INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
1560–8530/99/01–3–174–178

Review

Effect of Temperature Stress on Nutrient Utilization and Different Physiological Functions of Ruminant Animals

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ABSTRACT

Heat stress has resulted in reduced feed intake and low metabolic rate. These responses are related to thyroid activity which directly influence the gut motility and passage rate of the digesta. Changes in the quality and quantity of food alter the intensity of the metabolic heat load. Supplementing the diets with sodium bicarbonate and potassium or sodium salts alleviate the negative effects of heat stress. Cold stress increases portal blood flow and improves nutrient utilization. Forage intake, digestibility and time spent for grazing was positively correlated to the ambient temperature below 0 ^{0}C. Forage intake during extremely cold weather, was substantially below maintenance requirements under normal temperature. Digestibility of low quality forages during cold weather was lower by the grazing than that of confined animals. This large energy deficit could possibly be because of increased maintenance needs coupled with low intake, increasing gastrointestinal tract motility, resulting in a greater digesta passage rate which reduces digestibility. Reduction in milk production due to cold stress is attributed to greater uptake and oxidation of blood glucose to maintain body temperature. Winter management strategies should therefore, include consideration for increased energy requirements and low levels of forage intake as air temperature becomes cooler. such practices might include feeding supplements that enhance forage intake and digestibility, timing of supplementation so that grazing activities are not disrupted and range forage intake is not reduced and selection of winter grazing sites that provide feeding and resting sites protected from wind.

Key Words: Heat stress; Cold stress; Maintenance energy; Ruminants; Lactation; Feed intake; Digestibility

Temperature stress is a phenomenon that can impart physical and economical losses to livestock production in temperate, subtropic and tropical regions of the world. Temperature stressed animals undergo a series of metabolic and physiological changes. These changes are necessary for adaptability and survivability of the animal. Nutritional balance of the animal is an important factor in thermal stress, the disturbance of which may be deleterious to performance (Christopherson & Kennedy, 1983; Beede *et al.*, 1983)

Thermal stress in livestock production results in increased demand for net energy for maintenance and subsequent reduction in energy for tissue growth and production (Ames *et al.*, 1994). Interactions between nutrition and stress results in nutrient deficiencies which affects animal's ability to counter the stress (National Dairy Council, 1980). Thermal stress has negative effect on food consumption and metabolic activities.

Cold stress (below the thermoneutral zone) increased maintenance requirements of livestock (Hidiroglou & Lessard, 1970). At ambient temperatures below the lower limit of the thermoneutral zone, sheep convert more energy to heat (Graham *et al.*, 1959) and digest their feed less efficiently (National Research Council; NRC, 1989). Unless additional food energy is provided to compensate for increased energy demands in a cold environment, availability of metabolizable energy (ME) for productive processes would be limited (McBride & Christopherson, 1984). In addition, changes in the thermal environment caused by variations in temperature, wind, humidity, precipitation and radiation induce a variety of physiological responses in animals (Christopherson & Kennedy, 1983). Wind is known to have significant effect on heat loss from cattle (Webster, 1974). Ames and Insley (1975) suggested that the human-wind-chill relationship is quadratic in nature but this relationship is not valid for animals with natural covering, particularly at wind velocities greater than 40 km/h. Instead, the relationship between rate of heat loss and wind velocity for animals with hair or wool is predicted more accurately by a cubic function, which may account for the destruction of the external insulation occurring during wind speeds greater than 40 km/h. In general, environmental changes evoke predictable responses in the nervous, circulatory, renal and endocrine systems that allow animals to adjust to the altered environment (Christopherson & Kennedy, 1983). However, changes in thermal environment also induce alterations in activity and function of the digestive system that are independent of changes in feed intake. This paper will discuss energy requirements for forage intake, passage rate, digestibility, metabolism, milk production and body condition of livestock as affected by temperature stress.

Heat stress

Feed intake. A decrease in feed intake and reduction in metabolic rate resulted in cattle exposed to heat stress (Baccari *et al.,* 1983). These responses helped in maintaining heat balance (Beede *et al.,* 1983). However, in most temperate breeds of cattle, higher intake of good quality forage resulted in enhanced metabolic rate and increased requirements for water consumption for intermediary metabolism and thermoregulation (Springell, 1968).

Voluntary intake has been shown to be affected in feedlot cattle exposed to temperature outside their thermoneutral zone (NRC, 1984). The reduction in dry matter (DM) intake from roughage based diets becomes pronounced when environmental temperature increase is accompanied with high humidity (Bhattacharya & Hussain, 1993; Warren *et al.,* 1974). The feed intake, in intensively managed livestock, is less affected by the heat stress, compared to the grazing animals, in which reduction in grazing activity is to maintain heat balance (Beede *et al.,* 1983).

Thermal stress has an indirect relationship to feed intake. Westra and Christopherson (1976) showed that heat stress induces alterations in the activity of the digestive system. The environmental temperature has been associated with the activity of the thyroid gland (Gale, 1973), the reduction of which results in reduced gut motility and rate of passage of digesta (Kennedy *et al.,* 1982).

Digestibility. Exposure to heat stress has been shown to increase digestibilities of DM, crude protein, cell solubles and various fiber fractions, as a result of reduced passage rate and increased mean retention time (Lippke, 1975; Warren *et al.,* 1974). However, similar studies with sheep subjected to heat stress showed only improved fibre digestibility (Lippke, 1975; Bhattacharya & Hussain, 1993). A decrease in volatile fatty acids (VFA) production and alteration in the ratio of acetate to propionate has been reported in heat stress animal (Gengler *et al.,* 1968). Lomax and Baird (1982) investigated the effects of nutrient output on fasting cows. When the animals were fasted for 24 h, there was a decrease in the gut output of acetate, propionate, butyrate and ketone bodies. Christopherson and Kennedy (1983) indicated that digestibility of 100% concentrate diets appear not to be temperature dependent.

Metabolism. Rate of absorption and utilization of nutrients in heat stressed animals have not been well documented. However, Thatcher and Collier (1982) reported that vasodilalation and increased blood flow in heat stressed animals helps dissipation of excessive heat load. These changes result in a reduction of blood supply to the internal organs, including the ruminant forestomach (Englehardt & Hales, 1977). Lomax and Baird (1982) indicated that blood flow to the digestive tract is greatly influenced by the level of feed intake, a factor which is related to the environmental temperature (Attebery & Johnson, 1969).

Glucocorticoid levels increase during heat stress (Collier *et al.,* 1995). Association between circulatory glucocorticoids and proteolytic activity in digestive tract results in increased urinary nitrogen and creatinine excretion (Tepperman, 1980). Colditz (1972) indicated a greater protein catabolism and lower nitrogen retention in cattle kept at 48°C. Battacharya and Hussain (1993) concluded that heat stress resulted in a reduced ME and nitrogen retention. Ames and Brink (1977) reported that increase energy requirement by thermally-stressed animals significantly reduced the protein deficiency ratio. For efficient utilization of dietary protein during heat stress, Ames *et al.* (1994) suggested that protein intake should be adjusted in proportion to expected reduction in average daily gain.

Baccari *et al.* (1983) reported a reduction in plasma triiodothyronine, decrease in body weight gain and poor feed conversion, in heat stressed animals when compared to the animals in thermoneutral zone.

Heat stress results in the loss of large proportion of sodium, potassium, magnesium and chloride ions from the body (Jekinson & Mabon, 1973). At environmental temperature of 40°C, Collier *et al.* (1995) observed a 28-fold increase in the urinary excretion of potassium compared to cows maintained at 15°C. Addition of dietary potassium (Mallonee *et al.,* 1993) and sodium salt (Schneider *et al.,* 1986) has been shown to increase DM intake and milk production in heat stressed dairy cows.

Cold stress

Feed intake. Graham *et al.* (1982) reported that shorn sheep exposed to cold stress during grazing increased feed intake by 20 to 40% to compensate for heat loss. Likewise, Baile and Forbes (1974) reported increased voluntary food intake in cold stressed animals. This response is directly related to the activity of the thyroid gland (Gale, 1973). The elevation of thyroid activity results in increased ruminoreticulum motility and higher rate of passage of digesta (Westra & Christopherson, 1976; Gonyou *et al.*, 1979). In contrast, cows consuming only range forage ate less at lower temperature when compared to those kept at warmer winter temperature (Adams *et al.*, 1986). Further, a 44% reduction in feed intake was observed between two 5 days period when air temperature averaged about -15 and -27°C (Adams *et al.*, 1986). Kartchner (1996) also found that intake of cows grazing on winter forage was below maintenance during harsh than during mild weather. If energy requirements for grazing and cold environments are considered simultaneously, the relationship between intake and requirement would be even less favorable (Adams, 1987). Decreased intake of forage results in lesser production of thermoneutral heat which inturn mobilize body fat to bridge energy gap to maintain body temperature (Webster, 1974). During cold exposure, Young (1975) found elevated concentrations of glucose and free fatty acids in the blood. Baile and Della-Fera (1993) reported that elevated levels of free fatty acids in the blood are associated with reduced intake.

Passage rate. Increased ruminoreticulum motility during cold exposure enhances the rate of passage of small particles from the rumen by promoting their mixing, sorting and fluid propulsion (Gonyou *et al.*, 1979). Nicholson *et al.* (1980) reported that cold exposure reduces the digestibility of long, chopped and ground-pelleted forms of hay by about the same amount, suggesting that rate of particle size reduction for the long and chopped hay may have been enhanced by cold exposure. Feedlot cattle exposed to cold temperature showed increases in the rumination activity (Gonyou *et al.*, 1979). Pearce and Moir (1964) associated this increase in rumination to higher rate of passage of digesta through the gut and subsequent decrease in nutrient digestibility. Cold exposure might alter chemoreceptor reflexes by influencing ruminal blood flow and hence absorption. There is evidence for enhanced blood flow to the ruminant digestive tract during moderate cold stress (Thompson *et al.*, 1978) and reduced blood flow during heat stress (Hales, 1973). An increased blood flow may enhance VFA absorption from the rumen (Thompson *et al.*, 1978). This response is relative to the greater release of ruminal VFA into the portal blood. Leek and Harding (1975) reported that lowering the concentration of ruminal VFA would reduce one of the inhibitory inputs to the gastric centre which consequently results in increased motility. Kennedy *et al.* (1982) reported significant decrease in VFA production rate in the rumen of cold exposed sheep. These results are consistent with the hypothesis that reduction in VFA concentration increase ruminal motility and consequently passage rate.

Digestibility. Nicholson *et al.* (1980) has reported reduced feed digestibility in steers exposed to cold temperature. Graham *et al.* (1980) indicated that cold temperature increased both fecal and urinary energy losses, resulting in a decreased ME availability. It is generally accepted that cold exposure decrease digestibility of feeds in confined ruminants (Kennedy *et al.*, 1982). Likewise, reduced forage digestibility has been associated with cold in grazing animals (Adams *et al.*, 1986); however, in grazing ruminants, differences in forage digestibility between mild and harsh weather often have been large. In addition, Adams (1987) reported that low forage digestibilites during periods of cold weather would greatly limit nutrients to the animals and would affect their performance. Christopherson and Kennedy (1983) concluded that energy deficit of an animal modulates gut function. They suggested energy deficit increases gastrointestinal tract activity and increases passage of digesta, which reduces digestibility.

Milk production. Cold exposure directly limits the synthetic capacity of the mammary gland by reducing mammary gland temperature or may act indirectly by affecting blood supply to the udder (Thompson, 1980). Linzell and Peaker (1971) reported that milk consisted of 90% water and flow of water from blood to milk is probably by osmosis. Because lactose is the main osmolar component of milk, rate of milk secretion depends on lactose secretion. Hardwick *et al.* (1963) reported that blood glucose is the only precursor of milk lactose, therefore, glucose uptake by the udder is important for milk secretion. Cold exposure alters glucose metabolism in non-lactating animals, and blood glucose concentration, total turnover and oxidation of glucose are increased by cold exposure and thus, consequently, output of glucose from the liver increases (Depocas & Masironi, 1960). Bell *et al.* (1975) reported increased uptake of glucose by shivering muscle in cold-exposed animals. Similarly, Faulkner *et al.* (1980) reported that an increased circulating level of glucose and reduced glucose uptake and lactose synthesis by the udder are important factors that reduce milk secretion in goats during cold exposure. Further changes in endocrine balance induced by cold exposure might significantly alter the metabolism of the mammary gland. In an environment where both offspring and ewe are cold stressed, a reduction in milk supply is in direct conflict with increased energy demands of the lamb (McBride & Christopherson, 1984). Cold-induced depression in milk yield may be offset, at least in part, by changes in milk composition, increasing the energy value of the milk (Faulkner *et al.*, 1980).

Body condition. Winter energy requirements of beef cows are influenced by cow size and breed (Lemenager *et al.*, 1980), environment and body condition (Young & Dietz, 1971). Because of the insulation value of fat and its low maintenance requirements, fat cows may have lower winter energy requirements than thin cows (Pullar & Webster, 1977). Thus, manipulation of body condition may be important economically to cow-calf producers, and the ability to deposit external fat may be an important component of an animal's adaptability to a cold climate (Young & Dietz, 1971). Lower winter energy needs for fat cows have been attributed to a large supply of energy reserves and greater insulation against heat loss provided by subcutaneous fat layers (Young & Dietz, 1971). In contrast, Thompson *et al.* (1983) reported no advantages, in respect to energy required or cow-calf performance for Angus- Holstein fat cows compared to thin cows during the winter. However, there was an advantage in ME required for winter maintenance for Angus-Hereford fat cows during the winter.

Maintenance requirements include energy needs for protein and fat synthesis and turnover, ion transport across cell wall, thermogenesis and vital organ and nervous function (Thompson *et al.*, 1983). Protein synthesis and turnover, and ion transport have been identified as principal components in energy expenditures of animal maintenance-related metabolic functions, requiring in excess of 50 % of all energy expended for maintenance (Baldwin *et al.*, 1980). Protein synthesis and turnover may be responsible for higher maintenance requirements of cattle that mature at heavier weights (Garrett, 1971). Webster and Young (1970) indicated that cattle with a greater propensity to deposit fat subcutaneously were better able to increase thermal insulative efficiency than those depositing fat internally and thus were more tolerant and adaptable to cold environment. These findings are consistent with responses noted by Thompson *et al.* (1983), where dairy cross cows had higher maintenance requirements than beef cows in a cold environment and showed no reduction in maintenance energy needs with increased fatness.

CONCLUSIONS

Thermal stress exerts an influence on livestock productivity through an interaction between the animal's physiological changes and the energy requirement. Adjusting the dietary protein during thermal stress to estimated level of reduction in average daily gain would be economically efficient. Feeding management systems could be devised that are climate and animal type specific and that would establish optimum body condition during appropriate periods of the year. These could optimize the efficiency of using stored fat in minimizing maintenance energy requirements and maximize the economic efficiency of productive livestock.

REFERENCES

Adams, D.C., 1987. Influence of winter weather on range livestock. *Proc. Grazing Livestock Nutr. Conf.* pp 23-28. Jackson, Wyoming, July 23–24.

Adams, D.C., T.C. Nelsen, W.L. Reynolds and B.W. Knapp, 1986. Winter grazing activity and forage intake of range cows in the Northern Great Plains. *J. Anim. Sci.*,, 62: 1240–6.

Ames, D.R., D.R. Brink and C.L. Williams, 1994. Adjusting protein in feedlot diets during thermal stress. *J. Anim. Sci.*,, 72: 598–605.

Ames, D.R. and D.R. Brink, 1977. Effect of temperature on lamb performances and protein efficiency ratio. *J. Anim. Sci.*,, 44: 136–40.

Ames, D.R. and L.W. Insley, 1975. Wind chill effect for cattle and sheep. *J. Anim. Sci.*,, 40: 161–7.

Attebery, J.T. and H.D. Johnson, 1969. Effects of environmental temperature, controlled feeding and fasting on rumen motility. *J. Anim. Sci.*,, 29: 734–7.

Baccari, Jr. F., H.D. Johnson and G.L. Hahn, 1983. Environmental heat effects on growth, Plasma T_3 and postheat compensatory effects on holstein calves. *Proc.Soc.Exp. Bio. Med.*, 173: 312–8.

Baile, C.A. and M.A. Della-Fera, 1993. Nature of hunger and satiety control systems in ruminants. *J. Dairy Sci.*,, 76: 2899–2905.

Baile, C.A. and J. M. Forbes, 1974. Control of feed intake and regulation of energy in ruminants. *Physiol. Rev.*, 54: 160–7.

Baldwin, R.L., N.E. Smith, J. Tayllor and M. Sharp. 1980. Manipulating metabolic parameters to improve growth rate and milk secretion. *J. Anim. Sci.*,, 51: 1416–23.

Beede, D.K., P.G. Mallonee, P.L. Schneider, C.J. Wilcox and R.J. Collier, 1983. Potassium nutrition of heat-stressed lactating dairy cows. *South African J. Anim. Sci.*,, 13: 198–206.

Bell, A.W., J.W. Gardner,W. Manson and G.E. Thompson, 1975. Acute cold exposure and the metabolism of blood glucose, lactate and pyruvate and plasma amino acids in the hind leg of the fed and fasted young ox. *British J. Nutr.*, 33: 207–17.

Bhattacharya, A.N. and F. Hussain, 1993. Intake and utilization of nutrients in sheep fed different levels of roughage under heat stress. *J. Anim. Sci.*,, 71: 1761–6.

Christopherson, R.J. and P.M. Kennedy, 1983. Effect of the thermal environment on digestion in ruminants. *Canadian J. Anim.Sci.*, 63: 447–55.

Colditz, P.J., 1972. The effect of diet and heat stress on feed intake, growth and nitrogen metabolism in Friesian, F1 Braham x Friesian and Braham heifers. *Australian J. Agri. Res.*, 23: 717–23.

Collier, R.J., D.K. Beede, W.W. Thatcher, L.A. Israel and C.J. Wilcox, 1995. Influences of environment and its modification on dairy animal health and production. *J. Dairy Sci.,*, 78: 2221–9.

Depocas, F. and R. Masironi, 1960. Body glucose as fuel for thermogenesis in the white rat exposed to cold. *American J. Physiol.*, 199: 1051–55.

Engelhardt, W. Von and J.R.S. Hales, 1977. Partition of capillary blood flow in rumen, reticulum and omasum of sheep. *American J. Physiol.*, .232: 453–9.

Faulkner, A., E. M. Thomson, J.M. Bassett and G.E. Thomspon, 1980. Cold exposure and mammary glucose metabolism in the lactating goat. *British J. Nutr.*, 43: 163–70.

Gale, C.C., 1973. Neuroendocrine aspects of thermoregulation. *Ann. Rev. Physiol.*, 35: 391–9.

Garrett,W.N, 1971. Energetic efficiency of beef and dairy steers. *J. Anim. Sci.*, 32: 451–8.

Gengler, W.R., F.A. Martz, H.D. Johnson, G.F. Krause and L. Hahn, 1968. Effects of temperature on food and water intake and rumen fermentation. *J. Dairy Sci.*, 53: 434–40.

Gonyou, J.W., R.J. Christopherson and B.A. Young, 1979. Effects of cold temperature and winter conditions on some aspects of behaviour of feedlot cattle. *Appl. Anim. Ethol.*, 5: 113–9.

Graham, N., F.W. McWainman, K.L. Blaxter and D.G. Arstrong, 1959. Environmental temperature, energy metabolism and heat regulation in sheep. I. Energy metabolism in closely clipped sheep. *J. Agric. Sci.*, (Camb.) 52: 13–21.

Graham, A.D., A.M. Nicolson and R.J. Christopherson, 1982. Rumen motility responses to adrenaline and noradrenaline and organ weights of warm and cold acclimated sheep. *Canadian J. Anim. Sci.*, 62: 777–86.

Graham, A.D., R.J. Christopherson and J.R. Thompson, 1980. Endocrine and metabolic changes in sheep associated to acclimation to constant or intermittent cold exposure. *Canadian J. Anim. Sci.*, 61: 81–90.

Hales, J.R.S., 1973. Effects of exposure to hot environments on the regional distribution of blood flow and on cardiorespiratory function in sheep. *Pflugers Arch.*, 344: 133–41.

Hardwick, D.C., J.L. Linzell and T.B. Mepham, 1963. The metabolism of acetate and glucose by the isolated perfused udder. 2. The contribution of acetate and glucose to carbon dioxide and milk constituents. *Biochem. J.*, 88: 213–20.

Hidiroglou, M. and J.R. Lessard, 1970. Some effects of fluctuating low ambient temperature on beef cattle. *Canadian J. Anim. Sci.*, 51: 111–7.

Jekinson, D.M. and R.M. Mabon, 1973. The effect of temperature and humidity on skin surface pH and ionic composition of skin secretions in Ayshire cattle. *British Vet. J.*, 129: 282–90.

Kartchner, R.J., 1996. Effects of protein and energy supplementation of cows grazing native winter range forage on intake and digestibility. *J. Dairy Sci.*, 79: 639–46.

Kennedy,P.M., R.J. Christopherson and L.P. Milligan, 1982. Effect of cold exposure on feed protein degradation, microbial protein synthesis and transfer of plasma urea to the rumen of sheep. *British J. Nutr.*, 47: 521–35.

Leek, B.F. and R.H. Harding, 1975. Sensory nervous receptors in the ruminant stomach and the reflex control of reticula-ruminal motility. *In: Digestion and Metabolism in ruminants.* I.W. McDonald and A.C.I. Warner, editors. pp. 60–76. The University of New England Press, Armidale.

Lemenager, R.P.,L.A. Nelson and K.S. Hendrix, 1980.Influence of cow size and breed type on energy requirements. *J. Anim. Sci.*, 51: 566–74.

Linzell, J.L. and M. Peaker, 1971. Mechanism of milk secretion. *Physiol. Rev.*, 51: 564–72.

Lippke, H., 1975. Digestibility and volatile fatty acids in steers and wethers at 21 and 32°C ambient temperature. *J. Dairy Sci.*, 58: 1860–9.

Lomax, M.A. and G.D. Baird, 1982. Blood flow and nutrient exchange across liver gut of the dairy cow: effects of lactation and fasting. *British J. Nutr.*, 49: 481–9.

Mallonee, P.G., D.K. Beede, R.J. Collier and C.J. Wilcox, 1993. Production and physiological responses of dairy cows to varying dietary potassium during heat stress. *J. Dairy Sci.*, 76: 819–25.

McBride, G.E. and R.J. Christopherson, 1984. Effect of cold exposure on milk production and energy balance in the lactating ewe. *Canadian J. Anim. Sci.*, 64: 379–89.

National Dairy Council, 1980. Nutritional demands imposed by steers. *Dairy Council Digest*, 51: 1–8.

National Research Council, 1984. *Nutrient requirements of domestic animals.* No.4. Nutrient requirement of beef cattle. Sixth Revised Ed. National Academy of Sciences, Washington, D. C.

National Research Council, 1989. *Effect of environment on nutrient requirements of domestic animals.* National Academy Press, Washington, D.C.

Nicholson, J.W.G., R.E. McQueen and P.L. Burgess, 1980. Effect of cold on digestibility of chopped or pelleted hay by sheep. *Canadian J. Anim. Sci.*, 60: 571–8.

Pearce, G.R. and R.J. Moir, 1964. Rumination in sheep. 1. The influence of rumination and grinding upon the passage and digestion of food. *Australian J. Agri. Res.*, 15: 635–44.

Pullar, J.D. and A.J.F. Webster, 1977. The energy cost of fat and protein deposition in the rat. *British J. Nutr.*, 37: 355–63.

Schneider, P.L., D.K. Beede and C.J. Wilcox, 1986. Response of lactating cows to dietary sodium source and quantity and potassium quantity during heat stress. *J. Dairy Sci.*, 69: 99–110.

Springell, P.H., 1968. Water content and water turnover in beef cattle. *Australian J. Agri. Res.*, 19: 129–44.

Tepperman, J., 1980. *Metabolic and endocrine physiology.* Year Book Medical, Inc. Chicago.

Thatcher, W.W. and R.J. Collier, 1982. Effect of heat on animal productivity. *In: Handbook of Agricultural Productivity, Vol.II.* M. Rechcigl, Jr.(editor). pp. 77–105. CRC Press, Inc., Boca Raton, FL.

Thompson, G.E, 1980. The effect of cold exposure on fluid balance, circulating arginine and vasopressin concentration and milk secretion in goat. *Pflugers Arch.*, 383: 241–8.

Thompson, G.E., J.M. Bassett and A.W. Bell, 1978. The effect of feeding and acute cold exposure on the visceral release of volatile fatty acids, estimated hepatic uptake of propionate and release of glucose and plasma insulin concentration in sheep. *British J. Nutr.*, 39: 219–26.

Thompson, W.R., J.C., Meiske, R.D. Goodrich, J.R. Rust and F.M. Byers, 1983.Influence of body composition on energy requirements of beef cows during winter. *J. Anim. Sci.*,56: 1241–52.

Warren, W. P., F. A. Martz, K. H. Asay, E. S. Hilderbrand, C. G. Payne and J. R. Vogt, 1974. Digestibility and rate of passage by steers fed tall fescue, alfalfa and orchardgrass hay in 18 and 38°C ambient temperatures. *J. Anim. Sci.*, 39: 93–6.

Webster, A. J. F, 1974. Prediction of heat losses from cattle exposed to cold outdoor environments. *J. Appl. Physiol.*, 30: 634–43.

Webster, A.J.F and B.A. Young, 1970. Breed and strain differences in the cold tolerance of young cattle raised in different environments. *Canadian J. Anim. Sci.*, 51: 150–6.

Westra, R. and R. J. Christopherson, 1976. Effects of cold on digestibility, retention time of digesta, reticulum motility and thyroid hormones in sheep. *Canadian J. Anim. Sci.*, 56: 699–708.

Young, B.A., 1975. Temperature induced changes in metabolism in body weight of cattle (*Bos taurus*). *Canadian J. Physiol. Pharmacol.*, 53: 947–53.

Young, B.A. and W. Dietz, 1971. Effect of body condition and environment on the winter energy requirement of beef cows. *Canadian J. Anim. Sci.*, 52: 85–91.

(Received 15 January 1999; Accepted 03 April 1999)