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Review article

Effects of heat stress on the welfare of extensively managed domestic ruminants

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Abstract

High ambient temperatures, high direct and indirect solar radiation, and humidity are environmental stressing factors that impose strain on animals. This review concerns the heat stress–strain response of domestic ruminants from the viewpoint of animal welfare. Despite having well developed mechanisms of thermoregulation, ruminants do not maintain strict homeothermy under heat stress. There is unequivocal evidence that hyperthermia is deleterious to any form of productivity, regardless of breed, and stage of adaptation. The best recognized effect of raised body temperature is an adaptive depression of the metabolic rate associated with reduced appetite. Thus, in domestic ruminants a rise of body temperature marks the transition from aversive stage to noxious stage. Physiological (sweating, panting), hormonal (cortisol, thyroid gland activity), and behavioral thermoregulatory responses are discussed in respect to animal welfare. Factors such as water deprivation, nutritional imbalance and nutritional deficiency may exacerbate the impact of heat stress. The higher sensitivity of cattle to heat stress in comparison with sheep, and of animals at various productive stages in comparison with animals at maintenance is highlighted. Some practical measures that are applicable under extensive conditions, such as provision of shade shelter, are suggested.

Keywords: Welfare; Ruminants; Extensive conditions; Heat stress; Hot environments

1. Introduction

There is great public pressure concerning farm animal welfare in many European countries (Broom, 1992). Recent developments in housing and management practice of farm animals under intensive systems reflect the increase in moral concerns about animal welfare. The welfare of an individual is its state in regard to an attempt to cope with its environment (Broom, 1986). The effects of heat stress on the welfare of intensively managed cattle have been considered (Young, 1993; Jacobsen, 1996). However, there is very little discussion in the scientific literature regarding the interrelationships between heat stress and animal welfare under extensively managed systems. There is much knowledge regarding the interaction between heat stress and livestock productivity under intensive and extensive management systems. Heat is a major constraint on animal productivity in the tropical belt and arid areas (Silanikove, 1992). The effect of heat stress is also substantial in the subtropical-Mediterranean zones,

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and farm animals raised in central and western Spain, or in the southern areas of France, Italy and Greece, are exposed annually for 3–5 months to considerable heat stress. Growth, milk production and reproduction are impaired under heat stress as a result of the drastic changes in biological functions caused by the stress (Habeeb et al., 1992; Silanikove, 1992). However, these response are also indications for poor welfare (Broom and Johnson, 1993).

This paper reviews the heat stress–strain response of domestic ruminants from the viewpoint of animal welfare. We question whether recommendations can be drawn up to increase animal welfare under extensive conditions and, if yes, whether such measures are compatible with the input restraints on such systems.

2. Defining the relations among heat stress, strain and animal welfare

Thermal physiologists commonly use the term heat stress to mean the demand made by the environment for heat dissipation. Physiologists adopted the stress–strain relationship from physical sciences as a concept applicable to animals. Accordingly, strain refers to an internal displacement from the resting or basal state brought about by external stress (Finch, 1984). The internal readjustment to maintain homeostasis in the face of external temperature changes, is called an adaptation to the thermal environment (Finch, 1984). Behavioral adaptation to cope with environmental conditions is the learning process habituation (Broom and Johnson, 1993). Welfare is a characteristic of an animal, which varies from poor to very good and can be defined by discrete measures, such as changes in hormone level, body temperature, and normal behavior. Poor welfare will develop when an individual has difficulty in coping with its environment. There is a lot of overlap between productive and welfare measures, such as disease, mortality risk, growth, milk yield and reproduction. However, some physiological and behavioral measures of poor welfare may occur in the absence of productive responses, at least in the short term. It is within this latter frame of reference that the stress–strain–welfare relationships will be discussed in this review.

2.1. Indices of heat stress

In hot climates, high ambient temperatures, and high direct and indirect solar radiation, wind speed and humidity, are the main environmental stressing factors that impose strain on animals (Finch, 1984). The formulation of physiological temperature scales is important for delineating a suitable climatic space for a breed or species (Finch, 1984). Heat stress indices range from simple measurement of air temperature to indices that try to provide a weighted estimation of these factors. Black globe temperature combines the effects of total incoming radiation from the sun, horizon, ground and other subjects with air temperature and wind speed (Bond and Kelly, 1955). The combination of black globe temperature with wet bulb temperature provides a black globe-humidity index (Buffington et al., 1983). This index probably represents one of the best indices to represent heat stress in open areas; nevertheless, it accounted for only 24% of the variance of heat stress-related milk yield depression in dairy cows (Buffington et al., 1983). This is in part because of large variations between individuals and in part, because the animal is related to its environment in a much more complex manner than is represented by this index.

Solar radiation has a major effect on the thermoregulation of grazing ruminants (Gebremedhin, 1985). Yamamato et al. (1994) calculated the effective temperature (ET) from ambient temperature (dry bulb temperature, DBT) and radiation (black globe temperature, BGT) by multiple regression analysis using respiration rate and body temperature as the dependent response variable. They found that:

$$ET = 0.24DBT + 0.76BGT \quad (1)$$

This equation suggests that long-wave and short-wave (solar) radiation as measured by black globe temperature contributes substantially more to the heat load than does ambient temperature.

In addition, McDowell et al. (1976) suggested that the temperature–humidity index (THI), a parameter widely used to describe heat load on humans, is a good indicator of stressful thermal climatic conditions. The THI is arrived at from a combination of wet and dry bulb air temperatures for a particular day and expressed in a formula as follows:

$$\mathrm{THI} = 0.72(\mathrm{W}^\circ\mathrm{C} + \mathrm{D}^\circ\mathrm{C}) + 40.6 \quad (2)$$

where W°C = wet bulb and D°C = dry bulb. Temperature–humidity index values of 70 or less are considered comfortable, 75–78 stressful, and values greater than 78 cause extreme distress and animals are unable to maintain thermoregulatory mechanisms or normal body temperature. Lemerle and Goddard (1986) reported that, although rectal temperature only increased when THI was greater than 80, the respiration rate would increase from THI value of about 73 and probably more steeply above 80. This finding suggests that homeostatic mechanisms, including increased respiration, can prevent a rise in rectal temperature until the THI reaches 80. This is similar to the critical THI level of 78 quoted by McDowell et al. (1976).

The severity of heat stress depends to a large extent on the diurnal fluctuations of the ambient temperature. If the temperature drops at night to below 21°C for 3–6 h, the animal has sufficient opportunity to lose at night all the heat gained from the previous day (Igono et al., 1992; Muller et al., 1994a,b). In the Northern Hemisphere, the most severe heat stress is expected during the months of July and August, because in many instances the temperature does not drop below 21°C at night, and the capacity to completely dissipate heat gained during the preceding day is severely hampered.

However, so far there was no effort to develop an indices of heat stress that is based dry bulb, wet bulb and black globe temperature. Such a putative indices will take in account the three major factors (i.e. ambient temperature, humidity, and radiation) that influence the thermal balance between an animal and its environment, and therefore may provide a better measure of heat stress. Nowadays, the THI become the method of choice in most countries, because meteorological stations in most countries routinely provide this information.

2.2. Physiological thermoregulation

The ability to regulate temperature is an evolutionary adaptation that allows homeotherms to function in spite of variation in ambient temperature (Baker, 1989); this ability also allows temperature to be used as a signal to control physiological processes. Peripheral thermoreceptors and thermosensitive units in the central nervous system mediate temperature reception (Baker, 1989). Warming the pre-optic region of the hypothalamus activates all available physiological and behavioral heat-loss mechanisms (Baker, 1989). Heat stress causes the rostral cooling center of the hypothalamus to stimulate the medial satiety center which inhibits the lateral appetite center, resulting in reduced dietary intake and consequently lower milk production (Albright and Alliston, 1972). The general homeostatic responses to thermal stress in mammals include raised respiration rates (Yousef, 1985), panting, drooling, reduced heart rates and profuse sweating (Blazquez et al., 1994), decreased feed intake (Silanikove, 1992) as well as reduced milk production (Albright and Alliston, 1972; Lu, 1989).

2.3. Heat balance between an animal and its environment

The heat balance between an animal and its environment is given by the following equation (Berman et al., 1985):

$$\mathrm{M} = (\mathrm{HS} + \mathrm{K} + \mathrm{C} + \mathrm{R} + \mathrm{E}) \quad (3)$$

where: M = metabolic heat production, HS = heat storage, R = heat exchanged by radiation, E = heat exchanged by evaporation, C = heat exchanged by convection, K = heat exchanged by conduction.

2.4. Heat storage

In mammals, the body temperature is maintained at a relatively constant level because of the balance which exists between heat production and heat loss. Heat storage (gain) can be expressed as:

$$\text{(heat gained (in Joules)} = \text{mass (in kg)} \times \text{specific heat (in Joules)} \times \text{temperature change (in }^\circ\text{C)} \quad (4)$$

Factors that increase heat production over BMR include, exercise or shivering, imperceptible tensing of muscles, chemical increase of metabolic rate, heat increment and disease (fever). Factors decreasing heat loss are an internal shift in blood distribution, decrease in tissue conductance and counter-current heat exchange. On the other hand, heat loss from the animal is enhanced by sweating, panting, a cooler environment, increased skin circulation (vasodilatation), shorter fur insulation, increased sensible water loss, increased radiating surface, and increased air movement or convection.

2.5. Rectal temperature

Rectal temperature is an indicator of thermal balance and may be used to assess the adversity of the thermal environment which can affect the growth, lactation, and reproduction of dairy cows (Johnson, 1980; Hahn, 1999; Hansen and Arechiga, 1999; West, 1999). A rise of 1°C or less in rectal temperature is enough to reduce performance in most livestock species (McDowell et al., 1976; Shebaita and El-Banna, 1982), which makes body temperature a sensitive indicator of physiological response to heat stress in the cow because it is nearly constant under normal conditions. Scott et al. (1983) found significant negative relationships of feed consumption (in kilogram per day on the *y*-axis) and average THI as well as average dry bulb temperature (degrees Celsius on the *x*-axis) as expressed in the equations: $y = 101 - 5.4x$, $r^2 = -0.66$ ($P < 0.05$) for the THI, and $y = 57.3 - 5.7x$, $r^2 = -0.66$ ($P < 0.05$) for the average dry bulb temperature, respectively, in non-lactating Holstein dairy cows. The results of Scott et al. (1983) suggest that night cooling may be an effective natural method to alleviate thermoregulatory limitations of a hot climate on optimal animal performance. It appears that there are notable differences between breeds in their ability to regulate rectal temperature: the mean rectal temperature is higher in *B. taurus* than in *B. indicus* cattle (Finch, 1986) and, as a result, *B. taurus* cattle are more sensitive to heat stress than their *B. indicus* counterparts.

2.6. Heat loss

An animal loses heat by conduction, convection, radiation, evaporation of water, and through expired air. Heat dissipation is shifted from radiation and convection at lower environmental temperatures to vaporization at higher temperatures. Heat lost by the skin is dependent partly on the temperature gradient between skin and air and solid objects. Non-evaporative heat loss declines as ambient temperatures rise, making the animal more dependent upon peripheral vasodilatation and water evaporation to enhance heat loss and prevent a rise in body temperature (Berman et al., 1985). Peripheral vasodilatation however, is unlikely to be a major method of increasing heat dissipation in cattle because of their large body mass.

Berman et al. (1985) reported that the maximal rate of water evaporation in lactating cows was 1.5 kg/h, which translates to 4.3 kJ/day. This rate of heat loss is close to the heat production of a dry non-pregnant 600-kg cow but only about half of that produced by a cow yielding 30 kg/day. This may explain the low sensitivity of dry cows to high ambient temperatures. The importance of water as a medium for ridding the body of excess heat through sweating and respiration greatly increases as the ambient temperature rises (Richards, 1985).

In cattle under heat load, about 15% of the endogenous heat is lost directly from the body core via the respiratory tract (McDowell et al., 1976). The remainder of the metabolic heat must be transferred to the skin, where it is dissipated either non-evaporatively by radiation, convection and conduction, or evaporatively by sweating. For beef cattle standing in a hot radiant environment, metabolism accounts for about one-third of the total heat load (Finch, 1976), and the ability of animals to remove metabolic heat efficiently is important for maintenance of steady body temperature.

2.7. Heat loss and gain by radiation

The amount of heat absorbed by an object from direct (solar) radiated heat depends not only on the temperature of the object, but also on its color and texture, with dark surfaces radiating and or absorbing more heat than light colored surfaces at the same temperature. An animal with a black coat will therefore have an absorbance of 1 of the direct radiation; whereas, a white-coated one will have an absorbance of 0.37 and one with red fur has an absorbance of 0.65 (Cena and Monteith, 1975). Radiant heat transfer between bodies takes place in both directions, and if the bodies are at different temperatures there is a net transfer of heat from the warmer to the cooler body (Esmay, 1969). This net heat transfer involves the loss or gain of heat by the animal through absorption or reflection of electromagnetic infrared waves.

In experiments using artificial radiant heat loads, Stewart and Brody (1954), and Kibler and Brody (1954) found that cows did not respond to radiation at an ambient temperature of 7.2°C. However, at temperatures of 21.1 and 26.7°C, Jersey cows had a mean heat production rate 12–14% lower with maximum radiation load. On the other hand, Holstein cows showed heat production decreases of 26% at 21.1°C and of 9% at 26.7°C. In the same experiment, Brahman cows showed little response to radiation insofar as heat production was concerned. The authors concluded that the lack of response by Brahman cows was due to their low heat production rate; therefore, their heat dissipation requirement was not more than half that of the lactating Jerseys and Holsteins.

According to Bond and Kelly (1955) and Muller et al. (1994a), a well-designed shade structure should reduce total heat load by 30–50%. The beneficial effects of providing shade shelter to cattle and sheep in terms of thermoregulatory responses and productive responses have been demonstrated on numerous occasions (Roman-Ponce et al., 1977; Collier et al., 1981; Roberts, 1984; Legates et al., 1991; Muller et al., 1994a,b,c). The beneficial effects of providing shade shelter to cattle and sheep in improving their reproductive performance are also well established (Stott et al., 1972; Stephenson et al., 1984).

2.8. Evaporative heat loss: respiratory and cutaneous water (RCW) losses

The heat required to convert water into vapor is referred to as the latent heat of vaporization. The vaporization of 1 ml of water requires 2.43 Joules and this is the amount of heat lost when 1 ml of water evaporates from the skin or from the respiratory tract. Loss of RCW can be separated into passive and thermoregulatory components. Passive water loss is the respiratory and cutaneous diffusion losses, the latter constituting approximately two-thirds of passive water loss (Yousef, 1985). Thermoregulatory water loss is activated by panting and sweating. Passive (insensible) water loss (IW) relates to body weight according to the following formula of Chew (1965):

$$[\mathrm{IW\ (ml/h)} = 2.58 \times \mathrm{BW}^{0.826}\ \mathrm{(kg)}] \quad (4)$$

According to Chew (1965) formula, a 600-kg cow would lose 12 l of water/day, which is very close to the RCW loss of 13 l/day measured in dry cows under thermoneutral conditions (Silanikove et al., 1997).

The proportion of metabolic heat that is dissipated from an animal's body by evaporation increases with rising environmental temperatures and a decreasing temperature gradient between animal and air. Johnson (1976) showed that the differences in the ratio of evaporative cooling to total heat loss (heat produced) is species variable and that the evaporative ratio of cattle begins to increase markedly at 16.6–18.3°C. In hot climates, the potential for non-evaporative heat loss is reduced and animals rely on the evaporation of water to dissipate any excess heat generated by metabolism (McArthur and Clark, 1988). However, the efficiency of evaporative cooling declines with an increase in relative humidity. This was demonstrated by decline in milk production between 32°C with 20% relative humidity and 32°C with 45% relative humidity (Johnson and Vanjonack, 1976). This difference in relative humidity reduced respiratory and surface evaporation, which resulted in a rise in rectal temperature, reducing feed intake and milk production.

Under thermal stress, cattle increase evaporative heat loss by both panting and sweating, with sweating being quantitatively superior to panting (McLean, 1963). Heat transfer by evaporation is described by the equation:

$$Q_e = k_e A_e V_n (p_s - p_a) \quad (5)$$

where Q_e = evaporative heat transfer, k_e = evaporative constant, A_e = effective evaporative (wet) area, V_n = air velocity to some power n, p_s = vapor pressure of water on the animal's surface, p_a = vapor pressure of water in the air.

It is important to note that evaporative and convective effects on heat loss are not easily separable.

As indicated in Eq. (5), air velocity is one of the important factors influencing evaporative heat transfer. Ittner et al. (1951) reduced skin and body temperatures by increasing the air velocities over pigs and cattle subjected to high ambient temperatures. These findings were pivotal to the development of modern forms of air ventilation to ameliorate heat stress in domestic animals. However, the time that a volume of air at a speed of 1.6 km/h (typical breeze in the Mediterranean zone) passes over an 11-m long shade is too short (25 s) to induce a significant reduction in the heat load. Therefore, most of the benefit from shade for animals under extensive conditions should be gained from reducing the radiation.

Basal respiration rate is about 20 breaths per min. in cattle (Thomas and Pearson, 1986) and little bit higher (25–30 breaths per min) in goats (Robertshaw and Damiel, 1983) and sheep (Hales and Brown, 1974). Therefore, increase in breaths rate above 40 may be regarded as panting in order to increase body cooling by respiratory evaporation. Under severe heat stress the respiration rate reach values of 200 breaths per min in cattle (Thomas and Pearson, 1986), and 300 breaths per min in sheep (Hales and Brown, 1974). In sheep, panting is the major evaporatory heat loss mechanism and respiratory frequencies tend to follow closely the heat loss by evaporation (Hales and Brown, 1974). In non-sheltered sheep under summer Mediterranean conditions respiration rate (125 breaths per min) was 56% higher than in sheltered sheep (80 breaths per min) due to direct effect of solar radiation (Silanikove, 1987). Measuring breath rate and deciding if an animal is panting, and qualifying the severity of heat stress according to panting rate (low: 40–60 breaths per min, medium high: 60–80, high: 80–120, and severe heat stress: above 150 breaths per min in cattle, and above 200 in sheep) appears to be the most accessible and easiest method for evaluating the impact heat stress on farm animals under extensive conditions; all it requires is direct observation of the animal and a watch.

The measurement of sweating rate is difficult and results have been varied. Robertshaw and Vercoe (1980) reported a twofold increase in the rate of skin moisture loss (up to 77 $g/m^2/h$) from the scrotum after exposure to a temperature of 40°C. Blazquez et al. (1994) measured a fivefold increase in the rate of skin moisture loss (up to 279 $g/m^2/h$) from the scrotum at 36.2°C. Finch (1986) found that the sweating rates of *B. indicus* increased exponentially with rises in body temperature; whereas, in *B. taurus*, the sweating rates tended to plateau after an initial increase. Within *B. taurus* breeds, Singh and Newton (1978) found higher sweating rates ($P <$ 0.05) in Ayrshire calves than in Guernsey calves and suggested that Ayrshire calves were more capable of acclimation to hot weather than Guernsey calves.

The morphology and functioning of the apocrine sweat glands of cattle during hot climatic conditions has been extensively investigated (Montgomery et al., 1984). Blazquez et al. (1994) reported that increased blood flow to the skin is positively correlated to the sweating rate. Earlier, Kibler and Brody (1952) found similar sweating rates for *B. taurus* and *B. indicus* breeds; however, Allen (1962) showed that *B. indicus* and Zebu cattle had significantly higher sweating rates than breeds from temperate regions. Ferguson and Dowling (1955) and Allen (1962) ascribe elevated sweating rates of *B. indicus* and Zebu cattle to their higher density of sweat glands. Schmidt-Nielsen (1964) reported that as the environmental temperature rose, *B. taurus* cattle showed an appreciable increase in evaporation between 15 and 20°C, with a maximum rate of evaporation being reached before 30°C. On the contrary, Brahman cows (*B. indicus*) had initially lower evaporation rates, but rapid evaporation rates occurred when temperatures were between 25 and 30°C, and continued rising up to 40°C. Cattle in temperate and tropical regions possess the same type and number of sweat glands, one to each hair follicle (Findlay and Yang, 1950). However, tropical breeds have a higher density of hair follicles (1698/cm^2 for Zebu) than is the case in *B. taurus* breeds (1064/cm^2 for Shorthorn) according to Dowling (1955). Further, Dowling (1955) reported that Zebu have sweat glands that are located much closer to the skin surface than is the case in temperate breeds of cattle. Blazquez et al. (1994) did not attach significance to the number of sweat glands per unit area or to their individual size, but more to the product that these sweat glands produce.

2.9. Heat loss and gain by convection

When cool air meets a warm body, a layer of air surrounding the surface of the body is heated and rises moving away from the body, carrying with it heat, and thereby cooling the body through the process of convection. On the contrary, if air temperature is greater than skin temperature, then air movement will promote the movement of heat into the animal until air temperature equals skin temperature when transfer of heat ceases. The transfer of heat during respiration is a form of convective heat transfer. Inspired air is adjusted to the body temperature by the time it reaches the trachea (Yousef, 1985). The velocity of air movement affects the rate of convection and anything that resists air movement such as fur in cattle will decrease the rate of heat transfer by convection.

2.10. Heat loss and gain by conduction

The heat flow between two media or bodies in direct contact is described as conductive heat exchange. Conductive heat exchange is between the animal and its surrounding air environment, and between the animal and any other media, solid or otherwise that the animal may be in direct contact with. When the other media with which the animal is in contact with are either gases or liquid, the conductive heat exchange is further complicated by heat exchange through convection in these media. The flow of heat by conduction depends on the temperature difference, the conductance of the media, and the area of contact (Schmidt-Nielsen, 1964). Esmay (1969) reported a proportional relationship between the bulk density of materials and their conductivity, thus the more dense the material the greater the conductivity or inversely the less the resistance to heat flow. The conductive heat transfer was described in Yousef (1985) in a simple diffusion equation as:

$$K = Ah_c(t_s - t_a) \quad (6)$$

where K = conductive heat exchange, A = is surface area, h_c = is thermal conductivity of the material in contact with the skin, t_s = is mean skin temperature, t_a = is air temperature.

For the high producing dairy cow, it is important to know that the magnitude of conductive heat transfer depends on the nature of material in contact with its skin, in particular its thermal conductivity. To alleviate heat stress, utilization of bedding materials with high conductance may facilitate cooling of the animals. From experiments with different bedding materials (wood shavings, sand, ground limestone, shredded paper and rubber mats), Cummins (1998) found that cows had highest preference for ground limestone which had the lowest temperature of 25.9°C at 25 mm below the surface. This underscores the importance of bedding material selection as part of heat stress abatement strategies. In the standing animal, conductive heat loss is minimal because of the presence of a layer of air against the skin, which means that most of the heat transfer from the animal takes place to air, and air has a poor thermal conductivity (Yousef, 1985). Furthermore, in a standing animal, transfer of heat to the ground only takes place through the feet with a very small area of contact, and in cows the distance between the blood vessels and the surface is much greater in the feet than it is in the skin. On the other hand, an animal lying on a cool wet surface will have greater conductive heat transfer depending on the thermal conductance of the substrate as well as the temperature gradient and magnitude of the area of contact relative to the total surface area (Eq. (6)). If air temperature or temperature of the ground on which the animal is lying is greater than skin temperature, then the animal will gain heat by conduction, adding to the metabolic heat load.

2.11. Summary of factors governing the heat balance between an animal and its environment

The general homeostatic responses to thermal stress in mammals include reduction in fecal and urinary water losses, reduction in feed intake and production, and increased sweating, respiratory rates and heart rates. In response to stress, mammals sets physical, biochemical, and physiological processes into play to try and counteract the negative effects of heat stress and maintain thermal equilibrium. Most of the adjustments made by an animal involve dissipating heat to the environment and reducing the production of metabolic heat.

The heat stress imposed by the environment depends on the internal heat load and on the factors that govern heat exchange. The latter is dependent on the temperature and vapor pressure gradients that exist between the animal and the environment and the resistance to heat flow along these gradients. The color of the fur and its resistance can affect considerably the non-evaporative heat gain and losses

(Esmay, 1969; Yousef, 1985). The thermoregulatory responses of ruminant held in a climate-controlled room differ qualitatively and quantitatively from those in animals exposed to natural environment (Robertshaw and Damiel, 1983; Legates et al., 1991). This is because direct and indirect radiation and local heating of the skin have a large influence on stimulation of the sweat glands.

The complexities of the above described factors that govern heat exchange make it clear why any physical measurement of the environment is less than satisfactory as an index of thermal stress, hence animal welfare. The impact of the environment may be modified by animal behavior, and can differ on a species, breed, and individual levels. The susceptibility to other stresses may exacerbate the effects of heat stress. These considerations emphasize further the problematic nature of establishing a useful relationship between heat stress indices and animal welfare and productivity, particularly in extensive systems. Nevertheless, an environmental profile provides baseline data on which to estimate average expected climatic effects, their variation and the duration of any extremes. Such information is necessary for understanding animal responses to environmental conditions, defining the climatic space for a given species or breed, and as a first approximation in evaluating its susceptibility to exposure to conditions which will reduce its welfare. Thus this information is essential in making decisions to expend economic and energy resources in order to improve the climate for animal welfare and production.

3. Hormonal responses

3.1. Glucocorticosteroids

Activation of the pre-optic area stimulates the hypothalamus to release a corticotrophin-releasing factor that acts on the anterior pituitary to release adrenocorticotropic hormone. This stimulates the adrenal cortex to produce glucocorticosteroids (mainly cortisol). Activation of the hypothalamic–pituitary–adrenal axis and the consequent increase of plasma cortisol concentration are the most prominent responses of an animal to stressful conditions. The secretion of cortisol stimulates physiological adjustments that enable an animal to tolerate the stress caused by a hot environment (Christison and Johnson, 1972). Plasma cortisol may increase within 20 min of exposure to acute heat stress, and reach a plateau within 2 h (Christison and Johnson, 1972). Plasma cortisol rises markedly when cattle are acutely exposed to high environmental temperatures and decreases during the chronic phase (Habeeb et al., 1992). However, Muller et al. (1994b) found that shaded cows under South African Mediterranean summer conditions maintained lower plasma cortisol concentration, along with lower rectal temperatures and respiration rates, during periods of peak heat stress. This suggests that cows are sensitive to heat stress even in a temperate environment, and that basal cortisol concentrations may increase in chronically heat-stressed cows if heat stress intensifies.

Collins and Weiner (1968) suggested that the initial reactions of the animal to acute heat stress represent an emotional rather than a thermoregulatory response. However, under severe acute heat stress the hyperglycemic action of cortisol is most likely required to provide the expected increase in glucose utilization. It may be concluded that decline in plasma cortisol activity under chronic heat stress indicates adaptation to the stress, whereas an increase in the cortisol concentration over the basal level in animals that are chronically exposed to heat load is an indication that the animal became distressed.

3.2. Thyroid hormones

The anterior lobe of the pituitary gland produces the hormone thyrotropin, which acts primarily on the thyroid gland to produce thyroxin (T_4) and triiodothyronine (T_3). These hormones influence different cellular processes, in particular the thermogenesis activity that accounts for approximately 50% of the basal metabolic rate of normal animals (Habeeb et al., 1992). Certain physical stress factors tend to inhibit the secretion of the thyroid gland (Habeeb et al., 1992). The concentrations of T_4 and T_3 in blood plasma were found to decline under heat-stress conditions by up to 25% (Magdub et al., 1982; Beede and Collier, 1986). The response is slower than that described for cortisol, and it took several days for T_4 and T_3 levels to reach a new steady state (Kamal and Ibraim, 1969). The readjustment in thyroid response is chronic and, as a result, summer thyroid activity is lower than during winter (Habeeb et al., 1992). These modifications in thyroid activity are consistent with decrease in metabolic rate, feed intake, and growth and milk production under heat stress (Beede and Collier, 1986).

From the above discussion its appears that a reduction in thyroid activity reflects an animal under strain that is adapted to its environment, whereas elevated cortisol reflects distress. Consequently, it may be concluded that the welfare of an animal with elevated cortisol concentration is much poorer than in an animal with reduced thyroid gland activity.

4. Thermoregulatory behavior

Domesticated ruminants are mainly diurnal in their habits, being active during the day and resting at night. However, during hot weather in tropical and subtropical-Mediterranean conditions, grazing ruminants tend to lie down and to reduce their locomotion during the day. Instead, they tend to graze before sunrise, at dawn and during the night. Seeking shade, particularly during the heat of the day, is a conspicuous form of behavioral adaptation in these areas (Finch, 1984; Silanikove, 1987). If shade is not available, an animal will change its posture to the vertical position in respect to the sun in order to reduce the effective area for heat exchange (Hafez, 1968). Sheep tend to crowd, and to stand intimately side by side for the same purpose. Under severe heat stress, animals moisten their body surface with water saliva, or nose secretions. This range of behavioral response affects the heat exchange between the animal and its environment by reducing heat gain from radiation, and increasing heat loss via convection and conduction (Hafez, 1968).

5. The thermoneutral zone (TNZ) concept

TNZ concept is a convenient means to describe schematically the interrelationships between an animal and its environment. The lower critical ambient temperature range point and the upper critical ambient temperature range point define the limits of the TNZ (Robertshaw, 1981). However, whereas the definition of the lower critical point is precise and unambiguous, the upper critical point may be defined in several ways (Mount, 1973). The ambient temperature, below which the rate of heat production of a resting homeotherm increases to maintain thermal balance, is the lower critical temperature. The upper critical temperature may be defined as the ambient temperature when the: (a) metabolic rate increases; (b) evaporative heat loss increases; or (c) tissue thermal insulation is minimal.

Defining the upper critical temperature under natural conditions according to definitions (a) and (c) is very difficult. These criteria may be measured in climate-controlled chambers, but it is doubtful whether the results are applicable to outdoor situations because, in the chambers; diurnal and seasonal cycles of climate do not prevail; and the effect of radiation is not considered. Consequently, some researchers choose to define the upper critical temperature of cows as the point where evaporative heat loss in the form of panting increases (Berman et al., 1985; Igono et al., 1992). However, sweating and panting can be activated independently and, for goats (Robertshaw and Damiel, 1983) and cows (Silanikove et al., 1997), sweat secretion is activated long before panting. Furthermore, sweating in dairy cows apparently is activated at fairly low temperatures (12–14°C), which are considered to be well within the thermoneutral zone (Silanikove et al., 1997). In horses, the upper critical temperature point varied from 20°C (increased evaporation) to 25°C (increased metabolic rate) to 30°C (minimal tissue insulation), depending on which physiological parameter was used for definition (Morgan, 1998). These data and more information reviewed by Webster (1991) show that it is hard to establish a uniform definition for the upper critical temperature.

6. Thermal well-being in relation to the TNZ

The subdivision of the TNZ into a zone of thermal well-being, as for humans (Fig. 1), is suggested to be most suitable to describe the relation between an animal and its environment from the viewpoint of animal welfare. In humans, the original term that was

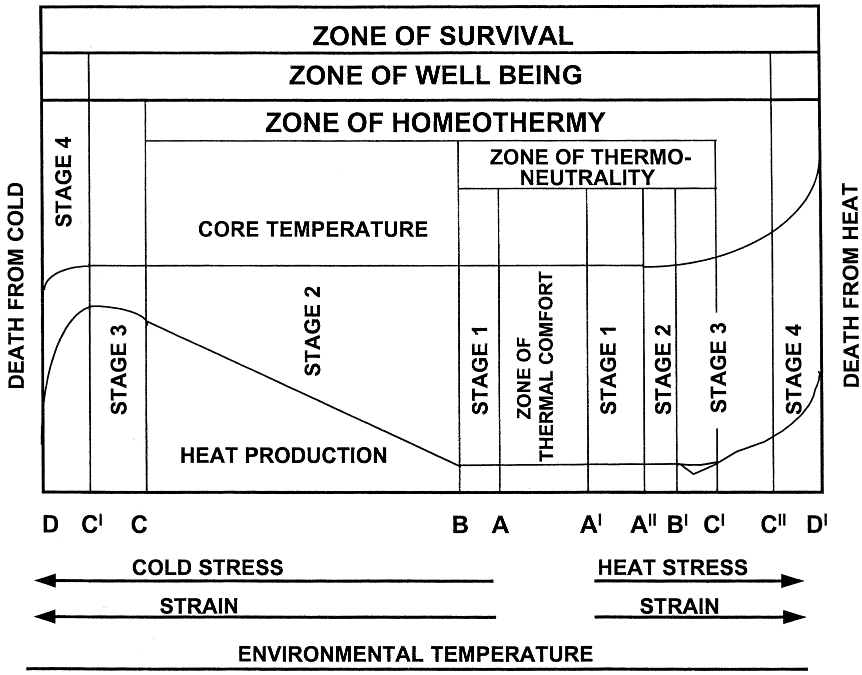

Fig. 1. Schematic presentation of the zones of survival, well being, and homeothermy in respect to environmental conditions in ruminants. See text for more detailed definitions of the four stages of diminished welfare.

used was thermal comfort. However, comfort implies cognitive recognition, whereas the decision regarding the animal state of welfare are made by those who raise the animals. Therefore, we prefer to use the objective term — thermal well-being, to describe the state of animal welfare in relation to its ambient environment.

6.1. Zone of optimal thermal well-being

Within the zone of optimal thermal well-being, the energetic and physiological efforts of thermoregulation (principally vasodilatation of peripheral blood vessels) are minimal, the animal's health is optimum, and growth rate and milk yield are maximized (Bianca, 1968).

6.1.1. Stage I: the innocuous stage

This stage is defined by the upper optimal thermal well-being point (A′) and a point (A″) that precedes the upper critical point (B′). When environmental temperature rises above the optimal thermal well-being (A′), strain defense mechanisms against overheating come into operation: in addition to general vasodilatation, sweating occurs in large and small ruminants (Berman, 1971; Robertshaw and Damiel, 1983; Silanikove et al., 1997). In small mammals such as goats, sweating may be associated at this stage with modest panting. In summary, the animals are under heat stress and activating strain responses. However, homeothermy is attained without difficulty, fitness is not hampered, and productivity is not necessarily affected.

6.1.2. Stage II: the aversive stage

This stage is defined by point A″ (the first sharp increase in evaporative cooling) and point B′ (upper critical point). Based on increases in body temperature, the upper critical point of sheep and cattle is around 24–26°C (Robertshaw, 1981; Igono et al., 1992; Hahn, 1999). Above point A′ the evaporative cooling mechanisms are intensified exponentially with the increase in internal and external heat loads (Silanikove et al., 1997). As a result, water consumption per unit of dry matter ingested by cows was constant between −12 and +4°C and rose at an accelerated rate between 4 and 38°C (Winchester and Morris, 1956). At this stage the animals are much more vulnerable to negative interactions with nutritional and other environmental stresses (Silanikove et al., 1997); some of these negative interactions are discussed later.

6.1.3. Stage III: the noxious stage

This stage is defined by point B′ and point C″ in which coping attempts to maintain homeothermy are unsuccessful and therefore fitness is impaired.

Above point B′, two physiological responses are possible:

1. Feed consumption and thermogenic hormone secretion decrease to lower the basal metabolism, resulting in a reduction of the internal heat load. This response will be activated whenever the increase in heat stress is gradual, allowing the animals to adapt to the new situation, and when the combined effects of reduced internal heat load and evaporative cooling enable the maintenance of homeothermy. If animals are at a productive stage (growth, lactation), the reduction in feed intake and internal heat production is reflected in a reduction in productivity (Silanikove, 1992).
2. If an animal does not have an opportunity for adaptation (B′ in Fig. 1) or with temperature rising further in adapted animals (C′ in Fig. 1), cooling is insufficient to maintain homeothermy despite intensification of evaporation, with the result that body temperature starts to rise.

Most of the efforts in farm animal management should be targeted in preventing the animals from entering stage III, because: (i) the danger of entering stage IV, which may fatal, and (ii) impaired fitness is associated with poor welfare, health, and reduced productive and reproductive performances.

For a variety of reasons, the incidence of health problems in livestock increases during warm summer months (Collins and Weiner, 1968; Niwano et al., 1990). Vectors and other disease causing agents thrive better under warm to hot and humid environmental conditions. In tropical locations, tick and internal parasite populations explode during summer, forcing farmers to dip and drench their livestock more frequently than during the cool winter months. Other than parasitic problems during warm months, it is apparent that heat stress itself can directly and adversely affect the health of the dairy cow (Collins and Weiner, 1968). Using data from dairy herds, DuBois and Williams (1980) calculated that 24% of cows (79 parturitions) that calved during the warm season of May through September had retained placenta and developed postpartum metritis, compared to 12% (98 parturitions) for the rest of the year when temperatures were low. This difference ($P<0.05$) was wholly attributed to the effects of heat stress on the dairy cows during the warm months. Further, DuBois and Williams (1980) found a difference in the gestation length (273 vs. 279 days) of cows having retained placenta and postpartum metritis than of cows not exhibiting these symptoms. Retained placenta and postpartum metritis occur with early parturition and are of major economic significance for dairy producers. Collins and Weiner (1968) reported that heat stress causes a variety of neuroendocrine changes, which may contribute to the shortening of the gestation period. Although literature on the effects of heat stress livestock health is scant, it seems logical to postulate that the influence of thermal stress on the physiological functions may trigger clinical or sub-clinical health conditions.

Cavestany et al. (1985) determined the relationship between ambient temperature and breeding efficiency and demonstrated that seasonal high environmental temperatures were associated with low breeding efficiency due to a variety of factors. High summer temperature above the TNZ of cattle and sheep drastically reduced conception rate and presumably increased embryonic loss (Cavestany et al., 1985; Holmes et al., 1986; Biggers et al., 1987; Dollah et al., 1990; Adballa et al., 1993) and perinatal losses (Lynch, 1985). Heat stress also adversely affects the ovum and sperm in the reproductive tract and early embryo development (Ingraham et al., 1979; Ocfemia et al., 1993), and may alter the hormonal balance of the dam (Stott et al., 1972; Thatcher, 1974).

6.1.4. Stage IV: the extreme stage

This stage is defined by point C″ (sharp increase in body temperature) and point D′ (death from heat), and occurs when a vicious circle of rising body temperature sets in. External emergency aid is needed to save the animal from immediate death.

If the strain is high, and body temperature continues to rise, the animal enters into an acute phase of heat stress that induces heavy panting and maximal sweating. Heat production will rise under this condition because of the acceleration in the biochemical processes (the van't Hoff effect) and because of the energetic cost of heavy panting (Hales and Brown, 1974). If these dramatic measures fail to stop the elevation in body temperature, a vicious circle set in and the animal succumbs to heat stroke and dies. Most mammals die when deep body temperature reaches 42–45°C (Bianca, 1968), which exceeds normal body temperature by about only 3–6°C.

Stages I, II, III, and IV in the zone below the lower critical temperature represent the deterioration in animal well-being in the cold environment. However, the detailed justifications of this are beyond the scope of this review.

7. Interaction with water metabolism

Under thermoneutral conditions, feed intake is the major determinant of water intake, or water turnover (Silanikove, 1989). Heat stress increases considerably water and ion losses of ruminants, and hence increases their requirements (Beede and Collier, 1986). Cerebral thermal sensors and sensors regulating thirst and release of vasopressin are interrelated at the hypothalamic level and heat defense mechanisms are adjusted to the water balance of the animal (Baker, 1982, 1989). Dehydration and increase of solutes concentration in the body fluid of mammals exposed to heat will reduce their thermoregulatory evaporation and allow the body temperature to rise (Silanikove, 1992). This readjustment in thermoregulation has been observed in both panting and sweating species and appears to be a regulated response that allows the dehydrated animal to save water. In species that both pant and sweat, such as the goat, progressive dehydration leads to suppressed sweating and increased panting (Baker, 1989). A panting animal does not lose salt and therefore blood plasma volume is better preserved. An additional advantage of panting relates to cooling of the blood passing the nasal area, which allows the brain temperature to be kept lower than the core body temperature (Robertshaw and Damiel, 1983). Thus, water scarcity, or water deprivation, will enhance the heat stress effect, and cause deterioration in the animal welfare due to the steeper increase in core body temperature.

On the other hand, heat load increases plasma and extracellular volume, apparently in proportion to the thermoregulatory requirement of the exposed animal (Silanikove, 1987; Chaiyabtur et al., 1990). This response may be interpreted as pre-adaptation to heat stress and water deprivation, as the expended fluid pools will buffer increase in body temperature and will resist dehydration longer. Maintaining feed intake and milk yield in heat-stressed desert goats even after exposure to 48 h of dehydration has been related to their ability to maintain a sufficient blood flow to the gut and the udder (Maltz et al., 1984). The increase in body water content in animals in a hot climate is considered, therefore, as an adaptive reaction to ameliorate heat stress. Thus, like the reduction in thyroid gland activity, an increase in body water content is a sign of an animal in stress that is adapted to its environment.

The reduced homeostatic efficiency of plasma monovalent ions in hot weather observed in lactating cows may consist of an accumulation of their deficiencies, enhanced secretion in sweat, and the transient sequestration of sodium and chlorine ions in the rumen (Maltz et al., 1994). Ruminants secrete large amounts of saliva to buffer their rumen content. The amount of sodium secreted with the saliva is 5–10-times greater than that present in plasma (Silanikove et al., 1987). Reabsorption of sodium from the rumen is an active process that accounts for ~50% of the sodium absorption from the gastro-intestinal tract (Silanikove and Tadmor, 1989). The reduction in feed intake and volatile fatty acid production under heat stress may, therefore, delay sodium absorption from the rumen (Maltz et al., 1994). Thus, an increase in the fluctuation of plasma ions, and a mid-day decrease in their concentration, may serve as an indication of failure of animals to ameliorate heat stress effectively.

8. Interaction with supplementation

Pastures along the summer dry belts on earth, such as the Mediterranean pasture, are dry during the summer, and their quality in most instances do not sustain the energy and nitrogen requirements of cattle and sheep for maintenance and pregnancy. These dry pastures are characteristically highly fibrous and release much heat during the processes of fermentation and absorption (heat increment). This heat increment exacerbates the heat load of the animal by increasing the internal heat load (Beede and Collier, 1986; Goetsch and Johnson, 1999; West, 1999). Thus, supplementing grazing ruminants with low-quality highly fibrous food may sustain the animals when those pastures are meager, but cannot improve their well being. On the other hand, supplementation of ruminal escape protein and fat may reduce the heat increment of food, improve nitrogen utilization, and therefore animal welfare (Bunting et al., 1992; West, 1999).

8.1. Nutritional imbalance

Nutritional imbalance and deficiencies may exacerbate the impact of heat stress (Manteca and Smith, 1994; West, 1999). Generally, an excess of degradable dietary protein is undesirable because of energy cost to metabolize and excrete excess N as urea (West, 1999). One particular case that will be discussed is the interaction between heat stress and supplementation based on foodstuff rich in non-protein nitrogen. Poultry litter is widely used as a cheap source of nitrogen in Israel and other countries. When pasture is plentiful, supplementing grazing beef cows with poultry litter provided their nutritional requirements for maintenance and early pregnancy (Silanikove et al., 1987). However, reduced pasture availability resulted in a considerable increase in poultry litter consumption (Silanikove and Tiomkin, 1992). Excessive consumption of poultry litter has been found to cause severe damage to the liver, which may be fatal when consumption increases from 2 or 3 to 10 kg/day (Silanikove and Tiomkin, 1992). Beef cows that had no access to shade consumed much more poultry litter than shaded cows, despite the fact that pasture conditions were similar (Silanikove and Gutman, 1992). Physiological indices (total body water content and breathing rate) suggest the non-shaded cows experienced much greater strain. This caused a shift in preference from the pasture — with its high heat increment effect — to poultry litter, and was reflected in extended negative energy balance in this group. The excess consumption in poultry litter induced toxic effects on the liver, and the combination of metabolic burden and negative energy balance increased embryo loss in the non-shaded cows. Thus, providing shade ameliorated the heat stress, prevented excessive reduction in pasture intake, allowed the cows to consume a better balanced diet, and prevented embryo loss.

8.2. Nutritional deficiency

Addition of solutes ($NaHCO_3$ and KCl) benefited heat-stressed cows in terms of milk yield, regulation of acid–base balance, and lowering body temperatures (Coppock et al., 1982; Schneider et al., 1986). These responses may be related to the deficiency of the major monovalent ions (sodium, potassium, and chlorine), particularly in early lactation under heat load (Shalit et al., 1991; Silanikove et al., 1997). Low quality grasses are also low in sodium content. It has been shown that sodium chloride application to pasture, or its direct supplementation, increased the productivity of dairy cows (Chiy and Phillips, 1991). Thus, NaCl supplementation to grazing cattle may improve their heat tolerance, although this is not yet tested.

9. Species, breed and productive state

Among the domestic ruminant species, goats are best adapted to harsh hot environments (see Silanikove, 1997, 2000, for recent reviews on the subject). Breeds of ruminants indigenous to tropical and subtropical environments generally performed better than their counterparts from more temperate zones in terms of survival, reproduction and expression of their genetic potential for growth and milk yield (Finch, 1984). These characteristics relate to their capacity to maintain their appetite under heat stress or during moderate growth and milk yield (Silanikove, 1992). Some comparative aspects such as the important of the color of the fur, morphology of sweat glands, and extend of sweating were already discussed. Additional physiological basis for this has been reviewed extensively over the years (MacFarlane and Howard, 1972; Robertshaw, 1981; Finch, 1984; Silanikove, 1992, 1994), and therefore will not considered in detail in this review. As cattle and sheep are the most prevalent and numerous ruminants in southern Europe, the differences between them in respect to resistance of heat stress will be highlighted in this review.

Cattle have a higher metabolic rate than most other domestic ruminants and a poorly developed water retention mechanism in the kidney and gut (MacFarlane and Howard, 1972). The rate of water use by cattle under summer Mediterranean conditions was approximately twice that of Merino sheep on a metabolic-weight basis (Silanikove, 1987; Silanikove et al., 1987). Voluntary feed intake and resting salivary flow-rate were both ~40% lower in the summer in stall-fed beef cows given water once daily in comparison with those given water twice daily (Silanikove and Tadmor, 1989). As European cattle suffer from even short periods of water deprivation, they respond to shadeless conditions much more acutely than do sheep (Silanikove and Gutman, 1992).

Sheep are able to maintain remarkable thermostability in spite of heat stress (Degen and Shkolnik, 1978; Silanikove, 1987). This ability relates to their excellent insulation capacity (Degen and Shkolnik, 1978). Depriving Merino sheep at a maintenance level of feeding from shade shelter had no effect on their voluntary food intake (Silanikove, 1987). However, shade-deprivation increased their strain, as reflected by an increase in plasma and total body water content (Silanikove, 1987).

Water deprivation and heat stress in pregnant and lactating ruminants would result in a more acute reduction in feed intake than in the same animals fed at near maintenance. This difference is because in highly productive animals dehydration is faster, and the interaction with the high internal heat load would tend to increase body temperature faster (Silanikove, 1992). Pregnant and lactating sheep increase their water intake markedly during heat stress. The result is voluntary overhydration (Adballa et al., 1993; Olsson et al., 1995), and in sheep this phenomenon was observed also in non-pregnant and non-lactating animals under shadeless conditions (Silanikove, 1987). Such a response allows the animals to buffer themselves against short periods of water deprivation, and therefore may be regarded as anticipatory drinking (Silanikove, 1987).

10. General discussion

According to the present definition of animal welfare, welfare is a characteristic of an animal that can be measured in a scientific way that is free from moral considerations (Broom and Johnson, 1993). Therefore, welfare measurements should be based on: (i) environmental indices of heat stress, (ii) the animal's response in coping with difficulties, and (iii) on signs that coping effects to maintain homeothermy are failing. In mammals, the body temperature is maintained at a relatively constant level because of the balance that exists between heat production and heat loss. Rectal temperature is an indicator of thermal balance and may be used to assess the adversity of the thermal environment that can affect the growth, lactation, and reproduction of farm animals. Despite having well-developed mechanisms of thermoregulation, both wild and domestic herbivores do not maintain strict homeothermy (McLean et al., 1983). For cattle under considerable heat stress the diurnal variation in body temperature may be as much as 3°C, although the rate of rise in core body temperature is slower in adapted breeds (Finch, 1984). Animals that are adapted to extremely hot environments, such as the oryx and the camel, can tolerate a rectal temperature of 45°C for 8 h without any apparent damage (Finch, 1984). This raises the question whether body temperature can be used as a general measure of an animal's welfare. With regard to domestic species, there is unequivocal evidence that hyperthermia is deleterious to any form of productivity, regardless of breed and stage of adaptation (Finch, 1984). This conclusion is also valid on the individual level; ewes of the same flock and breed that managed to maintain lower rectal temperature ($<$39.8°C) produced lambs with higher birth weight than sheep with higher rectal temperature ($>$39.8°C) (McCrabb et al., 1993a,b). McCrabb et al. (1995) concluded that measurement of rectal temperature in sheep exposed to a hot environment in any one year is an accurate measure of their rectal temperature during subsequent years.

Thus, the best physiological parameter to objectively monitored animal welfare in hot environment should be rectal temperature. In domestic ruminants a rise in body temperature marks the transition from aversive (stage II, coping with difficulty) to the noxious (stage III, coping attempts to maintain body temperature are unsuccessful and therefore fitness impaired) stage. The innocuous stage (stage I), which precedes the aversive stage, marks the ambient conditions where for the first time thermoregulatory mechanisms are operated, and the aversive stage marks the limit of the animal's ability to do so without a raise in body temperature. The extreme stage (stage IV) is defined as that in which a vicious cycle of rising body temperature starts. External emergency aid is needed to save the animal from immediate death.

The problem is that rectal temperature can not be simply measured in free ranging animal. In the future, developing cheap miniature telemetric equipment might solve this problem. In the mean time, stage III can be relatively easy identified by counting animal breaths rate of 100 per min and above. In sheep, where respiration rate follows closely evaporative water loss, counting breaths rate of 50–60 breaths per min most likely indicates that the animals are in stage II. THI of around 80 and above imply that most domestic ruminants would be in stage III, with danger in being drifted to stage IV.

11. Practical considerations

Relatively, there is a lot of basic knowledge on the interaction between heat stress and livestock production, reproduction, and health traits. The implementation of these knowledge to maintain the welfare of animals maintained under extensive management systems is difficult because of objective limitations to monitor heat stress and because of economical restriction in applying measures to relief heat stress. From welfare point of view, ideally the animals should be raised in the zone of optimal thermal well being. However, these would be almost impracticable goal to attain in large grazing part of the world. A more practical goal would be to maintain livestock within stages I and II of thermal well being, or in other words to prevent the animals entering stage III.

The following recommendations are general rules that can be applied under extensive conditions:

1. Provision of shade shelter: This measure is essential to the welfare of farm animals in areas where typical ambient temperature during summer exceeds 24°C and THI exceeds 70.
2. Provision of water: It is recommended that the distance between watering spot and grazing area be such that grazing cattle are able to visit the water spot at least twice a day, and goats and sheep at least once a day. In order to avoid negative interactions with other stressful factors, particular emphasize should be given to adequate supplementation and provision of clean water.
3. Limitation on type of breed: It would be unethical from welfare considerations to grow purebred breeds from temperate environments in areas where typical ambient temperature during summer exceeds 24°C and THI exceeds 70.
4. Limitation on transportation: Since adaptation takes time, it is recommended to avoid the transfer of farm animals from a relatively cool to a hot environment during the summer.

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References

Adballa, E.B., Kotby, E.A., Johnson, H.D., 1993. Physiological responses to heat-induced hypothermia of pregnant and lactating ewes. Small Rumin. Res. 11, 125–134.

Albright, J.L., Alliston, C.W., 1972. Effects of varying the environment upon performance of dairy cattle. J. Anim. Sci. 32, 566–577.

Allen, T.E., 1962. Responses of Zebu, Jersey and Zebu and Jersey crossbred heifers to rising temperatures with particular reference to sweating. Aust. J. Agric. Res. 13, 165–179.

Baker, M.A., 1982. Brain cooling in endotherms in heat and exercise. Annu. Rev. Physiol. 44, 85–96.

Baker, M.A., 1989. Effect of dehydration and rehydration on thermoregulatory sweating in goats. J. Physiol. Lond. 417, 421–435.

Beede, D.K., Collier, R.J., 1986. Potential nutritional strategies for intensively managed cattle during heat stress. J. Anim. Sci. 62, 543–550.

Berman, A., 1971. Thermoregulation in intensely lactating cows in near-natural conditions. J. Physiol. Lond. 215, 477–481.

Berman, A., Folman, Y., Kaim, M., Mamen, M., Herz, Z., Wolfenson, D., Arieli, A., Graber, Y., 1985. Upper critical temperatures and forced ventilation effects for high-yielding dairy cows in a subtropical climate. J. Dairy Sci. 68, 1488–1495.

Bianca, W., 1968. Thermoregulation. In: Hafez, E.S.E. (Ed.), Adaptation of Domestic Animals. Lea and Febiger, Philadelphia, PA, pp. 97–118, Chapter 7.

Biggers, B.G., Geisert, R.D., Wetteman, R.P., Buchanan, D.S., 1987. Effect of heat stress on early embryonic development in the beef cow. J. Anim. Sci. 64, 1512–1518.
Blazquez, N.B., Long, S.E., Mayhew, T.M., Perry, G.C., Prescott, N.J., Wathes, C.M., 1994. Rate of discharge and morphology of sweat glands in the perineal, lumbodorsal and scrotal skin of cattle. Res. Vet. Sci. 57, 277–284.
Bond, T.E., Kelly, C.F., 1955. The globe thermometer in agricultural research. Agric. Eng. 36, 251–260.
Broom, D.M., 1986. Indicators of poor welfare. Br. Vet. J. 142, 524–526.
Broom, D.M., 1992. Animal welfare: Its scientific measurement and current relevance to animal husbandry in Europe. In: Phillips, C., Pigginns, D. (Eds.), Farm Animals and the Environment. CAB, Wallingford, UK, pp. 245–253.
Broom, D.M., Johnson, K.G., 1993. Stress and Animal Welfare. Chapman and Hall, London.
Buffington, D.E., Collier, R.J., Canton, G.H., 1983. Shade management systems to reduce heat stress for dairy cows in hot, humid climates. Trans. Am. Soc. Agric. Eng. 26, 1798–1803.
Bunting, L.D., Sticker, L.S., Wozniak, P.J., 1992. Effect of ruminal escape protein and fat on nitrogen utilization in lambs exposed to elevated ambient temperatures. J. Anim. Sci. 70, 1518–1525.
Cavestany, D., El-Wishy, A.B., Foote, R.H., 1985. Effect of season and high environmental temperature on fertility of Holstein cattle. J. Dairy Sci. 68, 1471–1478.
Cena, K., Monteith, P., 1975. Transfer processes in animal coats. 1. Radiative transfer. Proc. R. Soc. Lond. B 188, 377.
Chaiyabtur, N., Buranakal, C., Loypetjra, P., Chanpongsang, S., 1990. Effect of prolonged exposure to the sun on body water turnover and volume of the blood in swamp buffaloes. Asian-Aust. J. Anim. Sci. 3, 47–52.
Chew, R.M., 1965. Water metabolism of mammals. In: Mayer, W.W., Van Gelder, R.G. (Eds.). Physiological Mammalogy, Vol. 2. Academic Press, New York, p. 43.
Chiy, P.C., Phillips, C.J.C., 1991. The effects of sodium chloride application to pasture or its direct supplementation on dairy cow production and grazing preference. Grass Forage Sci. 46, 325–332.
Christison, G.I., Johnson, H.D., 1972. Cortisol turnover in heat-stressed cows. J. Anim. Sci. 53, 1005–1010.
Collier, R.J., Eley, R.M., Sharma, A.K., Pereira, R.M., Buffington, D.E., 1981. Shade management in subtropical environment for milk yield and composition in Holstein and Jersey cows. J. Dairy Sci. 64, 844–849.
Collins, K.H., Weiner, H.S., 1968. Endocrinological aspects of exposure to high environmental temperature. Physiol. Rev. 48, 785–794.
Coppock, C.E., Grant, P.A., Portzer, S.J., Charles, D.A., Escobosa, A., 1982. Lactating dairy cows responses to dietary sodium, chloride, and bicarbonate in hot weather. J. Dairy Sci. 65, 566–576.
Cummins, K., 1998. Bedding plays role in heat abatement. Dairy Herd Manag. 6 (June), 20.
Degen, A.A., Shkolnik, A., 1978. Thermoregulation in fat-tailed Awassi, a desert sheep, and in German Mutton Merino, a mesic sheep. Physiol. Zool. 51, 333–339.
Dollah, M.A., Fradhlulah, A.M., Nordin, H.M., Ibrahim, C.E., 1990. Alleviation of environmental heat stress for improvement of reproduction of exotic sheep in humid tropics. In: Proc. 5th AAAP Animal Science Congress, May 27–June 1, 1990, Taipei, Taiwan, Republic of China, Vol. 3. AAAP Organization Committee, Chunan, Miaoli, Taiwan, p. 155.
Dowling, D.F., 1955. The hair follicle and apocrine gland populations of Zebu (*Bos indicus* L.) and (*Bos taurus* L.) cattle skin. Aust. J. Agric. Res. 6, 645–654.
DuBois, P.R., Williams, D.J., 1980. Increased incidence of retained placenta associated with heat in dairy cows. Theriogenology 13, 115–121.
Esmay, M.L., 1969. In: Principles of Animal Environment. AVI Publishing, New York, p. 319.
Ferguson, K.A., Dowling, D.F., 1955. The functions of cattle sweat glands. Aust. J. Agric. Res. 6, 640–644.
Finch, V.A., 1976. An assessment of the energy budget of Boran cattle. J. Therm. Biol. 1, 143–148.
Finch, V.A., 1984. Heat as a stress factor in herbivores under tropical conditions. In: Gilchrist, F.M.C., Mackie, R.I. (Eds.), Herbivore Nutrition in the Subtropics and Tropics. The Science Press, Graighall, South Africa, pp. 89–105.
Finch, V.A., 1986. Body temperature in beef cattle: Its control and relevance to production in the tropics. J. Anim. Sci. 62, 531–542.
Findlay, J.D., Yang, S.H., 1950. The sweat glands and Ayrshire cattle. J. Agric. Sci. Camb. 40, 126–133.
Gebremedhin, K.G., 1985. Heat exchange between livestock and the environment. In: Yosef, M.K. (Ed.). Stress Physiology in Livestock, Vol. 1. CRC Press, Boca Raton, FL, pp. 15–33.
Goetsch, A.L., Johnson, Z.B., 1999. Feed intake and digestion in the summer and fall by different breeds of ewes consuming forages differing in quality. Small Rumin. Res. 31, 109–116.
Habeeb, A.A.M., Marai, I.F.M., Kamal, T.H., 1992. Heat stress. In: Phillips, C., Pigginns, D. (Eds.), Farm Animals and the Environment. CAB International, Wallingford, UK, pp. 27–47.
Hafez, E.S.E., 1968. Behavioral adaptation. In: Hafez, E.S.E. (Ed.), Adaptation of Domestic Animals. Lea and Febiger, Philadelphia, PA, pp. 202–214, Chapter 15.
Hahn, G.L., 1999. Dynamic responses of cattle to thermal heat loads. J. Anim. Sci. 77 (Suppl. 2), 10–20.
Hales, J.R.S., Brown, G.D., 1974. Net energetic and thermoregulatory efficiency during panting in the sheep. Comp. Biochem. Physiol. 49A, 413–422.
Hansen, P.J., Arechiga, C.F., 1999. Strategies for managing reproduction in the heat-stressed dairy cow. J. Anim. Sci. 77 (Suppl. 2), 36–50.
Holmes, J.H.G., Prasetyo, S., Miller, H.M., Scheurmann, E.A., 1986. Effect of chronic heat load during pregnancy on birth weight, behaviour and body composition of Australian feral goat kids. Trop. Anim. Health Prod. 18, 185–190.
Igono, M.O., Bjotvet, G., Sanford-Crane, H.T., 1992. Environmental profile and critical temperature effects on milk production of Holstein cows in desert climate. Int. J. Biometeorol. 36, 77–87.
Ingraham, R.H., Stanley, R.W., Wagner, W.C., 1979. Seasonal effects of tropical climate on shaded and nonshaded cows as measured by rectal temperature, adrenal cortex hormones,

thyroid hormone, and milk production. Am. J. Vet. Res. 40, 1792–1797.

Ittner, N.R., Kelly, C.F., Guilbert, H.R., 1951. Water consumption of Hereford and Brahman cattle and the effect of cooled drinking water in a hot climate. J. Anim. Sci. 10, 742–751.

Jacobsen, K.L. (Ed.), 1996. The well-being of dairy cows in hot and humid climates. II. Reducing stress. Compendium of Continues Education in Practical Veterinary, Vol. 18. Veterinary Learning Systems, Trenton, NJ, pp. S242–S254.

Johnson, H.D., 1976. World climate and milk production. Biometeorology 6, 171–175.

Johnson, H.D., 1980. Depressed chemical thermogenesis and hormonal functions in heat. In: Physiology: Aging, Heat and Altitude. Elsevier, Amsterdam, pp. 3–9.

Johnson, H.D., Vanjonack, W.J., 1976. Effects of environmental and other stressors on bloodpatterns in lactating animals. J. Dairy Sci. 59, 1603–1617.

Kamal, I., Ibraim, I.I., 1969. The effect of natural environment of the Sahara and controlled climate on thyroid gland activity in Friesian cattle and water buffaloes. Int. J. Biometeorol. 13, 275–285.

Kibler, H.H., Brody, S. (Eds.), 1952. Relative efficiency of surface evaporative, respiratory evaporative and non-evaporative cooling in relation to heat production in Jersey, Holstein, Brown Swiss and Brahman cattle, 50 to 105°F. Agricultural and Experimental Station Research, University of Missouri, Bulletin 497.

Kibler, H.H., Brody, S. (Eds.), 1954. Influence of radiation intensity on evaporative cooling, heat production and cardiorespiratory activities in Jersey, Holstein and Brahman cows. Agricultural and Experimental Station Research, University of Missouri, Bulletin 574.

Legates, J.E., Farthing, B.R., Casady, R.B., Barrada, M.S., 1991. Body temperature and respiratory rate of lactating dairy cattle under field and chamber conditions. J. Dairy Sci. 74, 2491–2500.

Lemerle, C., Goddard, M.E., 1986. Assessment of heat stress in dairy cattle in Papua New Guinea. Anim. Health Prod. 18, 232–242.

Lu, C.D., 1989. Effect of heat stress on goat production. Small Rumin. Res. 2, 151–162.

Lynch, J.J., 1985. Perinatal and post-shearing losses in sheep. In: Moore, B.L., Chenoweth, P.J. (Eds.). Grazing Animal Welfare Symposium: Proc. Symp. held at the Bardon Professional Development Centre, Brisbane, on April 26th and 27th, 1985. Australian Veterinary Association (Queensland Division), Indooroopilly, QLD, pp. 83–94.

McArthur, A.J., Clark, J.A., 1988. Body temperature of homeotherms and the conservation of energy and water. J. Therm. Biol. 3, 9–13.

McCrabb, G.J., McDonald, B.J., Hennoste, L.M., 1993a. Lamb birthweight in sheep differently acclimatized to a hot environment. Aust. J. Agric. Res. 44, 933–943.

McCrabb, G.J., McDonald, B.J., Hennoste, L.M., 1993b. Heat stress during mid-pregnancy in sheep and the consequences for placental and fetal growth. J. Agric. Sci. Camb. 120, 265–271.

McCrabb, G.J., McDonald, B.J., Hennoste, L.M., McDonald, B.J., 1995. The thermal response of sheep to a hot environment in different years. J. Agric. Sci. Camb. 125, 153–158.

McDowell, R.E., Hooven, N.W., Camoens, J.K., 1976. Effects of climate on performance of Holsteins in first lactation. J. Dairy Sci. 59, 965–973.

MacFarlane, W.V., Howard, B., 1972. Comparative water and energy economy of wild and domestic mammals. Symp. Zool. Soc. Lond. 31, 261–296.

McLean, J.A., 1963. The partition of insensible losses of body weight and heat from cattle under various climatic conditions. J. Physiol. (Lond.) 167, 427–434.

McLean, J.A., Stombaugh, D.P., Downie, A.J., Glasbey, C.A., 1983. Body heat storage in steers (*Bos taurus*) in fluctuating thermal environment. J. Agric. Sci. Camb. 100, 315–322.

Magdub, A.B., Johnson, H.D., Belyea, R.L., 1982. Effect of environment heat and dietary fiber on thyroid physiology of the lactating cows. Int. J. Biometeorol. 25, 2323–2329.

Maltz, E., Olsson, K., Glick, S.M., Fyhrquist, F., Silanikove, N., Choshniak, H., Shkolnik, A., 1984. Homeostatic responses to water deprivation or haemorrhage in lactating and non-lactating Bedouin goats. Comp. Biochem. Physiol. 77A, 79–84.

Maltz, E., Silanikove, N., Shalit, U., Berman, A., 1994. Diurnal fluctuations in plasma ions and water intake of dairy cows as affected by lactation in warm weather. J. Dairy Sci. 77, 2630–2639.

Manteca, X., Smith, A.J., 1994. Effects of poor forage conditions on the behaviour of grazing ruminants. Trop. Anim. Health Prod. 26, 129–138.

Montgomery, I., Jenkinson, D.M., Elder, H.Y., Czarnecki, D., Mackie, R.M., 1984. The effects of stimulation on the ultrastructure of the human atrichial sweat gland. 1. The fundus. Br. J. Dermatol. 110, 319–320.

Morgan, M., 1998. Thermoneutral zone and critical temperatures of horses. J. Therm. Biol. 23, 59–61.

Mount, L.E., 1973. The concept of thermal neutrality. In: Monteith, J.L., Mount, L.E. (Eds.), Heat Loss from Animals and Man Assessment and Control. Butterworth, London, pp. 425–435.

Muller, C.J.C., Botha, J.A., Smith, W.W., 1994a. Effect of shade on various parameters of Friesian cows in a Mediterranean climate in South Africa. 1. Feed and water intake, milk production and milk composition. South Afric. J. Anim. Sci. 24, 49–55.

Muller, C.J.C., Botha, J.A., Coetzer, W.A., Smith, W.W., 1994b. Effect of shade on various parameters of Friesian cows in a Mediterranean climate in South Africa. 2. Physiological responses. South Afric. J. Anim. Sci. 24, 56–60.

Muller, C.J.C., Botha, J.A., Smith, W.W., 1994c. Effect of shade on various parameters of Friesian cows in a Mediterranean climate in South Africa. 3. Behavior. South Afric. J. Anim. Sci. 24, 61–66.

Niwano, Y., Becker, B.A., Mitra, R., Caldwell, C.W., Abdalla, E.B., Johnson, H.D., 1990. Suppressed peripheral blood lymphocyte blastogenesis in pre- and postpartal sheep by chronic heat-stress, and suppressive property of heat-stressed sheep serum on lymphocytes. Dev. Comp. Immunol. 14, 139–149.

Ocfemia, G.O., Sharun, A., Miller, H.M., Holmes, J.H.G., 1993. Reduced foetal growth and lactation by does heat-stressed from mid-pregnancy. Small Rumin. Res. 11, 33–43.

Olsson, K., Josater-Hermelin, M., Hossaini-Hillali, J., Cvek, K., Hydbring, E., Dahlborn, K., 1995. Heat stress causes excessive drinking in fed and food deprived pregnant goats. Comp. Biochem. Physiol. 110A, 309–317.

Richards, J.I., 1985. Milk production of Friesian cows subjected to high daytime temperatures when food either ad lib or at nighttime only. Trop. Anim. Health Prod. 17, 141–152.

Roberts, G., 1984. Plotting a better future for lambs: a practical guide to providing shade [Heat stress reduction, sheep production, *Tamarix articulata*, Queensland]. Queensland Agric. J. 110, 25–26.

Robertshaw, D., 1981. The environmental physiology of animal production. In: Clark, J.A. (Ed.), Environmental Aspects of Housing for Animal Production. Butterworth, London, pp. 3–17.

Robertshaw, D., Vercoe, J.E., 1980. Scrotal thermoregulation of the bull (*Bos* spp.). Aust. J. Agric. Res. 31, 401–407.

Robertshaw, D., Damiel, R., 1983. The effect of dehydration on the control of panting and sweating in the black Bedouin goat. Physiol. Zool. 56, 412–418.

Roman-Ponce, H., Thatcher, W.W., Buffington, D.E., Wilcox, C.J., van Horn, H.H., 1977. Physiological and production responses of dairy cattle to shade structure in a subtropical environment. J. Dairy Sci. 60, 424–430.

Schmidt-Nielsen, K., 1964. Desert Animals: Physiological Problems of Heat and Water. Clarendon Press, Oxford.

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

Scott, I.M., Johnson, H.D., Hahn, G.L., 1983. Effect of programmed diurnal temperature cycles on plasma thyroxine level, body temperature, and feed intake of Holstein Dairy cows. Int. J. Biometeorol. 27, 47–62.

Shalit, O., Maltz, E., Silanikove, N., Berman, A., 1991. Water, Na, K, and Cl metabolism of dairy cows at onset of lactation in hot weather. J. Dairy Sci. 74, 1873–1874.

Shebaita, M.K., El-Banna, I.M., 1982. Heat load and heat dissipation in sheep and goats under environmental heat stress. In: Proc. 6th Int. Conf. on Animal and Poultry Production, held at University of Zagazig, Zagazig, Egypt, 21–23 September 1982, Vol. 2. Egyptian Society of Animal Production, pp. 459–469.

Silanikove, N., 1987. Impact of shade in hot Mediterranean summer on feed intake, feed utilization and body fluid distribution in sheep. Appetite 9, 207–215.

Silanikove, N., 1989. Interrelationships between water, food and digestible energy intake in desert and non-desert goats. Appetite 12, 163–170.

Silanikove, N., 1992. Effects of water scarcity and hot environment on appetite and digestion in ruminants: a review. Livest. Prod. Sci. 30, 175–194.

Silanikove, N., 1994. The struggle to maintain hydration and osmoregulation in animals experiencing severe dehydration and rapid rehydration: the story of ruminants. Exp. Physiol. 79, 381–400.

Silanikove, N., 1997. Why goats raised on harsh environment perform better than other domesticated animals. Options Méditerranénnes 34 (Ser. A), 185–194.

Silanikove, N., 2000. The physiological basis of adaptation of goats to scarcity of food and water in harsh environments. Small Rumin. Res. 35, 181–193.

Silanikove, N., Tadmor, A., 1989. Rumen volume saliva flow-rate, and systemic fluid homeostasis in dehydrated cattle. Am. J. Physiol. 256, R809–R815.

Silanikove, N., Gutman, M., 1992. Interrelationships between lack of shading shelter and poultry litter supplementation: feed intake, body weight, water metabolism and embryo loss in beef cows grazing dry Mediterranean pasture. Anim. Prod. 55, 371–376.

Silanikove, N., Tiomkin, D., 1992. Toxicity induced by poultry litter consumption: Effect on parameters reflecting liver function in beef cows. Anim. Prod. 54, 203–209.

Silanikove, N., Holzer, Z., Cohen, D., Benjamin, R., Gutman, M., Meltzer, A., 1987. Interrelationship between metabolism of tritiated water, ^{22}sodium and dry matter intake in beef cows fed poultry litter and wheat straw in free choice. Comp. Biochem. Physiol. 87A, 113–118.

Silanikove, N., Maltz, E., Halevi, A., Shinder, D., 1997. Metabolism of water, sodium, potassium and chlorine by high yielding dairy cows at the onset of lactation. J. Dairy Sci. 80, 949–956.

Singh, S.P., Newton, W.M., 1978. Acclimatization of young calves to high temperatures:responses. Am. J. Vet. Res. 39, 795–797.

Stephenson, R.G.A., Suter, G.R., Le-Feuvre, A.S., 1984. Reduction of the effects of heat stress on lamb birth weight and survival by provision of shade. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in Sheep. Cambridge University Press, Cambridge, pp. 223–225, Australian Wool Corporation Technical Publication.

Stewart, R.E., Brody, S. (Eds.), 1954. Effect of radiation intensity on hair and skin temperatures and on rates of Holstein, Jersey and Brahman cattle at air temperatures 45, 70 and 80°F. Agricultural and Experimental Station Research, University of Missouri, Bulletin 561.

Stott, G.H., Wiersma, F., Woods, J.M., 1972. Reproductive health program for cattle subjected to environmental temperatures. J. Am. Vet. Med. Assoc. 16, 1339–1344.

Thatcher, W.W., 1974. Effects of season, climate and temperature on reproduction and lactation. J. Dairy Sci. 57, 360–368.

Thomas, C.K., Pearson, R.A., 1986. Effects of ambient temperature and heat cooling on energy expenditure, food intake and heat tolerance of Brahman and Brahman×Fresian cattle working on treadmills. Anim. Prod. 43, 83–90.

Webster, A.J.F., 1991. Metabolic responses of farm animals to high temperature. Eur. Assoc. Anim. Prod. 55, 15–22.

West, J.W., 1999. Nutritional strategies for managing the heat-stressed dairy cow. J. Anim. Sci. 77 (Suppl. 2), 21–35.

Winchester, C.F., Morris, M.J., 1956. Water intake rates of cattle. J. Anim. Sci. 15, 722–729.

Yamamato, S., Young, B.A., Purwanto, B.P., Nakamasu, F., Natsumoto, T., 1994. Effect of solar radiation on the heat load of dairy heifers. Aust. J. Agric. Res. 45, 1741–1749.

Young, B.A., 1993. Implication of excessive heat load to the welfare of cattle in feedlots. In: Farell, D.J. (Ed.), Recent Advances in Animal Nutrition in Australia. University of New England, Armidale, Australia, pp. 45–50.

Yousef, M.K. (Ed.), 1985. Stress Physiology in Livestock. Basic Principles, Vol. 1. CRC Press, Boca Raton, FL.