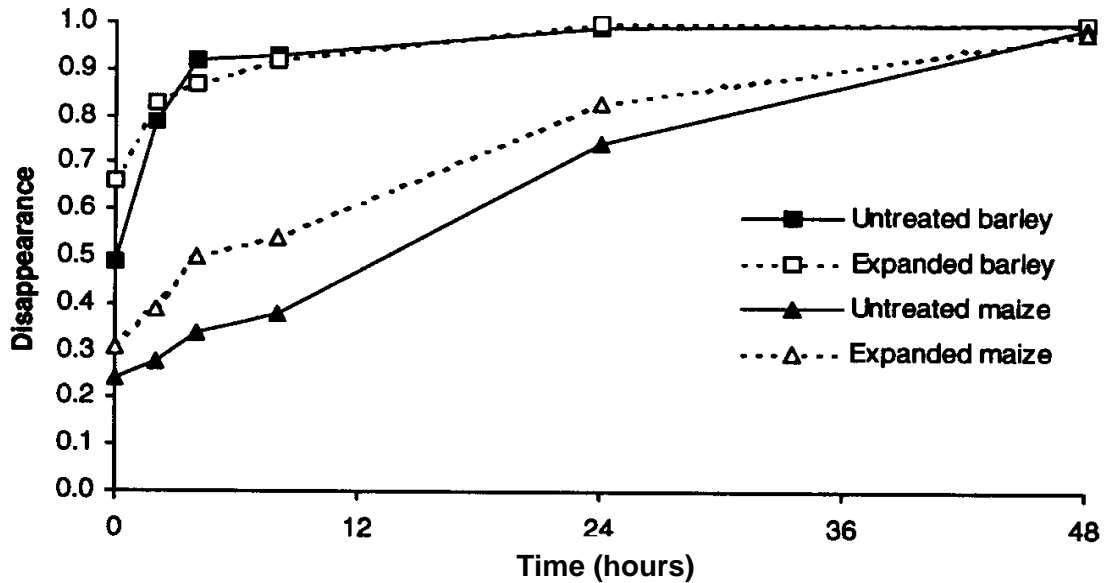


Figure 12. Disappearance of starch from nylon bags in the rumen (from Tothi et al. 2003).

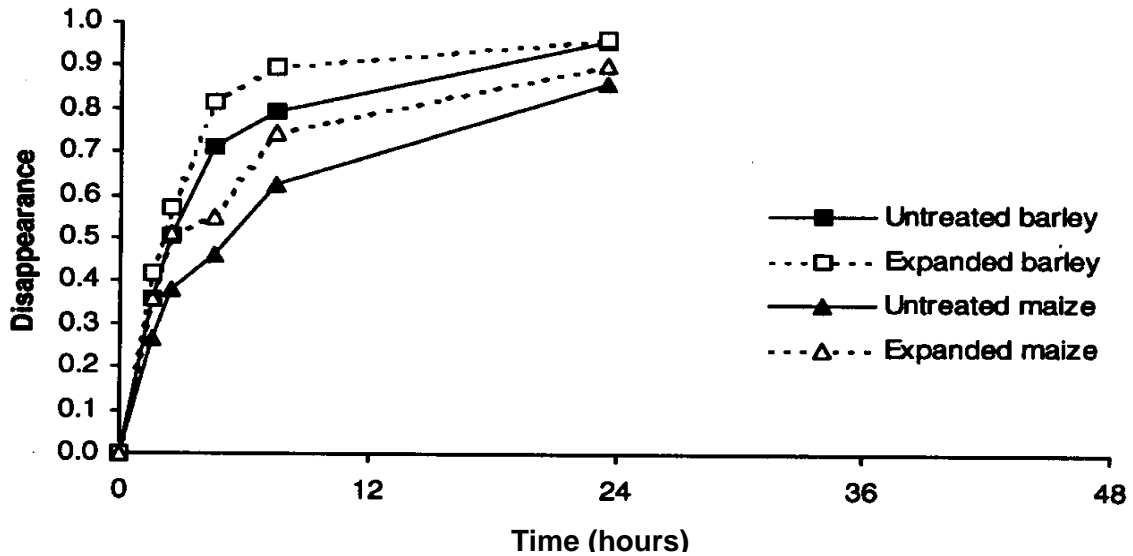


Figure 13. Predicted disappearance of starch in the rumen (from Tothi et al. 2003)

Figure 12 also depicts the effect of grain expansion in a screw press. The rate of starch disappearance was doubled for barley but was not affected for maize. The ability to substantially modify fermentation characteristics of grain by processing is well documented (e.g. Rowe et al. 1999) and provides the potential to modify site of digestion and HI without change of grain type. The predicted time course of starch fermentation in the rumen, derived using assumptions about rate of starch passage from the rumen and the digestion rates in nylon bags depicted in Figure 12, are shown in Figure 13.

The errors involved in such calculations are considered acceptable in the application of data in the Cornell Net Carbohydrate and Protein System to estimate feeding value (Sniffen et al. 1992) but it is less certain whether the approaches are sufficiently precise for satisfactory prediction of diurnal fluctuations in HI. Additionally, EHL in cattle will lead to short-term declines in feed intakes and in rate of passage of digesta from the rumen, with a resultant increase in time available for ruminal fermentation (NRC 1996). Variability in animal response to EHL as a result of changes in passage rates may be large, as there is substantial between-animal genetic variation in passage rate and efficient starch digestion for thermoneutral cattle (Channon and Rowe 2004). In the case of carbohydrate digestion, poor characterisation of short-term ruminal passage rate changes will lead to imprecision in estimates of site of digestion. This lack of precision may be substantial for concentrates containing large amounts of slowly-digestible starch, e.g. corn. Similar considerations apply to protein transactions in the rumen, which also are characterised by soluble, slowly digestible and undegraded fractions. This imprecision will then carry through to calculations of diurnal fluctuations of HI. Moss et al. (1998) used the nylon bag technique to measure degradability of protein concentrates available in northern Australia. The effective rumen degradability, calculated assuming a passage rate from the rumen of 8%/h, varied from 10 to 86% of protein content, and was determined largely by the content of the readily degradable (soluble) component. AUSBEEF uses data for starch digestion from a database compiled for Australian grains, in which rates of starch digestion were measured using an *in vitro* technique (Nagorcka, personal communication).

The potential of dietary manipulations to concentrate peak HI into a few hours post-feeding appears to be high. If HI_g comprises 44% of total heat production for cattle in which ME intake was 2.5 times maintenance requirements (data for Angus cattle, Ferrell and Jenkins 1998), and the feed can be 90% fermented in 6 hours (see Figure 13), then there is potential for approximately 70% of total metabolic heat to be evolved in 12 hours, providing the lag time for nutrient transactions in body tissues is small.

When management of feeding regime of high concentrate diets is seen to be desirable from the viewpoint of synchrony of HI with lower EHL, several other factors need consideration. Firstly, when frequency of meal numbers per day is reduced, there is likely to be lower minimum pH values (Mills et al. 1999), which may entail increased risks associated with fermentative acidosis. Damage to the rumen wall is likely to reduce blood flow and VFA absorption. In addition, increases in VFA absorption from the gut will impact on acid-base and electrolyte balances, and may lead to increased degradation of amino acids to provide ammonium ions, or lead to a loss of phosphorus from the body (Rowe and Channon 2001).

3.5 Conclusions

The limited evidence and simulations discussed above suggest that it may be possible to manipulate the postprandial pattern of heat production in feedlot cattle if the fermentation characteristics of the various dietary components are known. However, the potential of such dietary manipulations to provide management options to accelerate heat loss in the night-time will depend

on the post-feeding pattern of HI and the degree to which these fluctuations in HI can be exacerbated or dampened. It is obvious that an understanding of the time-course of heat production resulting from metabolism in the rumen, splanchnic bed and peripheral tissues will aid such manipulation. The existence and quantitative contribution of an immediate (central nervous system controlled) production of heat after feeding, if significant, may reduce the value of a tactical feeding option. Such studies need not encompass detailed blood flow measurements, but should include assessment of changes in site of starch digestion (rumen vs. small intestine) to allow interpretation. The technique of measuring O₂ consumption as an index of heat production has been applied to non-ruminant animals to describe the post-feeding time course of heat generation, however data for cattle are few. For individual cattle, heart rate can provide a proxy measurement for O₂ consumption (Brosh et al. 1998b) and therefore HI, but trained animals are required before calibration is done (Johnson et al. 2003). Between-animal variations in the relationship of heart rate with O₂ consumption preclude the application of a general equation predicting heat production from heart rate in a feedlot situation, however the technique would be of value in the scientific studies recommended in section 7 of this report.

Manipulation of feeding patterns to shift the peak of dietary-induced thermogenesis away from the hottest hours of the day towards the cooler night hours, when dissipation of heat load is higher, promises to be a cheap and effective tactic that could find acceptance in industry within the constraints of labour availability. Formulation of diets containing ruminally-digested components that are rapidly fermented, may allow the timing of peak fermentation heat to more precisely coincide with the coolest time of night. Because the heat load from tissue metabolism is larger than that from fermentation, then the timing of release of heat from intestinal absorption and metabolism will be critical. Close coincidence of evolution of metabolic and fermentation heat would aid application of a tactical feeding strategy. Even if the coincidence is poor, it is possible that temporal manipulation of the HI due to fermentation, despite it comprising only <10% of total HI, may still provide a useful outcome.

Appropriate experimentation is required to assess whether available data on rates of digestion of dietary components and assumptions about passage rates from the rumen can be used to adequately predict HI patterns, especially under EHL conditions which is known to affect gut motility. Discrimination between direct effects of EHL on gut motility and indirect effects due to intake changes and changes in nutrient supply to rumen microbes is desirable. Description of timing and origin of HI in respect to site and quantity of absorption of nutrients is central to understanding and to appropriate management of the endogenous component of the total heat load in cattle.

Research is warranted to determine interactions of meal quantity and feeding times with temperature, humidity, stocking density and feed and water trough spacings. The exact timing to facilitate most effective heat loss, e.g. where the peak of endogenous heat production should be planned relative to the coolest time of night, requires experimentation and it may vary according with the degree of night-time cooling. The role of breed differences in feeding behaviour may be pertinent.

4 Continuous monitoring of heat load during EHL

4.1 Data loggers

As discussed above (section 1.1), the accuracy and predictive value of THI indices may fall short of that required to assess confidently the degree of EHL on cattle in feedlots, especially where there are differences in microclimate within the feedlot. In order to judge when emergency measures are warranted, a device that accurately reflects the total heat load on the animal on a short-term basis during an impending heat wave is needed. Data loggers have been used with success to obtain continuous records of body temperature (Hahn 1999), however, animals equipped with these devices have to be restrained in order to download the data. This equipment is thus more suitable for research purposes than for commercial application. A more appropriate device for use in commercial feedlots has recently been developed (Sievers et al. 2004). This system consists of a small temperature probe that is dosed into the rumen and sends a continuous stream of data via radio-telemetry to a collar on the animal from which it is transmitted to a remote receiver connected to a computer. Continuous temperature readings in real time can be obtained from ten animals simultaneously. An early version of the system has been subjected to independent evaluation (Brown-Brandl et al. 2001) with favourable results, and it appears that rumen temperatures are as useful as tympanic or vaginal temperatures for assessment of effects of EHL (Colgan and Mader 2005).

4.2 Conclusions

Weather-based indices currently in use for prediction of severity of EHL events for feedlot animals, while subject to refinement, provide only a general indicator of heat-stress potential, and cannot account for differences in microclimate across the feedlot. The use of telemetric body temperature monitoring systems for tactical decision-making purposes in the feedlot environment offers several possibilities. The value is evident of a system in which body temperatures of a number of sentinel animals in various pens situated throughout the feedlot are displayed on a computer located in the supervisor's office and which is programmed to sound an alarm when a predefined limit is exceeded. Such systems would also be of value in testing strategies developed under simulated environmental conditions. Research aimed at assessing the utility and cost-effectiveness of the current commercially available telemetric temperature system under local feedlot conditions is warranted, and assessment of devices should also be included in more detailed experiments conducted in climate chambers.

5 Increasing tolerance to hyperthermia

While tactics such as that discussed above can assist in reactive mitigation of losses during heat waves, the issue of whether additional proactive measures can be instituted to induce greater tolerance against hyperthermia also deserves consideration. In order to evaluate strategies aimed at increasing thermotolerance, it is first necessary to discuss the sequence of events that precedes death from hyperthermia.

5.1 The pathophysiology of hyperthermia

If adaptation to stress results in decline in voluntary intake, it would be expected that there would follow changes in partitioning of nutrients according to priorities in intermediary metabolism. To minimise HI in this adaptive situation, it would be desirable to maintain or increase direct incorporation of nutrients into protein and fat and reduce turnover from those pools. It is known that direct incorporation, rather than de novo synthesis, is the preferred pathway for amino acids and for > 70% of fatty acids for fat synthesis.

However, stress resulting from increasing failure to dissipate EHL will involve the endocrine, immune and central nervous systems, in which communication between the three systems is mediated by neurotransmitters, hormones, cytokines and receptors (Husband 1995). As a result of stress, nutrients are directed away from growth processes to metabolic processes, which support the immunological response. Cytokines directly act on skeletal muscle, fat tissue, and liver and indirectly alter circulating hormone levels (Johnson 1997). The net result is increased fat deposition but reduced growth rate through increased protein turnover (Annison and Bryden 1999). However, these responses will also be affected by changes in voluntary feed intake. During feed restriction, lactate assumes a major role in gluconeogenesis. In the study of Lomax and Baird (1983) fasting for 1 day induced the following changes across the splanchnic bed: major declines in output of VFAs, increased uptake of lactate, and a 40% decline in O₂ use.

Exposure to EHL may also have implications for meat quality. Scanga et al. (1998) found increased incidence (by 85% for heifers, P<0.05) of dark cutters when average maximum temperature was >35°C, one to two days before slaughter, compared to <35 °C. Mitlöhner et al. (2002) found that there were significantly fewer dark-cutting heifers from shaded pens vs. non-shaded pens, but the authors could not attribute the effect entirely to EHL, as the shaded group engaged in less agonistic behaviour, which is also associated with dark-cutting meat.

Current thinking places membrane permeability of the gut at the centre of events leading to death as a consequence of hyperthermia (Lambert et al. 2002). Initially, exposure to a high temperature results in redirection of blood flow from the body core to the periphery; this increases the temperature gradient in the body allowing greater and more efficient dissipation of core heat to the environment via sweating. In order to defend normal systemic blood pressure, the increased blood flow to the skin is balanced by attenuated blood flow to the splanchnic bed. During the latter stages of hyperthermia, a sudden increase in splanchnic blood flow precipitates a drastic fall in blood pressure and circulatory collapse ensues. The consequent drop in blood supply to the brain results in the secretion of a wide range of neuropeptides and neuronal injury (Gisolfi and Mora 2000).

Although the exact reason for the sudden increase in splanchnic blood flow is not entirely clear, reviews by Jessen (2001) and Gisolfi and Mora (2000) point to a considerable body of evidence to substantiate the theory that damage to the gut wall plays a pivotal role. According to this hypothesis, the reduction in blood flow to the gut (ischemia) that accompanies exposure to heat impairs the barrier function of the gut. One of the primary consequences of ischemia is uncoupled oxidative phosphorylation and intracellular depletion of ATP; consequently, the vital role of ATP-dependent ion-pumping mechanisms is impaired, leading to imbalanced cellular osmotic pressure, increased cytosolic Ca⁺⁺ concentrations, generation of reactive O₂ species and loss of control of tight junctions between cells. The gut (especially the rumen) contains large amounts of endotoxins, lipopolysaccharides (LPS), derived from the cell walls of gram-negative bacteria. Ingress of LPS via the open junctions between cells lining the gut elicits the secretion of a variety of cytokines from

leucocytes resident between gut epithelial cells resulting in an acute phase immune response. As local vasodilation is characteristic of the immune response, this sequence of events may explain the sudden increase in vascular perfusion of the splanchnic bed that precedes circulatory shock in hyperthermia.

There are several lines of evidence that support the notion that gut integrity plays a critical role in the aetiology of hyperthermia. Elevated concentrations of LPS have been found in the portal vein of heat stressed monkeys, in heatstroke victims upon admission to hospital and in marathon runners who collapsed during competition (Gisolfi and Mora 2000; Jessen 2001). The first study to document pathophysiological changes over time during hyperthermia has been published (Eshel et al. 2001). In this study, anaesthetised dogs and monkeys were subjected to EHL to a degree sufficient to raise body temperature to 42 °C for 60 minutes or until cardiac arrest occurred. In animals that died during hyperthermia the main necropsy findings were gut oedema and minor petechial haemorrhages. Animals that were successfully resuscitated following hyperthermia began to show signs of secondary deterioration at times ranging from 4 to 18 hours after resuscitation and return to normothermia. These involved an abrupt drop in blood pressure followed 1 to 2 hours later by massive haemorrhages from the rectum and then cardiac arrest. Necropsies showed large amounts of blood in the gut and diffuse petechial haemorrhages in all viscera. It was suggested that the pattern of continuing deterioration even after return to normothermia indicates that tissue injury following hyperthermia continues even after cooling to normal body temperature. They concluded that the gut oedema found in animals that died during hyperthermia reflected the effects of splanchnic ischemia, and the intestinal haemorrhages in animals that survived for longer periods reflected the irreversible effects of cytokine activation and endotoxemia.

5.2 Acidosis

The important protective role played by the gut lining has significant implications for feedlot nutrition, as the rumen bacteria are a potential source of endotoxin and have been shown to be capable of inducing endotoxic shock (Nagaraja et al. 1979). Considerable quantities of endotoxin accumulate in the rumen under conditions conducive to the development of acidosis (Huber 1976). Rumen acidosis characteristic of many high-concentrate feedlot diets is known to compromise the integrity of rumen epithelium. Ingestion of concentrate-based diets can double the osmolality of rumen digesta, leading to a rise in the osmotic pressure gradient between the enteric circulation and the rumen contents; this results in rapid movement of water from the blood across the rumen epithelium, causing epithelial cells to separate from the basement membrane. The resulting necrosis affords endotoxins and bacteria entry to the body (Nagaraja and Chengappa 1998; Owens et al. 1998).

The high incidence of liver abscesses among feedlot animals (22%; Smith 1998), which is a direct result of the entry of endotoxins and bacteria to the circulation through a damaged rumen epithelial lining (Owens et al. 1998) suggests that these animals would be especially vulnerable to hyperthermia. In this regard, it is pertinent that “documentation linking the incidence of liver abscesses to feeding practices such as type of step-up is lacking” (Nagaraja and Chengappa 1998). It is also worth noting that Elam (1976) commented that “The highest incidence of acidosis and similar problems is observed in feedlots during the warmer seasons, and this is especially high during the summer months”. Similar peaks of feedlot deaths related to digestive causes during the summer months have also been reported by Miles et al. (1998). Research aimed at determining the link between acidosis and heat stress is clearly warranted.

5.3 Probiotics

The observation that reduction of gut flora in rabbits and dogs by administration of antibiotics or lavage attenuated the rise in body temperature during heat exposure and increased survival rate (Jessen 2001) may represent an opportunity that could be exploited to reduce the incidence of heat-related deaths in feedlots. Probiotic feed additives derived from fungal cultures are marketed as production-enhancing agents to the livestock industry, and have reportedly affected tolerance of dairy cows to EHL. Huber et al. (1994) reviewed trials in which the effects of one of these products (an *Aspergillus oryzae* extract) on rectal temperature and milk yield were examined. Body temperature and respiration rate was decreased by the fungal extract in several trials, and milk yield was increased in some, but not all trials. Although they concluded that the reason for these effects was unclear, the observation that temperature and respiration rates of probiotic-treated animals decreased during hot, but not cold weather is worthy of note. It is possible that the greater effects of probiotics during hot weather are linked with enhanced integrity of the gut wall. This possibility has not been investigated and deserves further consideration. It has been proposed that some yeast cultures can provide partial protection against sub-clinical acidosis (Sauvant et al. 2004), thus encouraging resilience of the rumen ecosystem during exposure to EHL. Probiotics might reduce the risk of subacute acidosis, but the effect is dependent on feeding an appropriate microbial species e.g. *Lactobacillus acidophilus* (Krehbiel et al. 2003).

5.4 Betaine

Betaine is one of several organic osmolytes used by mammalian cells to maintain osmotic equilibrium. Low molecular weight osmolytes such as betaine do not interfere with the normal function of intracellular enzymes and are selectively absorbed or secreted by a wide variety of cells, including the cells of the gut (Kettunen et al., 2001a) in response to osmotic challenges. *In vitro* studies using gut tissues from poultry chicks supplemented with betaine showed that the treatment altered the movement of water across the intestinal epithelium during hyperosmotic challenges (Kettunen et al. 2001c). Histological evidence from broiler chicks shows that the crypt-villus ratio of the small intestine was altered by dietary betaine supplementation, and it was concluded that betaine supplementation stabilizes mucosal structure in healthy birds and also alleviates parasite infection when challenged with coccidia (Kettunen et al. 2001b).

Recently, Moeckel et al. (2002) have shown large effects of betaine on ion-pump activity in membranes of red blood cells: Ca^{++} -ATPase activity was inhibited by 73% and $\text{Na}^{+}/\text{K}^{+}$ -ATPase was decreased by 64%. Although the exact mechanism is unclear, it is likely that inhibition of gut ion-pump activity of this magnitude would effect a substantial reduction in the HI associated with the gut. Research on the effects of betaine supplementation in ruminant diets is limited and equivocal. In experiments with lambs fed a finishing diet, betaine had no effect on mass gain but decreased fat deposition (Fernández et al. 1998; Fernández et al. 2000), but carcass fat and marbling score were increased in trials with feedlot cattle (Loest et al. 2002). None of these studies took cognisance of environmental temperatures or the potential osmotic effects of betaine; further research is needed to determine whether betaine can be used to confer thermotolerance on feedlot cattle.

5.5 Fatty acids

The use of protected fats to alter cell membrane function may offer novel opportunities for enhancing resistance to heat stress. Ion transport systems in cell membranes play a key role in the maintenance of ion gradients within defined limits, and are essential for normal cell functioning. It is estimated that the Na^+, K^+ -ATPase system generates 20-40% of the total amount of heat produced by mammals (Kelly and McBride 1990). It accounts for 17-61% of total heat production by the gut, 18-51% of that of the liver and 18-45% of that of skeletal muscle (Kelly and McBride 1990). The high activity and heat production associated with this system in mammals is considered to be one of the primary features that distinguishes them from reptiles, and it is thought that this is due to the several-fold greater ion permeability of mammalian cell membranes (Else and Hulbert 1987). Because ions enter the cell more readily, more heat is generated in maintaining transmembrane ion gradients. Membrane permeability and Na^+, K^+ -ATPase activity are, in turn, regulated to a large extent by the fatty acid composition of the cell membrane (Haines 2001). Although temperature-induced changes in body fat composition of reptiles and mammals such as sheep (Marchello et al. 1967) and cattle (Kelly et al. 2001) have long been interpreted in the context of adaptive thermogenesis (Gisolfi and Mora 2000), the potential of manipulating membrane composition in order to change thermotolerance has only recently been investigated.

Schmeeda et al. (2002) examined the relationships between the fatty acid composition of cell membranes and heat stress in rats. They observed that heat acclimation and acute heat stress resulted in substantial increases in the polyunsaturated fatty acid content of tissues, in particular the content of docosahexaenoic acid (22:6). They then used liposomes containing phosphatidylcholine to modify membrane lipid composition and demonstrated that this treatment conferred a 38% increase in endurance to thermal stress. This is a substantial increase, equivalent to that occasioned by a 30-day heat acclimation period. Although the exact mechanism responsible for this effect is not clear, they speculated that it might be associated with an increased glandular capacity to secrete water. If so, this could explain the increased evaporative water loss that accompanied elevated intakes of lipid in the experiment of O'Kelly (1987). Studies using fish and canola oils that have been protected from rumen microbial attack show that the fatty acid composition of phosphatidylcholine in skeletal muscle membranes in cattle can be extensively manipulated by dietary means (Scott and Ashes 1993), but as far as can be ascertained, the possible thermoregulatory implications of this have not been explored. Manipulation of membrane fatty acid composition would have a substantial impact on the feedlot industry if tolerance to heat load by could be increased by a factor as large as that reported for rats (38%). Research aimed at developing strategies to confer similar protection on feedlot cattle should be further considered, given that products capable of changing membrane lipid composition in cattle are currently available. Lipid from marine organisms is the principal source of C22 fatty acid; other rumen-inert lipid products on the market provide mainly C16 and C18 fatty acids (Loften and Cornelius 2004).

5.6 Heat Shock Proteins

Exposure to heat stimulates the intracellular production of heat shock proteins (Moseley 1997). The 70-kDa heat shock protein (HSP70) binds to denatured proteins and restores functionality by folding them back to their normal tertiary structures. The protective effect of HSP70 was demonstrated by Moseley (1994) who was able to attenuate the temperature-induced increase in membrane permeability of an epithelial cell culture by allowing them to accumulate HSP70 after prior exposure to short periods of intense thermal stress. It has been proposed that the development of strategies aimed at promoting the accumulation of HSP70 under normothermic conditions may enable humans to expand their normal 4 °C thermoregulatory zone to include temperatures above 41 °C or improve

the success of organ and tissue transplantation (Gisolfi and Mora 2000). Recently Yavelsky et al (2004) suggested that HSP90 (the 90-kDa protein) played a pivotal role in the cell response to hyperthermia. Advances in this rapidly expanding field of research may well have implications for thermotolerance in livestock species.

5.7 Conclusions

Research aimed at quantifying the potential contribution of gut lining integrity to thermotolerance in cattle warrants attention in the light of the fact that there is abundant evidence that many feedlot diets result in gross damage to the rumen epithelium. If confirmed, the adaptation of existing practices relating to feeding strategies, diets, buffers and probiotics would represent an acceptable and cost effective strategy that could have a considerable impact on welfare concerns relating to the feedlot and live export industries. Research aimed at establishing whether the protective effects of betaine observed in other species are applicable to cattle should receive priority.

6 Summary of findings and R&D opportunities

6.1 Gaps in current scientific knowledge

Gaps in current scientific knowledge identified in this review are:

- definition of physiological responses to increasing duration of hyperthermia.
- the degree to which associative effects arising from co-feeding of diet components, results in poor prediction of HI of the total diet when using feeding standards with feedlot diets.
- the paucity of data in ruminants describing the source (fermentative, metabolic) of HI and its time-course following feeding.
- the uncertainty concerning the degree to which available data can be used to predict the time-course of HI from feed digestion characteristics, and the influence of site of digestion.
- the precision of AUSBEEF predictions of the time-course of HI.
- the affect of exposure of cattle to EHL, on site of digestion and subsequently on time-course of HI.
- the degree of night-time cooling necessary before there is an advantage in tactical changes in time of feeding to enhance heat dissipation from feedlot cattle.
- the role of gut integrity and acidosis in the causes of hyperthermia; definition of the benefits of probiotics and betaine in maintaining gut integrity.
- the role of protected fats in altering membrane function, and of heat shock proteins in increasing the resistance of cattle to hyperthermia.

6.2 Refinement of a risk assessment model for heat load in cattle

One of the main recommendations of a previous review of heat load in feedlot cattle (Sparke et al. 2001) entailed the development of an 'Excessive Heat Load Environment Index' that was proposed to be coupled to an 'Excessive Heat Load Weather Alert Forecast Service'. The development of such a system could have a substantial impact on industry, and is probably no coincidence that the live export industry has interests in research designed to develop a heat stress risk management model for cattle on ships (Maunsell Australia Ltd 2003).

For both the live export industry and the feedlot industry, the development of an efficacious and versatile risk assessment system, and hence its uptake by industry, will be constrained by lack of critical data, including the role and time course of acclimation of animals to EHL and the interaction with diet composition.

Research is warranted on definition of limits for the extent and duration of exposure of cattle to hyperthermia (i.e. an elevated body temperature) in terms of:

- acclimation to environmental conditions.
- feed intake and the diurnal pattern of feed intake.
- growth rate during heat exposure and impact of diurnal patterns of EHL.
- mortality.
- metabolic disturbance.
- morbidity and susceptibility to production diseases post EHL exposure.
- tissue injury, if it affects product quality.
- behaviour and other indices of animal welfare.

6.3 Discrimination of components of HI & effect of feeding times

The main aim of this review was to focus on possibilities of manipulating HI using diet formulation or feeding regimes which could minimise heat generation and/or to maximise heat dissipation. The scientific evidence documented above shows that the heat of fermentation in the ruminant gastrointestinal tract contributes less than 20% of the total heat generated by digestion and metabolism of feed. Nevertheless, control of HI may be best achieved by changes in production of fermentation heat through dietary means such as by changes in grain type or processing method to alter the balance of starch digestion in the rumen and intestines. It is unlikely in practice that fermentation heat can be reduced by more than 25%, which equates to only to 5% of total HI. There is a limit to which dietary carbohydrate can be substituted by lipid. If 5% of inert rumen lipid can be included in the diet for several days before the onset of an EHL, then the resultant maximum reduction of HI should be of the order of 5%. We could not readily determine the extent to which the feedlot industry employs nutritional tactics to ameliorate the effects of EHL, but we suspect it is minimal.

As part of an experimental approach to the problem, a few methodological issues need solution. Pertinent issues include:

- In conditions where cattle are unable to further increase heat dissipation to the environment, does the change in post-feeding HI precede or coincide with, changes in intra-ruminal or tympanic temperatures in a predictable manner? Related to this question is the cause of the 2-3 hr delay in increases in body temperature following an increase in EHL (see Sparke et al 2001).
- Are whole-animal techniques using respiration rate, heart rate, core body temperature sufficiently sensitive to monitor changes in HI? Does measurement of HI from gas exchange (by itself or by using heart rate as a proxy measurement) add unique beneficial information not provided by conventional measurements of body temperature, respiration and heart rates, in evaluation of time course of HI?
- Can the heat of fermentation be experimentally distinguished from metabolic heat arising from tissues and is discrimination between these heat sources needed for development of tactical management techniques for the feedlot operator?
- Is the pattern (extent, duration) of post-feeding HI for a given diet predictable by current methodology (e.g. using rumen passage data and rate of fermentation from nylon bag or in vitro measurements) to assess digestion patterns? Is the prediction reliable in the face of imposed EHL?
- Is the act of eating associated with a HI component that is not explicable in terms of metabolism of ingested nutrients (i.e., is there a central nervous control of a portion of the HI) If so, how large is this HI component and does it vary with meal size?

Following validation of the above aspects of methodology and definition of the time course of response of HI, the following can be addressed:

- Does the period of prior adaptation to high EHL affect the HI response (amount or time-course)?
- Can a practical diet formulated by inclusion of rumen-inert fats, modification of grain processing or other dietary manipulation, result in lowered daily HI and/or a time profile of HI amenable to enhanced heat loss through appropriate feeding management?
- If there are benefits to changes in diet composition or of feeding time, how long is required for maximal benefits to be seen, and what degree of night-time cooling is required?
- Can AUSBEEF or other ruminant models satisfactorily predict HI patterns?

6.4 Potential of feed additives for hyperthermic cattle

Several compounds exist that have the potential to confer protection against exposure to hyperthermia. Development of such compounds may find greater acceptance with the feedlot industry than more invasive and disrupting practices that entail restriction of the amount fed, inclusion of large quantities of roughage in the diet or feeding at night. Potential candidates that may confer resilience to hyperthermia that deserve specific investigation are:

- Rumen inert lipids: Research on the use of rumen inert lipids in feedlot diets should be extended to determine whether the 38% increase in tolerance to heat that was observed in rats following manipulation of membrane fatty acid composition is applicable to cattle.
- Betaine research aimed at establishing whether the protective effects of betaine observed in other species are applicable to cattle is warranted.

The industry is well placed to evaluate such feed additives in practical conditions.

6.5 Evaluation of management aids

Telemetric body temperature monitoring systems may represent a useful and accurate index of hyperthermia for tactical decision-making purposes in the feedlot environment, and would complement the existing panting score system. Sentinel animals fitted with telemetric devices distributed throughout feedlots could provide immediate warning of EHL. Research aimed at assessing the utility and cost-effectiveness of commercially available telemetric temperature systems for use as a tactical decision-making tool by feedlot operators is warranted. In addition to its utility to feedlot owners, such a system would be of great assistance in enabling research to be carried out under practical conditions (Lefcourt and Adams 1996). Rumen temperatures appear to be a good proxy for body temperatures as measured in the ear and vagina (Colgan and Mader 2005), and intra-ruminal devices can be remotely interrogated without interference to the cattle following insertion of the device by balling gun.

It appears that validating this technology is best achieved in a feedlot setting.

7 Recommended research and development plan.

The following recommendations are made with the premise that feedlot operators would prefer tactical dietary-related technologies that can be employed to counter threatened high heat loads caused by adverse weather conditions, rather than invest in the more costly option of long-term conditioning of cattle by dietary supplementation to be more tolerant of exposure to extreme heat, which may occur unpredictably and infrequently.

Research on shorter-term modification of diets and changes in feeding times seems likely to provide an appropriate diet-based methodology capable of reducing the effects of EHL on feedlot animals, and can be considered to encompass two tactics.

The first tactic of selecting diet components which will potentially result in reduction of total HI, whilst minimising disruption to growth rate, is soundly based scientifically, but the variable results reported in the literature may indicate that meaningful HI reductions may be difficult to demonstrate without

conducting controlled experiments using a controlled climate facility. Incorporation of compounds such as free fatty acids as a supplemental rumen-inert lipid source may require a longer adaptation period than is feasible in the face of a threatened EHL event. On the other hand, a change in processing method of grain may be readily made. These response times require definition. The required experimental techniques are established.

It is **recommended** that a trial be commissioned, using an appropriate commercially-available rumen-inert lipid (hydrolysed pure fatty acids) added to a feedlot ration under controlled conditions to assess that product under thermoneutral and EHL conditions. A significant fast reduction of HI of the order of 5% would be required before justifying the extension of the research to consideration of adaptation time required for the full benefit to be achieved, and lipid by diet interactions.

The second tactic of organising feeding time so that the heat generated from the diet, which occurs several hours post-feeding, coincides with the coolest part of the day when the rate of radiative dissipation of heat stored in the animal is maximal, are more complex. The success of this tactic will depend on the time profile of generation of diet-derived heat and the potential of matching this with the decline of ambient temperatures during the night, and the degree of night-time relief of EHL. Such studies are therefore best done in a climate chamber.

It is **recommended** that research be commissioned to characterise the time profiles of HI of some typical feedlot diets, containing a number of appropriate grains, that theoretically differ in rates of rumen fermentation determined with currently available techniques. The experiments would determine whether the measured HI matched the HI profile predicted from fermentation characteristics in cattle in both thermoneutral and EHL conditions, and whether the precision of prediction during EHL was markedly affected by changes of ruminal rate of passage of starch diet components, or about lag times attributable to metabolism of absorbed nutrients in the tissues. Data for fermentation rates of Australian grain types and the effect of processing, have already been collated (Premium Grains for Livestock Program), and they may provide a framework for this research, not only in respect to selection of experimental diets, but also for use in formulation of rations to relieve heat stress. Data on rates of passage are also required for calculation of amounts of starch being digested in the rumen versus intestines. The experiments should include the effects of grain processing on HI patterns, and the role of adaptation of cattle to EHL. Techniques are currently available for animal trials, pending resolution of methodological issues noted above, although methodology for passage rate is indirect and not sensitive to within-day fluctuations of rumen function as might be experienced during EHL. The measured patterns of HI would be used to test against model-based predictions from AUSBEEF.

Because feed intake occurs over a number of hours, and feeding bunks may need to be filled on several occasions in the day, a **second phase** of experimentation may be required to consider options in allocation of the ration between morning and evening feeding, and the degree of night-time cooling required to produce a worthwhile mitigation of heat load at night while maintaining a satisfactory level of energy intake.

During this experimentation, it is recommended that telemetric devices be used to log core temperatures, with the aim to assess these devices for feedlot use.

Industry outcomes of this research would be:

- Evaluation of the use of hydrolysed fatty acids (rumen inert lipid) to reduce HI of a typical feedlot diet.
- Evaluation of the utility of available data on dietary degradation of starch in the rumen or of rumen models (e.g. AUSBEEF) in prediction of amount and timing of heat profiles.
- Clarification of whether and when changes of feeding time and amounts lead to benefits in reduced maximum or average heat load.
- Data on what night-time relief of EHL is needed for tactics to be useful.
- The role of adaptation to EHL on the HI response.
- Assessment of use of sentinel animals as a system to warn of adverse heat loads.

8 References

Ames DR, Brink DR, Willms CL (1980) Adjusting protein in feedlot diets during thermal stress. *J. Anim. Sci.* 50, 1-6.

Annisson EF, Bryden WL (1999). Perspectives on ruminant nutrition and metabolism. II Metabolism in ruminant tissues. *Nutr. Res. Rev.* 12, 147-177.

Arieli A (1994) Effect of whole cottonseed feeding on partitioning of energy and nitrogen balance in sheep exposed to thermoneutral and high environmental temperatures. 'Energy Metabolism of Farm Animals; proceedings of the 13th symposium' Eds. PW Moe, HF Tyrell, PJ Reynolds (Rowman and Littlefield, Totawa New Jersey). pp 355-357.

Arieli A, Rubinstein A, Moallem U, Aharoni Y, Halachmi I (2004). The effect of non forage fibre on energy balance and feeding behavior of heat stressed cows. *J. Anim. Feed Sci.* 13(Suppl 1)S615-618.

Armstrong DG, Blaxter KL (1984) Maintenance requirement: Implications for its use in feed evaluation systems. In 'Herbivore Nutrition in the Subtropics and Tropics' Eds. FMC Gilchrist, RI Mackie (The Science Press Pty Ltd: Craighall, South Africa) pp 631-647.

Baldwin RL, France J, Gill M (1987) Metabolism of the lactating cow. I. Animal elements of a mechanistic model. *J. Dairy Res.* 54, 77-105.

Baldwin RL, Smith NE, Taylor J, Sharp M (1980) Manipulating metabolic parameters to improve growth rate and milk secretion. *J. Anim. Sci.* 51, 1416-1428.

Beatty D, Barnes A, Petick DW, Taylor E, Dunshea FR (2004). *Bos indicus* cattle can maintain feed intake and fat reserves in response to heat stress better than *Bos taurus* cattle. *J Anim. Food Sci.* 13 (Suppl 1) 619-622.

Beede DK, Collier RJ (1986) Potential nutritional strategies for intensively managed cattle during thermal stress. *J. Anim. Sci.* 62, 543-554.

Beever DE (1993) Rumen function. In 'Quantitative Aspects of Ruminant Digestion and Metabolism' Eds. JM Forbes & FJ Forbes (CAB International: Wallingford, UK) pp 188-215.

Blaak EE, Saris WHM (1995) Health aspects of various digestible carbohydrates. *Nutr. Res.* 15, 1547-1573.

Blackshaw JK, Blackshaw AW (1994) Heat stress in cattle and the effect of shade on production and behaviour: a review. *Aust. J Exp. Agric.* 34, 285-295.

Blaxter KL (1962) 'The Energy Metabolism of Ruminants.' (Hutchinson Scientific and Technical: London).

Blaxter KL (1989) 'Energy Metabolism in Animals and Man' (Cambridge University Press: Sydney).

Brosh A, Aharoni Y, Degen AA, Wright D, Young BA (1998a) Effects of solar radiation, dietary energy, and time of feeding on thermoregulatory responses and energy balance in cattle in a hot environment. *J. Anim. Sci.* 76, 2671-2677.

Brosh A, Aharoni Y, Degen AA, Wright D, Young BA (1998b) Estimation of energy expenditure by heart rate measurements in cattle maintained under different conditions. *J. Anim. Sci.* 76, 3054-3064.

Brown-Brandl TM, Yanagi T, Xin H, Gates RS, Bucklin R, Ross G (2001) Telemetry system for measuring core body temperature in livestock and poultry. *Amer. Soc. Agric. Engin.* 01-4031, 1-14.

Channon AF, Rowe JB (2004) Manipulating gastrointestinal starch digestion to improve the efficiency of feed utilisation. *Aust. J. Exp. Agric.* 44, 475-482.

Colgan SL, Mader TL (2005) Effect of roughage and high energy diets on body temperature. 2005 Nebraska Beef Report, pp73-75.

Collier RJ, Beede DK, Thatcher WW, Israel LA, Wilcox CJ (1982) Influences of environment and its modification on dairy animal health and production. *J. Dairy Sci.* 65, 2213-2227.

Cronje PB, Nolan JV, Leng RA (1991) Acetate clearance rate as a potential index of the availability of glucogenic precursors in ruminants fed on roughage-based diets. *Br. J. Nutr.* 66, 301-312.

Czerkawski JW (1986) 'An Introduction to Rumen Studies' (Pergamon Press: Oxford, UK).

Davis MS, Mader T (2002) Effect of altered feeding and sprinkling on performance and body temperature of steers finished in summer. 2002 Nebraska Beef Report pp 61-65.

Davis MS, Mader T, Holt S, Cerkoney W (2001) Effects of feeding regimen on performance, behaviour and body temperature of feedlot steers. 2001 Nebraska Beef Report pp 69-73.

Davis MS, Mader TL, Holt SM, Parkhurst AM (2003) Strategies to reduce feedlot cattle heat stress: Effects on tympanic temperature. *J. Anim. Sci.* 81, 649-661.

Derno M, Klein M, Lohrke B, Matthes, H-D, Jentsch W (2001). Short time response in the metabolic rate to daily changes of energy level and ambient temperature in young bulls. In 'Energy Metabolism in Animals' Eds. Chwalibog A, Jakobsen K (Wageningen Pers, Wageningen Netherlands) pp 129-132.

Drackley JK, Cicela TM, LaCount DW (2003) Responses of primiparous and multiparous cows to additional energy from fat or concentrate during summer. *J. Dairy Sci.* 86, 1306-1314.

Elam CJ (1976) Acidosis in feedlot cattle: practical observations. *J. Anim. Sci.* 43, 898-901.

Else PL, Hulbert AJ (1987) Evolution of mammalian endothermic metabolism: "leaky" membranes as a source of heat. *Am. J. Physiol.* 253, R1-7.

Eshel GM, Safar P, Stezoski W (2001) The role of the gut in the pathogenesis of death due to hyperthermia. *Am. J. Forensic Med. Pathol.* 22, 100-104.

Fernández C, Gallego L, Lopez-Bote CJ (1998) Effect of betaine on fat content in growing lambs. *Anim. Feed Sci. Technol.* 73, 329-338.

Fernández C, López-Saez A, Gallego L, de la Fuente JM (2000) Effect of source of betaine on growth performance and carcass traits in lambs. *Anim. Feed Sci. Technol.* 86, 71-82.

Ferrell CL, Jenkins TG (1998) Body composition and energy utilization by steers of diverse genotypes fed a high-concentrate diet during the finishing period: II. Angus, Boran, Brahman, Hereford, and Tuli sires. *J. Anim. Sci.* 76, 647-657.

Finch VA (1984) Heat as a stress factor in herbivores under tropical conditions. In 'Herbivore Nutrition in the Subtropics and Tropics' Eds. FMC Gilchrist, RI Mackie (The Science Press: Craighall, South Africa) pp 89-105.

Finch VA (1986) Body temperature in beef cattle: Its control and relevance to production in the tropics. *J. Anim. Sci.* 62, 531-542.

Gaughan JB, Mader TL, Savage D, Young BA (1996) Effect of feeding regime on feed intake of cattle exposed to heat. *Proc. Aust. Soc. Anim. Prod.* 21, 223-226.

Gisolfi CV, Mora F (2000) 'The Hot Brain: Survival, Temperature, and the Human Body' (MIT Press: London, England).

Hahn GL (1999) Dynamic responses of cattle to thermal heat loads. *J. Anim. Sci.* 77 (suppl 2) / *J. Dairy Sci.* 82 (suppl 2), 10-20.

Haines TH (2001) Do sterols reduce proton and sodium leaks through lipid bilayers? *Prog. Lipid Res.* 40, 299-324.

Hocquette JF, Ortigues-Marty I, Pethick D, Herpin P, Fernandez X (1998) Nutritional and hormonal regulation of energy metabolism in skeletal muscles of meat-producing animals. *Livestock Prod. Sci.* 56, 115-143.

Holt SM, Gaughan JB, Mader TL (2004) Feeding strategies for grain-fed cattle in a hot environment. *Aust. J. Agric. Res.* 55, 719-725.

Huber JT, Higginbotham G, Gomez-Alarcon RA, Taylor RB, Chen KH, Chan SC, Wu Z (1994) Heat stress interactions with protein, supplemental fat, and fungal cultures. *J. Dairy Sci.* 77, 2080-2090.

Huber TL (1976) Physiological effects of acidosis on feedlot cattle. *J. Anim. Sci.* 43, 902-909.

Hunter RA, Sillence MN, Gazzola C, Spiers WG (1993) Increasing annual growth rates of cattle by reducing maintenance energy requirements. *Aust. J. Agric. Res.* 44, 579-595.

Huntington GB (1999). Nutrient metabolism by gastrointestinal tissues of herbivores. In 'Nutritional Ecology of Herbivores' (American Society of Animal Science: Soyoy, Illinois, USA) pp. 312-336.

Husband AJ (1995) The immune system and integrated homeostasis. *Immunol. Cell Biol.* 73, 377-382.

Illius AW, Jessop NS (1996) Metabolic constraints on voluntary intake in ruminants. *J. Anim. Sci.* 74, 3052-3062.

Jessen C (2001) 'Temperature Regulation in Humans and other Mammals' (Springer: New York).

Jessop NS (2000) Aspects of cellular energetics. In 'Farm Animal Metabolism and Nutrition'. Eds. JPF D'Mello (CAB International: Wallingford, UK) pp 149-160.

Johnson DE, Ferrell CL, Jenkins TG (2003). The history of energetic efficiency research: Where have we been and where are we going? *J. Anim. Sci.* 81(E. Suppl) E27-E38.

Johnson, RW (1997). Inhibition of growth by pro-inflammatory cytokines: an integrated view. *J. Anim. Sci.* 75:1244-1255.

Kelly JM, McBride BW (1990) The sodium pump and other mechanisms of thermogenesis in selected tissues. *Proc. Nutr. Soc.* 49, 185-202.

Kelly MJ, Tume RK, Newman SA, Thompson JM (2001) Environmental effects on the fatty acid composition of subcutaneous beef fat. *Aust. J. Exp. Agric.* 41, 1023-1031.

Kettunen H, Peuranen S, Tiihonen K (2001a) Betaine aids in the osmoregulation of duodenal epithelium of broiler chicks, and affects the movement of water across the small intestinal epithelium in vitro. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 129, 595-603.

Kettunen H, Peuranen S, Tiihonen K, Saarinen M (2001b) Intestinal uptake of betaine in vitro and the distribution of methyl groups from betaine, choline, and methionine in the body of broiler chicks. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 128, 269-278.

Kettunen H, Tiihonen K, Peuranen S, Saarinen MT, Remus JC (2001c) Dietary betaine accumulates in the liver and intestinal tissue and stabilizes the intestinal epithelial structure in healthy and coccidia-infected broiler chicks. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 130, 759-769.

Kim EJ, Dhanoa, MS, Gooden JM, Dawson, JM, Buttery PJ, Scollan ND (1998) The effect of dietary asynchrony on circadian changes in net nutrient fluxes across the portal-drained viscera in calves. In 'Energy Metabolism in Farm Animals' Eds. KJ McCracken, EF Unsworth, ARG Wylie (CAB International: Wallingford, UK) pp 15-18.

Kirchgessner M, Miller HL (1998) Dietary separation of protein and carbohydrate intake. In 'Energy Metabolism in Farm Animals' Eds. KJ McCracken, EF Unsworth, ARG Wylie (CAB International: Wallingford, UK) pp 135-142.

Knapp DM, Grummer RR (1991) response of lactating cows to fat supplementation during heat stress. *J. Dairy Sci.* 74, 2573-2579.

Kohn RA, Boston RC (2000) The role of thermodynamics in controlling rumen metabolism. In 'Modelling Nutrient Metabolism in Farm Animals' Eds. JP McNamara, J France, DE Beever (CAB International: Wallingford, UK) pp11-24.

- Kobayashi A, Osaka T, Inoue S, Kimura S (2001) Thermogenesis induced by intravenous infusion of hypertonic solutions in the rat. *J. Physiol.* 535, 601-610.
- Krehbiel CR, Rust SR, Zhang G, Gilliland SE (2003) Bacterial direct-fed microbials in ruminant diets: Performance response and mode of action. *J. Anim. Sci.* 81 (Suppl 2), E120-E132.
- Kreikemeier WM (2003) Growth promoting agents to reduce climate stress in feedlot cattle. PhD Dissertation. University of Nebraska.
- Lambert GP, Gisolfi CV, Berg DJ, Moseley PL, Oberley LW, Kregel KC (2002) Molecular Biology of Thermoregulation: Selected Contribution: Hyperthermia-induced intestinal permeability and the role of oxidative and nitrosative stress. *J. Appl. Physiol.* 92, 1750 – 1761.
- Lefcourt AM, Adams WR (1996) Radiotelemetry measurement of body temperatures of feedlot steers during summer. *J. Anim. Sci.* 74, 2633-2640.
- Leng RA (1990) Factors affecting the utilization of "poor quality" forages by ruminants particularly under tropical conditions. *Nutr. Res. Rev.* 3, 277-303.
- Lobley GE (1991) Organ and tissue metabolism: Present status and future trends. In 'Energy Metabolism of Farm Animals' Ed C Wenk, M Boessinger (ETH: Zurich) pp. 80-88.
- Loest CA, Titgemeyer EC, Drouillard JS, Coetzer CM, Hunter RD, Bindel DJ, Lambert BD (2002) Supplemental betaine and peroxide-treated feather meal for finishing cattle. *J. Anim. Sci.* 80, 2234-2240.
- Lofgreen GP, Otagaki KK (1960) The net energy of blackstrap molasses for fattening steers as determined by a comparative slaughter technique. *J. Anim. Sci.* 19, 392-403.
- Lofgreen GP, Givens RL, Morrison SR, Bond TE (1975) Effect of drinking water temperature on beef cattle performance. *J. Anim. Sci.* 40, 223-229.
- Loften JR, Cornelius SG (2004). Review: responses of supplementary dry, rumen-inert fat sources in lactating dairy cow diets. *Prof. Anim. Sci.* 20, 461-469.
- Lomax MA, Baird, GD (1983). Blood flow and nutrient exchange across the liver and gut of the dairy cow. *Br. J. Nutr.* 49, 481-496.
- Mader TL, Holt SM, Hahn GL, Davis MS, Spiers DE (2002) Feeding strategies for managing heat load in feedlot cattle. *J. Anim. Sci.* 80, 2373-2382.
- MAFF (1975). 'Energy Allowances and Feeding Systems for Ruminants' (Ministry of Agriculture, Fisheries and Food: London).
- Marchello JA, Cramer DA, Miller LG (1967) Effects of ambient temperature on certain ovine fat characteristics. *J. Anim. Sci.* 26, 294-297.
- Maunsell Australia Ltd (2003). Development of a heat stress risk management model. Meat and Livestock Australia. No. Live.116 ISBN 1740364430

Maust LE, McDowell RE, Hooven NW (1972) Effect of summer weather on performance of Holstein cows in three stages of lactation. *J. Dairy Sci.* 55, 1133-1139.

McDonald P, Edwards RA, Greenhalgh JFD (1981). 'Animal Nutrition' (Longman: London).

McLeod KR, Baldwin RL, Harmon, DL, Richards, CJ, Rumpler WV. (2001). Influence of ruminal and postruminal infusion on energy balance in growing steers. In 'Energy Metabolism in Farm Animals' Eds. A Chwalibog, K Jakobsen (Wageningen Pers, Wageningen Netherlands) pp 385-388.

Mitlöhner FM, Galyean ML, McGlone JJ (2002). Shade effects on performance, carcass traits, physiology, and behavior of heat-stressed feedlot heifers. *J. Anim. Sci.* 80, 2043-2050.

Miles DG, Hoffman BW, Rogers KC, Sears JE (1998) Diagnosis of digestive deaths. *J. Anim. Sci.* 76, 320-322.

Milgen van J, Noblet J, Dubois S. (2001) Dynamic aspects of gas exchange measurements. In 'Energy Metabolism in Farm Animals' Eds. A Chwalibog, K Jakobsen (Wageningen Pers, Wageningen Netherlands) pp 437- 440.

Mills JAN, France J, Dijkstra J. (1999) A review of starch digestion in the lactating dairy cow and proposals for a mechanistic model. I. Dietary starch characterisation and ruminal starch digestion. *J. Anim. Feed Sci.* 8, 291-340.

Mitlöhner FM, Galyean ML, McGlone JJ (2002). Shade effects on performance, carcass traits, physiology, and behavior of heat-stressed feedlot heifers. *J. Anim. Sci.* 80, 2043-2050.

Moe PW (1992) Comparative aspects of the concepts in animal and human energy metabolism. *Proc. Nutr. Soc.* 51, 109-115.

Moeckel GW, Shadman R, Fogel JM, Sadrzadeh SMH (2002) Organic osmolytes betaine, sorbitol and inositol are potent inhibitors of erythrocyte membrane ATPases. *Life Sciences* 71, 2413-2424.

Moseley PL (1994) Mechanisms of heat adaptation: thermotolerance and acclimatization. *J. Lab. Clin. Med.* 123, 48-52.

Moseley PL (1997) Heat shock proteins and heat adaptation of the whole organism *J. Appl. Physiol.* 83, 1413-1417

Moss, RJ, Buchanan IK, Casey AL, Matschoss AL, Martin PR (1998) Degradability of protein concentrates available in north Australia. *Anim. Prod. in Australia* 22, 340.

Nagaraja TG, Bartley EE, Anthony HD, Leipold HW, Fina LR (1979) Endotoxin shock in calves from intravenous injection of rumen bacterial endotoxin. *J. Anim. Sci.* 49, 567-582.

Nagaraja TG, Chengappa MM (1998) Liver abscesses in feedlot cattle: a review. *J. Anim. Sci.* 76, 287-298.

Nienaber JA, Hahn GL (1991) Associations among body temperature, eating and heat production in swine and cattle. In 'Energy Metabolism of Farm Animals' Eds. C Wenk, M Boessinger (ETH: Zurich) pp 458-461.

NRC (1981) 'Effect of Environment on Nutrient Requirements of Domestic Animals. (National Academy Press: Washington, D.C., USA)

NRC (1996) 'Nutrient Requirements of Beef Cattle' Seventh Edition (National Academy Press: Washington, D.C., USA).

O'Kelly JC (1987) Influence of dietary fat on some metabolic responses of cattle to hyperthermia induced by heat exposure. *Comp. Biochem. Physiol. A* 87, 677-682.

Ominski KH, Kennedy AD, Wittenberg KM, Moshtaghi Nia SA (2002) Physiological and production responses to feeding schedule in lactating dairy cows exposed to short-term, moderate heat stress. *J. Dairy Sci.* 85, 730-737.

Osaka T, Kobayashi A, Inoue S (2001) Thermogenesis induced by osmotic stimulation of the intestines in the rat. *J. Physiol.* 532, 261-269.

Ørskov ER, McDonald I (1979) Utilization of volatile fatty acids for maintenance and for energy retention. In 'Studies in the Agricultural and Food Sciences' Ed. LE Mount (Butterworths: Sydney) pp147-150.

Ørskov ER, Grubb DA, Smith JS, Webster AJF, Corrigan W (1979) Efficiency of utilization of volatile fatty acids for maintenance and energy retention in sheep. *Br. J. Nutr.* 41, 541-551.

Owens FN, Secrist DS, Hill WJ, Gill DR (1997) The effect of grain source and grain processing on performance of feedlot cattle: a review. *J. Anim. Sci.* 75, 868-879.

Owens FN, Secrist DS, Hill WJ, Gill DR (1998) Acidosis in cattle: a review. *J. Anim. Sci.* 76, 275-286.

Palmquist DL (1994) The role of dietary fats in efficiency of ruminants. *J. Nutr.* 124, 1377S

Park KK, Goetsch AL, Johnson ZB, Rossi JE (1997) Temporal net flux pattern of nutrients across splanchnic tissues in wethers consuming different forages. *Small Rumin. Res.* 25, 107-118.

Peracchi M, Santangelo A, Conte D, Fraquelli M, Tagliabue R, Gebbia C, Porrini M (2000) The physical state of a meal affects hormone release and postprandial thermogenesis. *Br. J. Nutr.* 83, 623-628.

Piccione G, Caola G, Refinetti R (2002) Maturation of the daily body temperature rhythm in sheep and horse. *J. Thermal Biol.* 27, 333-336.

Ray, DE, Hale WH, Marchello JA (1969) Influence of season, sex, and hormonal growth stimulants on feedlot performance of beef cattle. *J. Anim. Sci.* 29, 490-495.

Reinhardt CD, Brandt RT (1994) Effect of morning vs. evening feeding of limit-fed Holsteins during summer months. Cattlemen's Day Reports 704. Kansas State Agric. Exp. Stat., Manhattan.

Remond D, Bernard L, Chauveau B, Noziere P, Poncet C (2003) Digestion and nutrient net fluxes across the rumen, and the mesenteric- and portal-drained viscera in sheep fed with fresh forage twice daily: net balance and dynamic aspects. *Br. J. Nutr.* 89, 649-666.

Robinson DL, Oddy VH (2004). Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livestock Prod. Sci.* 90 255-270.

Rowe J, Channon A (2001) How site of gastrointestinal digestion affects efficiency of feed utilisation. In 'Feed Efficiency in Beef Cattle, Proceedings of the Feed Efficiency Workshop' Eds. JA Archer, RM Herd, PF Arthur (CRC for Cattle and Beef Quality, Armidale NSW) pp 69-72.

Rowe JB, Choct M, Pethick DW (1999) Processing cereal grains for animal feeding. *Aust. J. Agric. Res.* 50, 721-736.

Sanchez WK, McGuire MA, Beede DK (1994) Macromineral nutrition by heat stress interactions in dairy cattle: review and original research. *J. Dairy Sci.* 77, 2051-2079.

Sauvant D, Giger-Reverdin S, Schmidely P (2004) Rumen acidosis: modelling ruminant response to yeast culture. In 'Nutritional Biotechnology in the Feed and Food Industries ' Eds. TP Lyons, KA Jacques (Nottingham University Press, Nottingham, UK) pp 221-230.

SCA (1990) 'Feeding Standards for Australian Livestock. Ruminants' (Standing Committee on Agriculture, Ruminants Subcommittee. CSIRO Melbourne).

Scanga JA, Belk KE, Tatum JD, Grandin T, Smith GC (1998) Factors contributing to the incidence of dark cutting beef. *J. Anim. Sci.* 76, 2040-2047.

Shmeeda H, Kaspler P, Shleyer J, Honen R, Horowitz M, Barenholz Y (2002) Heat acclimation in rats: modulation via lipid polyunsaturation. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 283, R389-399.

Schoorlemmer GH, Evered MD (2002) Reduced feeding during water deprivation depends on hydration of the gut. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 283, R1061-1069.

Scott TW, Ashes JR (1993) Dietary lipids for ruminants: protection, utilization and effects on remodelling of skeletal muscle phospholipids. *Aust. J. Agric. Res.* 44, 495-508.

Sievers AK, Kristensen NB, Laue H-J, Wolffram S (2004) Development of an intraruminal device for data sampling and transmission. *J Anim. Food Sci.* 13 (Suppl 1) 207-210.

Sniffen CJ, O'Connor JD, Van Soest PJ, Fox DG, Russell JB (1992) A net carbohydrate and protein system for evaluating cattle diets: II. Carbohydrate and protein availability. *J. Anim. Sci.* 70, 3562-3577.

Smith RA (1998) Impact of disease on feedlot performance: a review. *J Anim Sci.* 76, 272-274.

Sole Del MJ, Recavarren ML, Milano GD (2004) Splanchnic energy expenditure and net nutrient flux in sheep fed diets with varying concentrate:forage ratios. *J. Anim. Food Sci.* 13 (Suppl 1) 307-310.

Sparke EJ, Bently R, Wood IM (1997) 'Alternative Energy Dense Feedstuffs for the Cattle Feedlot Industry' Project number FLOT.101 (Meat and Livestock Australia, North Sydney).

Sparke EJ, Bently R, Wood IM (1998) 'Fats & Oils Alternative Energy Dense Feedstuffs for the Cattle Feedlot Industry- Phase 2' Project number FLOT.106 (Meat and Livestock Australia, North Sydney). ISBN 1740364562

Sparke EJ, Young BA, Gaughan JB, Holt SM, Goodwin PJ (2001) 'Heat Load in Feedlot Cattle' Project number FLOT.307/308/309 (Meat and Livestock Australia, North Sydney). ISBN 1740362306.

St-Pierre NR, Cobanov B, Schnitkey G (2003) Economic losses from heat stress by US livestock industries. *J. Dairy Sci.* 86(E. Suppl), E52-E77.

Sukhija PS, Palmquist DL (1990) Dissociation of calcium soaps of long-chain fatty acids in rumen fluid. *J. Dairy Sci.* 73, 1784-1787.

Takahashi J, Chaudry AS, Beneke RG, Young BA (1999) An open-circuit hood system for gaseous exchange measurements in small ruminants. *Small Rumin. Res.* 32, 31-36.

Taniguchi K, Nakamura K, Yoneyama T, Ito T, Sugino T, Obitsu T (2004) Effects of short-term exposure to heat stress on splanchnic metabolism in sheep. *J Anim. Food Sci.* 13(Suppl 1) 359-362.

Taylor RB, Huber JT, Gomez-Alarcon RA, Weirsmas F, Pang X (1991) Influence of protein degradability and evaporative cooling on performance of dairy cows during hot environmental temperatures. *J. Dairy Sci.* 74, 243-251.

Thomas PC, Robertson S, Chamberlain DG, Livingstone RM, Garthwaite PH, Dewey PJS, Smart R, Whyte C (1988) Predicting the metabolizable energy (ME) content of compounded feeds for ruminants In Eds. W Haresign and DJA Cole 'Recent Advances in Animal Nutrition 1988' (Butterworths London) pp127-146.

Tothi R, Lund P, Weisbjerg MR, Hvelplund T (2003). Effect of expander processing on fractional rate of maize and barley starch degradation in the rumen of cows estimated using rumen evacuation and in situ techniques. *Anim. Feed Sci. Technol.* 104, 71-94.

Turner HG (1984) Variation in rectal temperature of cattle in a tropical environment and its relation to growth rate. *Anim. Prod.* 38, 417-427.

Tyrrell HF, Moe PW, Flatt WP (1970) Influence of excess protein intake on energy metabolism of the dairy cow. In 'Proc 5th Symposium on Energy Metabolism in Farm Animals' (Junis Drunk + Kenlag: Zurich) pp 69-71.

Wainman FW and Dewey PJS (1987) The energy value to sheep of saturated and unsaturated fat fed singly or in combination. *Anim. Prod.* 44, 227-232.

Wakamura T, Tokura H (2002) Circadian rhythm of rectal temperature in humans under different ambient temperature cycles. *J. Thermal Biol.* 27, 439-447.

Warwick PM, Baines, J (2000) Point of view: energy factors for food labelling and other purposes should be derived in a consistent fashion for all food components. *Br. J. Nutr.* 84, 897-902.

Webster AJF (1980) Energy costs of digestion and metabolism in the gut. In 'Digestive Physiology and Metabolism in Ruminants' Eds. Y Ruckebusch, P Thivend (AVI Pub. Co. Inc: Westport, Connecticut, USA) pp 469-484.

West JW (1999) Nutritional strategies for managing the heat-stressed dairy cow. *J. Anim. Sci.* 77 (suppl2) / *J. Dairy Sci.* 82 (suppl 2) 21-35.

West JW (2003) Effects of heat-stress on production in dairy cattle. *J. Dairy Sci.* 86, 2131-2144.

Westerterp KR (2004) Diet induced thermogenesis. *Nutr. Metab. (Lond).* 1 (5). doi: 10.1186/1743-7075-1-5. Published online 2004 August 18.
(<http://www.nutritionandmetabolism.com/articles/browse.asp?date=8-2004>).

White TW, Bunting LD, Sticker LS, Hembry FG, Saxton AM (1992). Influence of fish meal and supplemental fat on performance of finishing steers exposed to moderate or high ambient temperatures. *J. Anim. Sci.* 70, 3286-3292.

Williams CB, Jenkins TG (2003a). A dynamic model of metabolizable energy utilization in growing and mature cattle. I. Metabolizable energy utilization for maintenance and support metabolism. *J. Anim. Sci.* 81, 1371-1381.

Williams CB, Jenkins TG (2003b). A dynamic model of metabolizable energy utilization in growing and mature cattle. III. Model evaluation. *J. Anim. Sci.* 81, 1390-1398.

Yavelsky V, Vais O, Piura B, Wolfson M, Rabinovich A, Fraifield V (2004). The role of Hsp90 in cell response to hyperthermia. *J. Theoret. Biol.* 29, 509-514.

Zinn RA (1994). Effects of excessive supplemental fat on feedlot cattle growth and performance and digestive function. *Prof. Anim. Sci.* 10, 66-72.