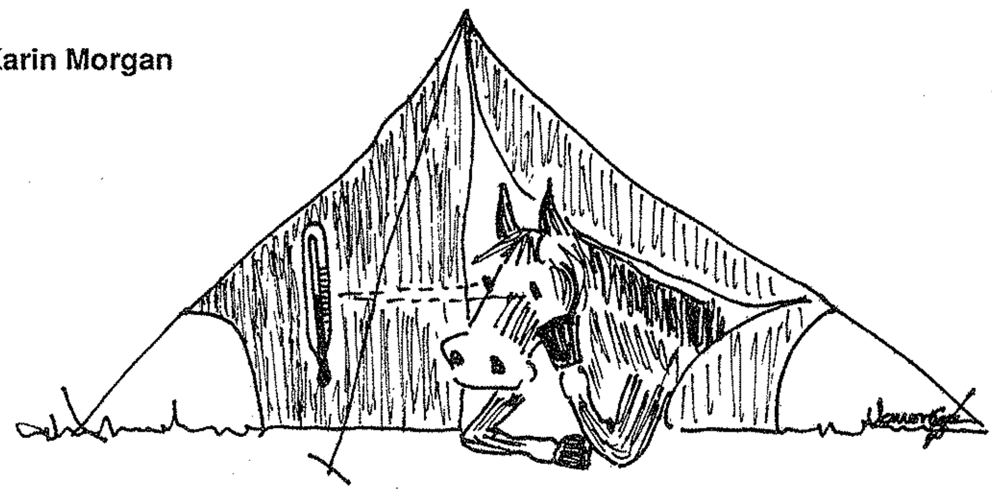
SHORT-TERM THERMOREGULATORY RESPONSES OF HORSES TO BRIEF CHANGES IN AMBIENT TEMPERATURE

Karin Morgan



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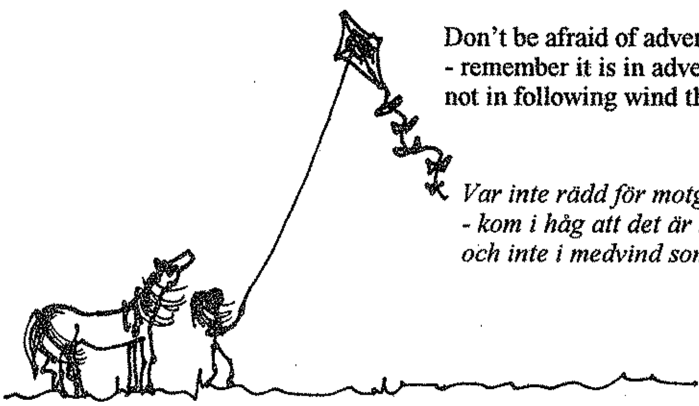
To my dear family and friends



Don't be afraid of adversity
- remember it is in adverse wind and
not in following wind that the kite flies.

Unknown

Var inte rädd för motgång
- kom i håg att det är i motvind
och inte i medvind som en drake stiger

Okänd

ABSTRACT

The first objective of this thesis is to study thermoregulation in standing horses, especially the short-term physiological responses to brief changes in the thermal environment. My hypothesis is that the characteristics of the thermoregulatory system reflects the evolutionary background of horses. Horses evolved on the steppe, where they lived in herds and fled when in danger. As homeothermic animals, they have to maintain an almost constant body core temperature by losing excess heat from a constantly on-going internal heat production despite changes in the thermal environment. On the steppe, temperature, radiation and wind can vary greatly, which affects the means of heat loss. In case of flight, the horse has to lose the heat load induced by muscular work so as to restore the body temperature.

A second objective is to measure the thermal properties and heat losses of horses to improve the management and housing of horses.

The study was performed in a climatic chamber on five horse at six different temperature levels: -3°C, 6°C, 15°C, 20°C, 30°C and 37°C. The results, discussed in the frame story, are presented in four articles:

I. Dissipation of heat from standing horses exposed to ambient temperatures between -3°C and 37°C.

II. Thermal insulance of peripheral tissue and coat in horses.

III. Effects of short-term changes in ambient air temperature or altered insulation in horses.

IV. Climatic energy demand of horses.

I found that horses increase evaporative heat loss (50 - 450 W m^{-2}) by sweating and by increasing respiratory rate in warm and hot environments. This is a mechanism, that is evolved to handle the exercised-induced heat load. The evaporative heat loss is regulated by both body core and skin temperature. The tissue thermal insulance (0.015 - 0.100 m^2 K W^{-1}) is an evolutionary compromise to provide insulation but not to be limiting to the processes of sweating. The coat, being a thin insulating layer of hair, is probably the best physical compromise for allowing the skin to lose heat by evaporation whilst providing protection from heavy solar loads during the day and radiative heat loss at night. However, in cold environments the insulation may not be sufficient to maintain body temperature. Since horses evolved to graze for most of the day, they can compensate for an excessive heat loss by regulating the feed intake. In cold climates, the horse needs extra feed, called climatic energy demand, which is estimated to 2.78 W m^{-2} per degree Celcius below the lower critical temperature. The thermoneutral zone for the horses in the study is estimated to range from 5°C to 25°C. The fact that horses live in a herd is an advantage since it enables the herd members to protect and help each other to handle different thermal environments, e.g. by standing close together to limit the exposed area.

In conclusion my synthesis of the study is that the thermoreglatory system of the horse has characteristics that are advantageous for an animal that has been evolved to be able to flee when in danger and to live freely on the steppe.

Keywords: horse; thermoregulation; heat loss; heat dissipation; evaporative heat loss; latent heat loss; non-evaporative heat loss; sensible heat loss; thermal property; thermal insulance; thermal resistance; body temperature; heart rate; respiratory rate; altered insulation

CONTENTS

PRESENTATION OF THE THESIS

The thesis deal with both the physiological responses of the horse and the interaction with the physical environment through the heat loss in relation to brief changes in ambient temperature. Some short-term mechanisms of regulation are discussed. In the general discussion some practical aspects of the thermoregulation and thermal comfort are discussed dealing with housing and management of horses. This thesis is based on four articles listed below. The first article deals with heat loss from the horse and how the heat loss divides in non-evaporative and evaporative heat loss, when the ambient temperature changes. The second article deals with the insulation and the thermal properties of the the tissue and the coat. The third article presents the physiological responses of body temperature, heart rate and respiratory rate when the ambient temperature changes or when the ambient temperature is constant but the insulation of the horse is altered. The fourth article presents how much extra feed the horse needs when the ambient temperature is below the lower critical temperature. In the text, they are referred to by their respective Roman numerals. The results from the seperate articles are summarized and discussed in the frame story, where a physiological parameter is related to the relevant means of heat loss.

I. **Morgan. K., Ehrlemark, A. and Sällvik, K.** Dissipation of heat from standing horses exposed to ambient temperatures between -3°C and 37°C. The manuscript was submitted to *Journal of Thermal Biology* in March 1996.

II. **Morgan, K.** Thermal insulance of peripheral tissue and coat in horses. The manuscript was submitted to *Journal of Thermal Biology* in February 1996.

III. **Morgan, K.** Effects of short-term changes in ambient air temperature or altered insulation in horses. The manuscript was submitted to *Journal of Thermal Biology* in March 1996.

IV. **Morgan, K.** 1995. Climatic energy demand of horses. *Equine Veterinary Journal Supplement* **18**, pp. 396-399.

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A SHORT GLOSSARY

Some of the key words are explained in English and in Swedish (*italics*)to help the reader unfamiliar with the subject. The glossary is from Bligh & Johnson (1973).

AMBIENT TEMPERATURE: The average temperature of the gaseous or liquid environment (usually air or water) surrounding the body, as measured outside the thermal and hydrodynamic boundary layers overlaying the body. *Omgivningens temperatur.*

CALORIMETRY: The measurement of heat. In thermal physiology, the measurement of heat transfer between a tissue, an organ or an organism and its environment. *Värmemätning. I termisk fysiologi mäter man värmeöverföring mellan vävnad, organ eller mellan en organism och omgivningen.*

EVAPORATIVE HEAT LOSS: The heat loss by evaporation of water from the skin and the surfaces of the respiratory tract. Synonym of latent heat loss. *Vämeavgivning på grund av avkylning när vatten avdunstar från huden eller slemhinnorna i andningsvägarna. Även kallad bunden värmeavgivning eller latent värmeavgivning. Storleken av värmeavgivningen beror främst på skillnad i ångtryck mellan huden/slemhinnan och omgivningen.*

HEAT LOSS: The heat transfer from an organism to the environment, or from one part of an organism to another, by conduction, convection, radiation, evaporation, or a combination of these. Synonym of heat dissipation. *Värmeöverföring från en organism till omgivningen, eller från en del till en annan inom en organism, genom ledning, strömning, strålning och avdunstning eller en kombination av dessa.*

METABOLISM: The sum of the chemical changes in living matter in which energy is transformed. *Ämnesomsättning.*

METABOLIC RATE: The free energy production in the organism per unit time. *Ämnesomsättning per tidsenhet.*

NON-EVAPORATIVE HEAT LOSS: The sum of heat losses by radiation, convection and conduction. Synonym of dry heat loss, sensible heat loss, Newtonian heat loss. *Fri värmeavgivning, summan av värmeförluster genom strålning, strömning och ledning. Storleken på den fria värmeavgivningen beror till stor del på temperaturskillnaden mellan två medier, men även faktoer som lufthastighet samt objektets storlek och form, mm. inverkar.*

RATE OF HEAT LOSS: The heat loss of a given surface area in unit time [W m^{-2}]; short for density of heat flow rate. *Värmeflödestäthet, dvs hur mycket värmeenergi som förloras per tidsenhet per ytenhet* [W m^{-2}].

THERMAL COMFORT: Subjective satisfaction with the thermal environment. *Subjektiv tillfredsställelse med omgivningsklimatet.*

THERMAL INSULANCE: Thermal insulation expressed for a layer and insulance defines the thermal property of a material [$m^2 K W^{-1}$]. The thermal insulance is not related to the size of the horse. *Värmemotstånd - ett mått som beskriver en materialegenskap, dvs. isolering över ett skikt av materialet. Värmemotståndet är oberoende av hästens storlek* [$m^2 K W^{-1}$].

THERMAL RESISTANCE: Measurement of thermal insulation for a whole animal [KW^{-1}]. The thermal resistance is related to the size of the actual horse. *Värmeresistans - ett mått på hela djurets värmeisolering* [$K W^{-1}$].

It is important for the reader to know and understand that heat loss [W] and thermal resistance [$K W^{-1}$] are related to the entire animal. The rate of heat loss [$W m^{-2}$] and the thermal insulance [$m^2 K W^{-1}$], on the other hand, are related to a specific area of the animal. This is illustrated in Figure 1.

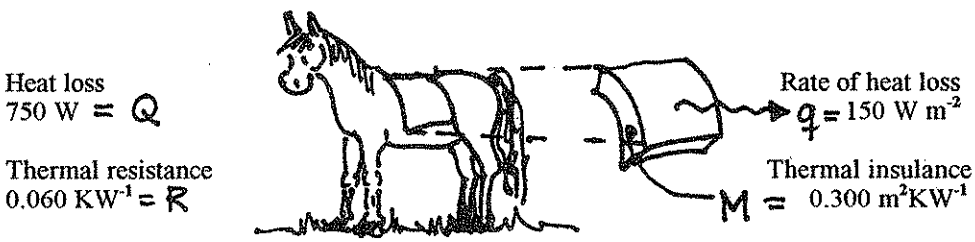


Figure 1. An example of a 500 kg horse illustrating the difference between heat loss and rate of heat loss and thermal resistance and thermal insulance.

INTRODUCTION

Horses have evolved to live free on the steppe. They live in herds and flee in the threat of danger. They seek food and graze for the most part of their time. The digestive system, with a small stomach and large intestines, is designed for an even and constant feed intake. Their thermal environment changes with time and location. It is a challenge for a homeothermic animal like the horse to maintain a constant body core temperature. The internal physiological systems must make alterations dynamically to adjust to the changing external physical environmental conditions created by wind speed, radiation, humidity, air temperature and rain or snow and to internal heat production.

In the management of the horse the thermal environment will change with time and location. In Sweden horses are mainly kept in insulated and ventilated stables, where the inside air temperature usually maintains between 5 and 15°C during the winter. They are let outside to a paddock during the day. The thermal environment outside will often differ from the stable indoor climate. In winter, outdoor temperatures can be 40°C colder than the indoor temperature. In the summer, it can be 15°C warmer outdoors as compared to in the stable. When the horse exercises, it will acquire an extra heat load which must be dissipated during and after the work. Today, horses travel to different part of the world to compete and thus can be exposed to a totally new climatic situation. The new and different thermal environment may affect the performance of the horse. Transportation per se can also entail thermal stress on the horse. Hence there is a need to improve knowledge about the thermoregulatory system of horses, for a better understanding of how the thermal environment will affect the horse and to enable facilitation of the thermal comfort of the horse in different situations. Increased knowledge of the thermoregulatory system and its controlling strategies in horses can improve the management and housing of horses with regard to thermal comfort.

Body temperature

A homeothermic animal such as the horse regulates its body temperature to an almost constant level. The normal body temperature for horses is 37.2°C - 38.2°C measured as rectal temperature. A number of conditions can influence body temperature, including exercise, time of day, environmental temperature, digestion, and drinking of water. Also, different parts of the body can differ in temperature because of differences in metabolic rate, blood flow, or distance from the surface. (Reece 1991)

Control of body temperature

The aim for the control system for the body temperature is to keep the body temperature at a constant level. This is a very important function of the body. The feed-back gain of the total mechanism for control of body temperature is extremely high. For instance, it is more than ten times faster than the feed-back gain of the baroreceptor arterial pressure control system. The temperature level that the temperature control system aim to keep can be called the set-point. All temperature control mechanisms continuously attempt to bring the body temperature back to this set-point. The set-point for the body temperature can vary and shift within a narrow limit due to skin temperature, season, fever etc (Guyton, 1991; Christopherson, 1994). Horses maintain homeothermy in high temperatures by regulating evaporative heat loss to keep body temperature down to a set-point (Webster, 1991). The controlling mechanisms of temperature has been descibed by Guyton (1991), as follows. The temperature of the body is controlled almost entirely by nervous feedback mechanisms, and almost all of these operate through the temperature-regulating centres located in the hypothalamus. The anterior hypothalamic-preoptic area contains a large number of heat-sensitive neurons and about a third as many cold-sensitive neurons. There are also peripheral temperature receptors in the skin and deep body tissue. The latter are located mainly in the spinal cord, abdominal viscera and in and around major veins. The peripheral receptors are mainly concerned with detecting cool and cold temperatures. The thermal senses respond markedly to changes in temperature in addition to being able to respond to steady states of temperature. The signals transmitted as impulses and the frequency of discharge is used as information. The temperature signals from the peripheral receptors and the temperature sensitive neurons in the anterior hypothalamic-preoptic area are transmitted to the posterior hypothalamus. The temperature signals are combined and compared with the set-point in the posterior hypothalamus and the deviation from the set-point generate heat-producing and heat-conserving reactions in the body. (Guyton, 1991).

Bligh & Johnson (1973) calculated a mean body temperature index in man which differs between warm and cold environment (Equations 1a and 1b).

$t_{body} \cong 0.90\ t_{tympanic} + 0.10\ t_{skin}$ man in warm environment (1a)

$t_{body} \cong 0.67\ t_{tympanic} + 0.33\ t_{skin}$ man in cold environment (1b)

where

t_{body}	body temperature	[°C]
$t_{tympanic}$	tympanic temperature	[°C]
t_{skin}	skin temperature	[°C]

My interpretation of the Equations 1a and 1b is that in a warm environment the central body temperature, $t_{tympanic}$, is most important for regulation. In a cold environment the skin temperature, t_{skin}, is of importance, even though, the central temperature still is of major importance. This agrees with Guyton's (1991) statement that the skin receptors are most sensitive for cold and the central receptors are most sensitive for warm temperatures.

Heat balance

The almost constant body temperature is accomplished by a balance between produced heat and dissipated heat. In some situations, for instance during exercise, heat production will be greater than the heat loss. Part of the produced heat will then be stored in the body and the body temperature increases. At rest, there is usually no heat storage. The basic heat balance is described on a general basis by Equation 2 (Bianca, 1968);

Heat production = Heat loss ± Heat storage (2)

Heat production

Heat is produced as a by-product of the metabolism when feed is converted and also from muscular activity or hormonal processes (Young, 1975; Guyton, 1991). The energy supplied to the metabolism derives from the feed. The utilization of the intake of feed energy within the animal is shown in Figure 2. The total energy intake divides into digestible energy and energy in faeces. The digestible energy separates into metabolisable energy and energy in urine and gases. The major part of metabolisable energy will be heat and a minor part will be stored in the body's tissues or products.

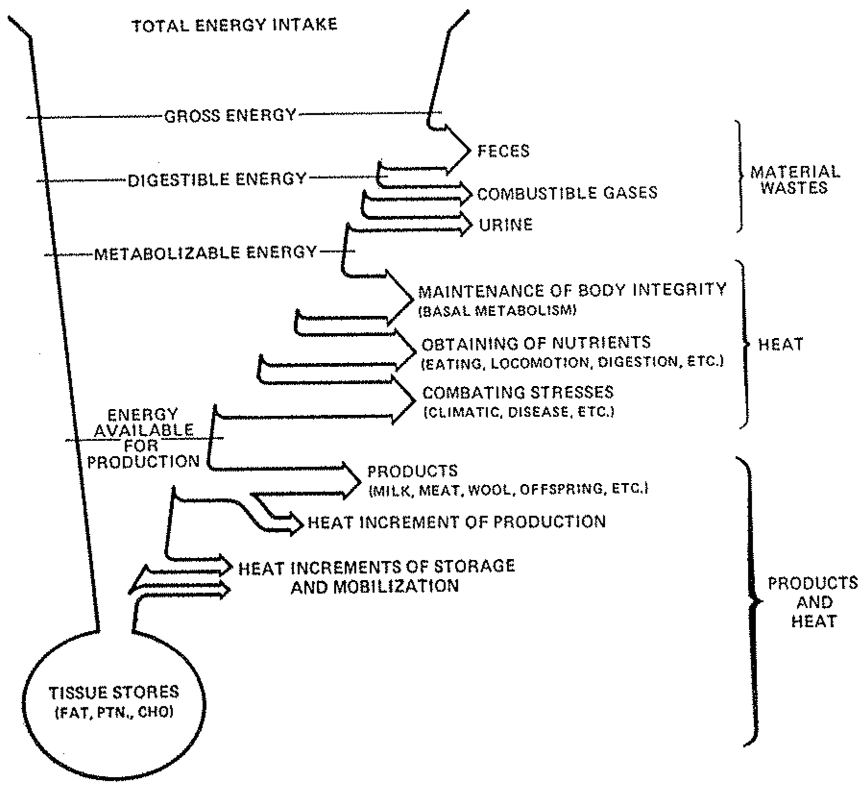


Figure 2. Schematic representation of the flow of energy through an animal (Young, 1975).

Pagan & Hintz (1986) and Wooden *et al* (1970) have studied the heat production of horses in a thermoneutral environment. The four horses in the study of Pagan & Hintz (1986) were fed a pelleted feed containing 75% alfalfa meal and 25% oats. The two horses in the study of Wooden *et al* (1970) were fed hay and concentrate.

The results of these studies are presented and analysed in the diagram in Figure 3. There seems to be a relationship between the amount of metabolizable energy (ME) and the proportion of heat production (HP/ME). An analysis of the relationship gives a linear equation with a regression coefficient R^2=0.93. (Equation 3). The equation can be considered valid when feeding both hay and concentrate and within this particular span of energy intake.

$$HP/ME = 1.2 - 0.649 * ME \qquad (3)$$

where

HP/ME ratio heat production to metabolisable energy

ME daily metabolisable feed intake energy [MJ $kg^{-0.75}$]

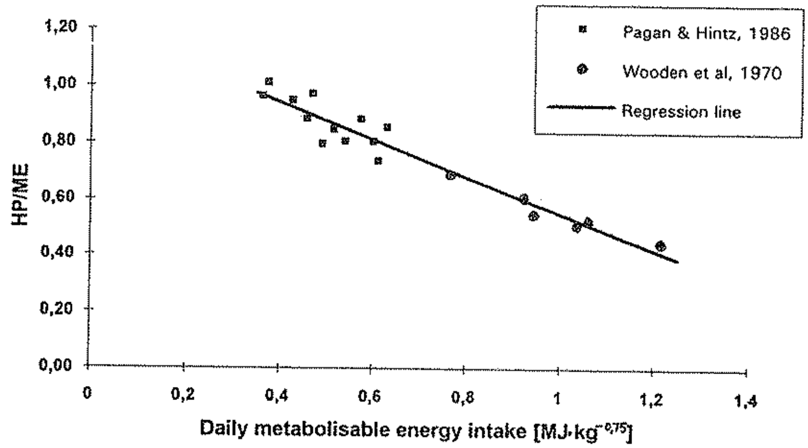


Figure 3. The diagram shows the ratio between heat production and metabolisable feed energy intake in relation to metabolisable feed energy intake, from analysis of Pagan & Hintz (1986) and Wooden *et al* (1970).

Studies of energy metabolism such as these by Pagan & Hintz (1986) and Wooden *et al* (1970) are performed with the horse in a metabolism stall and in a thermoneutral environment. However, a normal activity compared to immobility in a metabolism stall or decreased ambient temperatures will demand more feed energy. Cymbaluk (1990) argued that a correction of 29% more energy is needed for horses under normal activity compared to results of studies like Pagan & Hintz (1986) and Wooden *et al* (1970), since the results are based on horses in metabolism stall and in a thermoneutral environment. McBride *et al* (1983) measured heat production in six mature Quarter Horse geldings. They were fed 12 kg medium quality hay (90% brome, 10% legume) per day. The horses were housed in outdoor pens. They were brought inside a climatic chamber for a measuring period of six hours. Data for oxygen uptake and carbon dioxide output were collected to calculate heat production. The results for heat production were related to ambient temperature inside the climatic chamber and are presented diagrammatically in Figure 4.

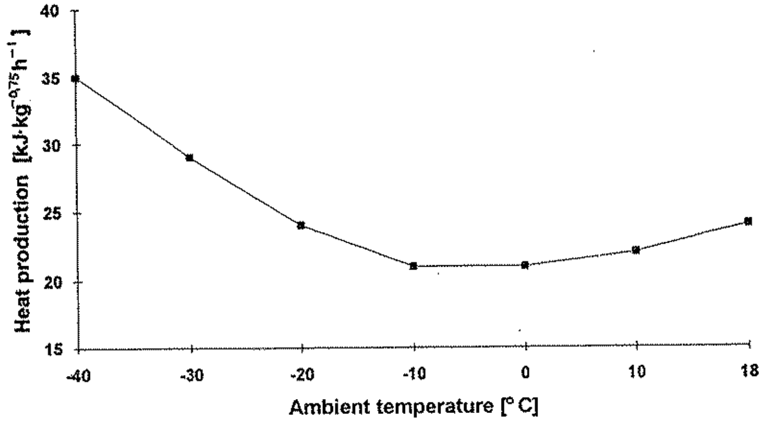


Figure 4. Heat production of horses in relation to ambient temperature (McBride *et al*, 1983).

The conclusion is that the heat production will vary with both the feed energy intake (Pagan & Hintz, 1986; Wooden *et al*, 1970) and with the ambient temperature (McBride *et al*, 1983). When the horse is fed for maintenance the qoutient HP/ME = 1.0 per definition. There will be no energy gain in or loss from the body. If HP/ME > 1.0 energy will be taken from the reserve of energy stored in the body and the animal will lose weight. When HP/ME < 1.0 energy will be stored in the tissue. When the ambient temperature changes this will affect the slope of the line since, the digestibility of the feed can change in relation to environmental conditions (Cymbaluk & Christison, 1990). A sudden change in metabolic heat production, like shivering, will create a step to a new level of heat production.

Heat loss and its regulation

The total heat loss is divided into radiation, convection, conduction and evaporation from the surface of the animal and convection and evaporation from the respiratory system. The different means of heat loss is shown in figure 5. The area on the horses for the different means of heat loss vary. The total heat loss from a horse will be the respiratory heat loss and the sum of the rates of heat loss times the exposed area, Equation 4:

$$Q_{tot} = A_{rad} * q_{rad} + A_{conv} * q_{conv} + A_{cond} * q_{cond} + A_{evap} * q_{evap} + Q_{resp} \quad (4)$$

where

Q_{tot}	total heat loss	[W]
A_{index}	exposed area of heat loss	[m^2]
q_{index}	rate of heat loss, where index gives type of heat loss	[W m^{-2}]
Q_{resp}	respiratory heat loss	[W]

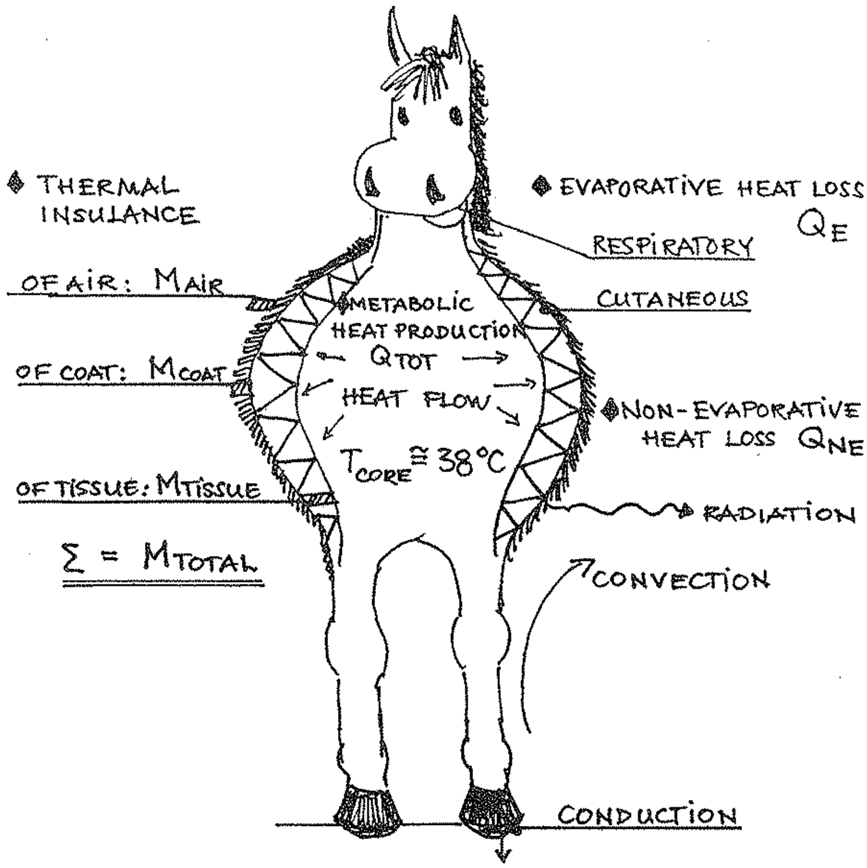


Figure 5. The principle of heat production in and heat loss from a horse. The three layer of thermal insulation are also shown.

There are, however, difficulties in estimating heat loss from animals, since the surface area is a very important factor. Non-evaporative heat exchange between a solid body and its surroundings takes place at a well defined surface. In contrast the surface of an animal's hair covered body is not distinct. Measurement of the area of this interface presents difficulties (McArthur & Monteith, 1980). Another difficulty is that the non-evaporative heat loss (radiation, convection and conduction) and evaporative heat loss can interact, which can affect how the heat loss divides.

To illustrate the principle of estimating heat loss from an animal an analogue with Ohm's law of potential difference, resistance and currrent is often used (McArthur, 1987; Ehrlemark, 1988). Figure 6-8 and Equations 5-7 show the principle of Ohm's law and the analogue with non-evaporative and evaporative heat loss.

$I = (U_1 - U_2) / r$ (5)

where

I	current	[A]
$U_1 - U_2$	potential difference	[V]
r	resistance	[Ω]

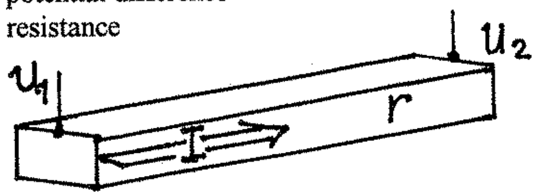


Figure 6. Schematic representation of Ohm's law, where I is current, $(U_1 - U_2)$ represents the potential difference and r is the resistance.

$Q_{ne} = (T_1 - T_2) / M$ (6)

where

Q_{ne}	non-evaporative heat flow	[$W\ m^{-2}$]
$T_1 - T_2$	temperature difference	[K]
M	thermal insulance	[$m^2\ K\ W^{-1}$]

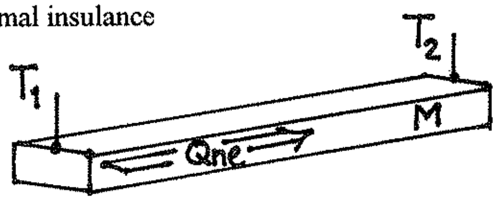


Figure 7. Schematic representation of the non-evaporative heat loss, where Q_{ne} is the non-evaporative heat flow, $(T_1 - T_2)$ represents the temperature difference and M is the thermal insulance.

$Q_{evap} = \lambda * (e_1 - e_2) / z$ (7)

where

Q_{evap}	evaporative heat flow	[$W\ m^{-2}$]
λ	latent heat of vaporisation of water	[$J\ kg^{-1}$]
$e_1 - e_2$	difference in water vpour concentation	[$kg\ m^{-3}$]
z	resistance to water vapour transfer	[$s\ m^{-1}$]

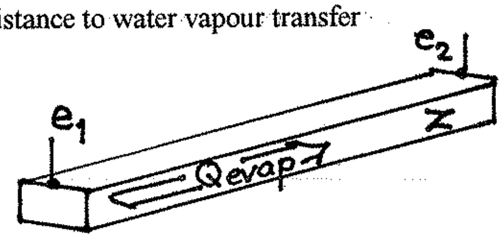


Figure 8. Schematic representation of the evaporative heat loss, where Q_{evap} is the evaporative heat flow, $(e_1 - e_2)$ is the difference in water vapour concentration and z is the resistance to water vapour transfer.

Regulation of non-evaporative heat loss

The rate of non-evaporative heat loss is directly proportional to a temperature difference; Equation 6 and Figure 7. To regulate the non-evaporative heat loss, either the thermal insulance M or the temperature difference (T_1 - T_2) in Equation 6 can be altered. The thermal insulance M is the insulating properties of the animal. An increase in insulation will directly decrease the non-evaporative heat loss, but will also operate indirectly since it affects the temperature difference. Greater insulation will lower the surface temperature, hence the temperature difference between the surface and the environment decreases and consequently the non-evaporative heat loss will decrease.

The total insulation between an animal's body core and its environment is provided by three thermal insulating layers acting in series: the peripheral body tissue, the coat and the boundary layer of air (McArthur, 1981, 1991) (Figure 5). The insulation can be regulated by both short-term and long-term measures. Vasocontrol of rate of blood flow to the peripheral tissue is a short-term physiological regulator of the insulation (Worstell & Brody, 1953; McArthur, 1987). The ratio between minimal tissue insulance at vasodilation and maximal tissue insulance at vasoconstriction is approximately 1 to 8 in man (Guyton, 1991). Piloerection of the coat is another short-term physiological regulator of the insulation. Young & Coote (1973) found in horses that the coat depth increased by 10-30% due to piloerection in acute cold. In a long term perspective in a cold climate, animals develop insulation to ensure that non-evaporative heat loss is within their capacity to produce heat (McArthur & Clark, 1987) The amount of subcutaneous fat and the coat length, depth and density can be altered to affect the insulation. The fat conducts heat only one-third as readily as other tissues (Guyton, 1991). In sheep, McArthur & Monteith (1980b) found that the thermal properties of fleece depend on the depth and type of wool. The level of insulation of the coat will also depend on the physical environment. The thermal properties of the hair layer depend in part on differences in temperature and vapour pressure across it (McArthur, 1990). Insulation is always decreased by the effects of wind, but the extent of the decrease depends on both the type of coat and on the wind direction (Cena & Clark, 1979). The change in the coat length, depth and density of a horse can be compared to the process in cattle. Christopherson & Young (1986) described the thickness of haircoat in cattle as a function of rates of hair growth and shedding. Increased winter hair growth is induced by shorter daily photoperiods and cold exposure reduces shedding. Cymbaluk (1990) also states that hair shedding and growth in horses varies with photoperiod: however, with the same light régime the temperature, as well as the photoperiod, has a regulatory function. Furthermore that study found that cold housed horses had 1.4-2 times higher a haircoat weight than warm housed horses (Cymbaluk, 1990).

Regulation of evaporation

When the ambient air temperature increases the potential for non-evaporative heat loss is reduced. In order to maintain heat balance the animal must rely on the evaporation of water to dissipate heat generated by metabolism (McArthur & Clark, 1987). The evaporative heat loss divides in evaporation in the respiratory tract and evaporation from the skin. The potential rate of evaporation is determined by the vapour pressure difference between the surface and the air. At high temperatures, for both man and equidae heat loss by sweat is limited by the physical resistance to transfer of water vapour through the coat or clothes rather than by physiological control of sweat secretion (Cena & Clark, 1979).

Man, horse and cow are species that respond by sweating when there is an increase in either or both the ambient temperature and the internal heat load. Man has both eccrine and apocrine sweat glands whilst the horse and cow have only apocrine sweat glands (Reece, 1991). The sweat glands of man and horse respond to stimulation by adrenaline and acetylcholine (Guyton, 1991; Jenkinson, 1972). The sustained activity of hunting, as in man (predator) and horses (prey), gives sweating a distinct advantage over panting (Bligh, 1972). Cows differ from horses, since cows pant to a larger extent and the respiratory evaporative heat loss is one-third of the total evaporative heat loss in a hot, dry environment (Jenkinson, 1972).

The regulation of evaporative heat loss in relation to core, skin and ambient temperature has been investigated in humans, cattle and donkeys (Gagge, 1937; Wurster *et al*, 1966; Whittow & Findley, 1968; Bullard *et al*, 1970; Berman, 1971; Gatenby, 1986). Gagge (1937) found that sweating in humans began to increase at a certain ambient temperature. Gatenby (1986) showed in cattle an exponential relation between sweat rate and skin temperature in a hot environment. Bullard *et al* (1970) showed the onset of sweating in donkeys to be a step function where sweat rate was correlated to mean body temperature, which depended on both skin and core temperature. The overall sweating in the donkeys did not stop until general body cooling had occurred. Wurster *et al* (1966) in their study on humans concluded that during a non steady state, neither tympanic nor mean skin temperature may be considered solely responsible for the onset or cessation of sweating. Both tympanic and skin temperature have relevance to central nervous control. Whittow & Findley (1968) found that a localized heating of the anterior hypothalamus in oxen significantly increased respiration rate and also increased cardiac output. Hot and humid environmental conditions also increased respiration rate and cardiac output in oxen. Berman (1971) studied seasonal differences on regulatory responses measured in the summer (25-39°C) and in the winter (9.5 - 24°C). A small change in mean tympanic temperature was found, but variations in the effects of skin and tympanic temperature on the thermoregulatory responses (Berman, 1971). Guyton (1991) stated that the regulation of thermoregulatory physiological responses is performed by the posterior hypothalamic area, where signals from the anterior pre-optic area and signals from peripheral receptors are integrated. According to what thermal environment an animal is acclimatized, the specific hypothalamic set-point level at which sweating begins is determined by internal head temperature and skin temperature. This is illustrated in Figure 9. Based on this background of regulation of evaporative heat loss, I decided to evaluate the importance of both skin and body core temperature in the regulation of evaporative heat loss from my results.

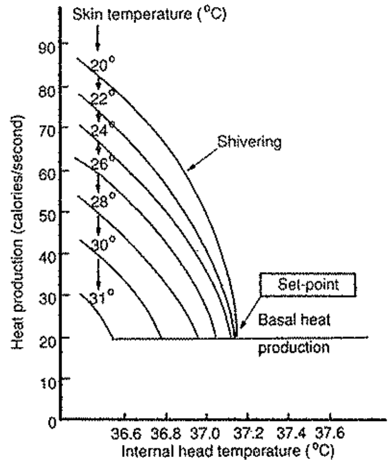


Figure 9. The relationship between internal head temperature and skin temperature in regulation of sweating (Guyton, 1991).

Acclimatisation

Horses that are moved permanently to hot conditions will acclimatize to adjust the evaporative heat loss so that total heat loss equals heat production. Burton *et al* (1940) showed that slow adaption of men to heat had two phases. The first phase entailed an increased evaporative rate as non-evaporative heat loss fell. In the second phase, the evaporative rate gradually reduced and non-evaporative heat loss increased. The sweat response curve was displaced to lower temperatures, but in the second phase it moved towards higher temperatures. An acclimatised man can withstand a higher mean skin temperature in order to save water. Gatenby (1986) commented that animals with lower insulation are able to lose a given amount of heat through a reduced thermal gradient and can thus afford higher skin temperature. An upwards shift of set-point during the hot season has been seen as a physiological response of the horse to a hot arid environment (Honstein & Monty, 1977). The onset of sweating can also depend on the fitness of the horse. Thomas (1992) states that a fit horse starts to sweat more slowly and more gradually and loses fewer proteins and electrolytes in its sweat.

Thermoneutrality

The concept of thermal neutrality was discussed thoroughly at the Twentieth Easter School in 1973 and concluded by Mount (1973). The basic principles of heat loss from an animal are described in the thermoneutral diagram by Mount (1973). The relationship between body temperature, heat production, evaporative and non-evaporative heat loss is presented schematically in Figure 10 (Mount, 1973). It was suggested as defining a number of environmental zones that are neutral in different respects, e.g. a zone with minimal metabolism bounded on each side by rising metabolic rate; a zone of least thermoregulatory effort bounded at the colder limit by raising metabolic rate at the warmer limit by increasing evaporative loss. Zones could also be defined for particular purposes, for instance preferred thermal environment, animal productivity or zones optimal in any given respect such as growth rate. These specially designated zones do not necessary coincide with either minimal metabolism or least thermoregulatory effort.

Different thermal zones with limits, A-F, are presented in Figure 10. Zone A is the zone of hypothermia, where the body temperature declines due to a higher heat loss than heat production. In the zone BC the rate of non-evaporative heat loss will increase due to an increased temperature difference between the animal and the environment. Within the zone BC, the animal can increase heat production to cover the increase in heat loss. The zone CD is the zone of least thermoregulatory effort. The lower limit of this zone is the (lower) critical temperature marked C. The upper limit, D, is the environmental temperature at which a marked increase in evaporative heat loss occurs. Between environmental temperatures C and F metabolism will be minimal. The range of environmental temperatures BE is called the thermoregulatory range. In zone F, the zone of hyperthermia, the body temperature will rise since the environmental conditions limit heat loss.

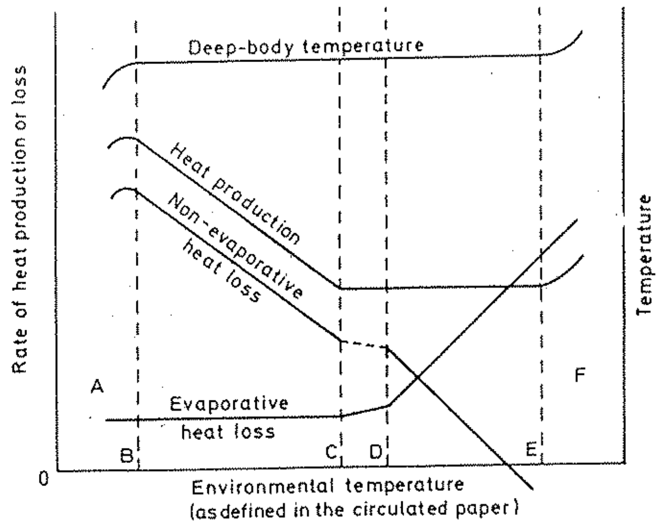


Figure 10. Diagrammatic representation of relationships between heat production, evaporative and non-evaporative heat loss and deep-body temperature in a homeothermic animal (Mount 1973). A: zone of hypothermia; B: temperature of summit metabolism and incipient hypothermia; C. critical temperature; D: temperature of marked increase in evaporative heat loss; E: temperature of incipient hyperthermal rise; F: zone of hyperthermia; CD: zone of least thermoregulatory effort; CE: zone of minimal metabolism; BE: thermoregulatory range.

Measurements of heat production and heat loss

Heat production measurement methods

Indirect calorimetry estimates the heat production from quantitative measurements of materials consumed and produced during metabolism. Most methods involve estimation of respiratory gas exchange and may be classified according to their operating principles as confinement, closed-circuit, total collection and open-circuit (McLean & Tobin, 1987). For farm animals, the amount of heat produced is usually calculated according to Brouwer (1965) (Equation 8):

$$P = 16.18 * V_{O_2} + 5.02 * V_{CO_2} - 5.99 * N - 2.17 * V_{CH_4} \qquad (8)$$

where

P	heat production	[kW]
V_{O_2}	oxygen uptake	[$l\ s^{-1}$]
V_{CO_2}	carbon dioxide output	[$l\ s^{-1}$]
N	urinary nitrogen	[$g\ s^{-1}$]
V_{CH_4}	methane production	[$l\ s^{-1}$]

According to McLean & Tobin (1987), the methane term and the nitrogen term each contribute to the estimated heat production by 1% each. If these terms are ignored the estimation will be affected by ± 1.2%.

Heat loss measurement methods

Direct calorimetry measures the rate of heat dissipation from a subject, often with the aim to estimate heat production of the subject. The general principal of a direct calorimeter is that the subject is enclosed in a well-insulated chamber. The heat dissipation can then be measured as an increase in temperature and in air humidity, the principle is shown in Figure 11 (McLean & Tobin, 1987).

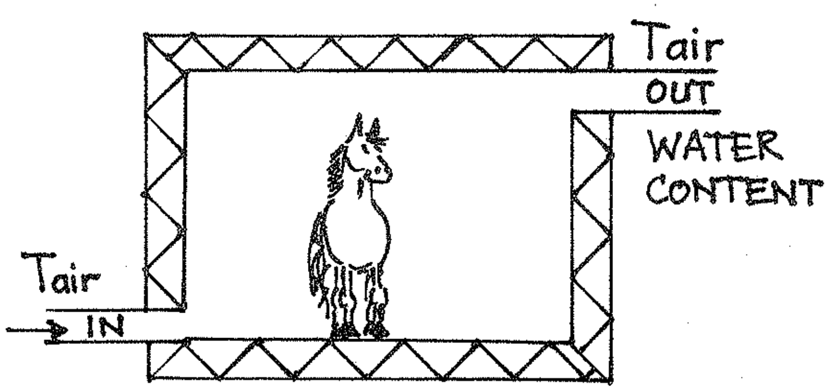


Figure 11. Illustration of the principle of a direct calorimeter.

The evaporative and non-evaporative heat loss can be estimated indirectly in other ways. Examples of some indirect methods of measuring evaporative heat loss are shown in Figure 12. Heilemann *et al* (1990) used a ventilated facemask to measure respiratory evaporative heat loss. The cutaneous evaporative heat loss in horses has been measured using a ventilated capsule, by Allen & Bligh (1969) and Johnson & Creed (1982). The total (both respiratory and cutaneous) evaporative heat loss can be measured by means of a hygrometric tent (Yeck & Kibler, 1956), in which the gain in water content of the air passing through the tent is measured. The rate of non-evaporative heat loss can be calculated according to laws of physic from the temperature difference between the surface of the animal and the environment.

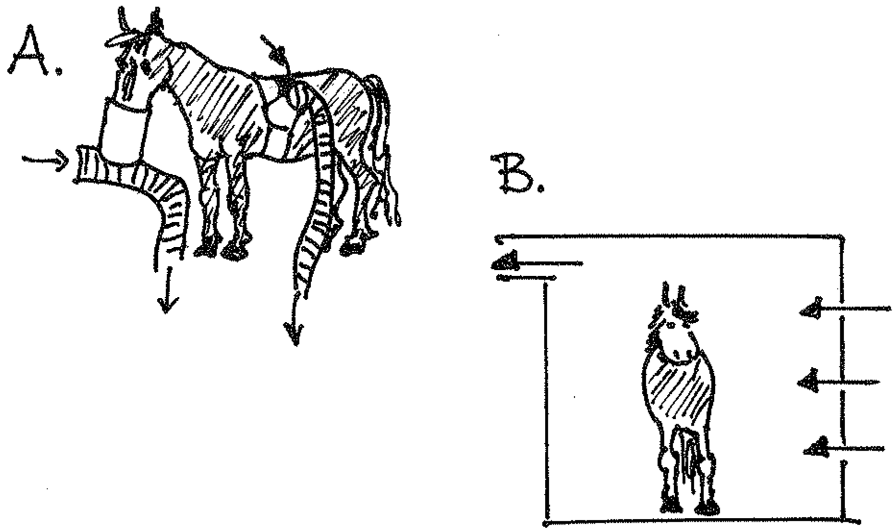


Figure 12. Illustration of A. ventilated facemask for measuring respiratory evaporative heat loss and ventilated capsule for measuring cutaneous evaporative heat loss and B. hygrometric tent for measuring both respiratory and cutaneous evaporative heat loss.

Identification of problem, hypothesis and objective

Problem

A horse constantly produces heat internally which must be transferred to the body's periphery and dissipated to the environment, in order to maintain an almost constant body core temperature. This rate of heat transfer from the body core to the periphery is regulated by physiological processes. The internal heat transfer is done by conduction and convective transportation with the blood. The physical status may be a limiting factor. The possibilities for dissipating heat from the periphery and the means by which heat can be dissipated are governed by the physical environment. The environment may limit the heat loss or create a heat loss that exceeds the heat production. In the light of this background following two questions can be raised.

Since the horse's heat production is constant, can the horse maintain homeothermy despite a brief and acute change in ambient air temperature?

When the ambient temperature changes, how will the thermoregulatory system of the body respond in a short-term to the change in the possibility to dissipate heat?

Hypothesis

The hypothesis is that the thermoregulatory system and strategies of the physiological functions are evolved to cope with, and will reflect, situations associated with the fundamental living conditions and natural behaviour of the horse. This means that the thermoregulatory system of the horse is evolved to maintain an almost constant body core temperature despites changes in the thermal environment within a fairly with range. The thermoregulatory system is also evolved to dissipate an exerise-induced heat load from a flight.

Objectives

The objective of this thesis was to study the thermoregulation in a horse, especially the short-term physiological responses in relation to brief changes in thermal environment.

A second objective was to measure the thermal properties and heat losses of horses in order to improve management and housing of horses.

MATERIALS AND METHODS

In the experiment, the horse was taken from an environment with the stable temperature (18°C) to which the horse was acclimatized for at least 18 hours. When entering the climatic chamber the horse was exposed to a sudden change in ambient temperature, except for the times when the chamber's ambient air temperature was almost the same as the ambient temperature of the stable. The change in ambient air temperature lasted for the time the horse spent in the chamber, approximately 1.5 - 2 hours. The set-up was chosen to study the physiological response in relation to a brief change in ambient air temperature which changed the prerequisites for means of heat loss. In the present study, I elected to measure and estimate rate of heat loss [W m^{-2}], since I did not have access to a direct calorimeter. The rate of non-evaporative heat loss was calculated from the temperature difference between the surface of the horse and the environment. The total evaporative heat loss was measured using a hygrometric tent. The rate of evaporative heat loss was estimated by dividing the total evaporative heat loss by the surface area of the horse. The rate of total heat loss was estimated by adding the rates of non-evaporative and evaporative heat loss. The thermal properties of the horse's insulation were estimated as thermal insulance [m^2 K W^{-1}], since the rate of non-evaporative heat loss was estimated.

Climatic chamber and horses

The climatic chamber was large enough for one horse. The temperature can be altered according to specification from -10°C to 40°C. The six different target temperature levels in the experiment were set to: -10°C, 0°C, 10°C, 20°C, 30°C and 38°C. However, the actual temperatures, (with the relative humidity given within brackets) was: -3°C (50%), 6°C (55%), 15°C (55%), 20°C (45%), 30°C (40%) and 37°C (40%). The velocity of the air was <0.1 m/s. Each horse participated once for each temperature level in a randomised order. For each occasion, a horse was kept in the climatic chamber for approximately one and a half hours. The horse was given a small amount hay (≈1kg) to keep it occupied and to distract it from interfering with the measuring equipment.

The horses in the study are presented in Table 1. All the horses were individually fed for maintenance and light work at 0.71 MJ $kg^{-0.75}$ metabolisable energy per day, in agreement with feeding recommendations of the NRC (1973). The horses were acclimatised to an indoor temperature of 15-20°C. The horses were turned out in a paddock during the daytime for four hours, on days when they did not take part in the experiment. The experiment was carried out mainly during the winter season. The experiments for each horse were carried out within a period of two weeks. All horses were trained to be in the climatic chamber and were accustomed to the measuring equipment prior to the commencement of experimental series.

Table 1. Presentation of the horses used in the study by breed, sex, age and body weight

Horse	**1**	**2**	**3**	**4**	**5**
Breed	Shetl. pony	Std bred	Std bred	Std bred	Std bred
Sex	Stallion	Gelding	Gelding	Gelding	Mare
Age [years]	3	14	5	13	7
Weight [kg]	135	540	530	465	475

A complementary set of experiment were done to measure the effect of an altered insulation of the horse. However the Shetland pony was not used in the measurements of altered insulation, instead a Standardbred trotter gelding weighing 455 kg was used. Because of the shearing procedure the experiment were carried out in a specific order:

1. a control where the coat remained intact on the horse
2. an intact coat covered with a rug
3. a sheared horse
4. a rug covered the sheared horse.

The same rug was used for all horses and was a thinner type of winter rug, so called "thermo-rug". The ambient air temperature (relative humidity) in the climatic chamber was 6°C (55%) for this complementary set of experiments. This temperature level was chosen to represent a common ambient air temperature for a horse in southern part of Sweden during the winter season.

Experimental procedure

The schedule for the experimental procedure is presented in Figure 13. The horse was prepared in an examination stall, where the room temperature was approximately 18°C, the ordinary stable temperature for the horse. After preparation, it entered the chamber, where the ambient air temperature had stabilized to the desired level. Radiant temperatures of the walls, ceiling and floor inside the tent were measured before and after the experimental period. The tent was closed and respiration rate, heart rate, temperatures and evaporation were measured for one hour. The measured parameters indicated steady state conditions after half an hour or less. The last 30 minutes of the measuring period were used to calculate an average for each parameter. The horse was given a food reward before exiting the climatic chamber.

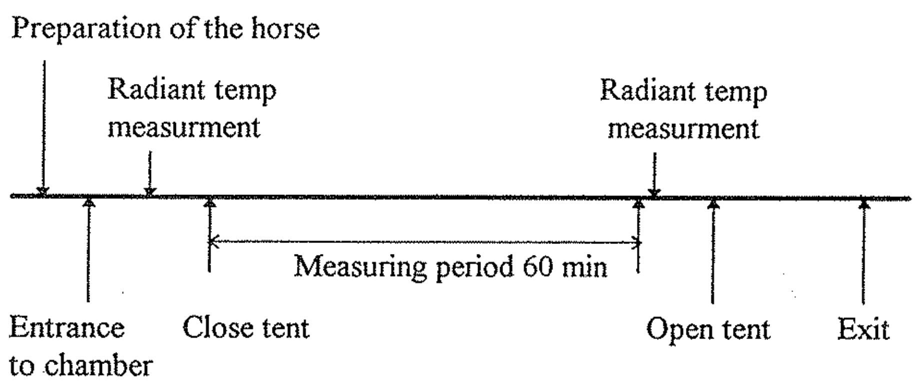


Figure 13. Experimental procedure and time schedule for the experiment.

Aim of statistical analyses

Results from five horses is a limited dataset when it comes to statistics. However, ethical and economical aspects set limits to biological studies. The results can exemplify the physiological response but in detail cannot give absolute values for the horse population. The five horses were chosen to represent different sizes and sexes. The order of exposure to the different levels of ambient air temperature was randomised. The aim of the statistical analyses was to look for trends in the results of the measured parameters and to be able to compare the trends of physiological parameters with the trends of heat loss to establish possible relationships and models of explainations. The trend was represented with a regression line that was fitted according to the principle of least squares. In the complementary set of experiment on altered insulation nonparametric analyses were carried out to detect any significant differences. The nonparametric analyses were Friedman ANOVA followed up by Wilcoxon matched pairs test. The statistical analyses were conducted with the statistical program Statistica 4.5 and 5.0 (Statsoft, 1995).

Measured parameters and measuring equipment

The set-up with the measuring equipment is presented in Figure 14 and Table 2. The research parameters with their code number in Figure 14 are as follows. Respiration rate (No. 2) and heart rate (No. 3) were recorded at three-minute intervals during the measuring period. The evaporative heat loss was calculated from the air temperature (Nos. 10 and 11), the dew-point temperature of the air (Nos. 12 and 13), the air flow (No. 14) and the atmospheric air pressure which was measured with a mercury barometer. To estimate the thermal insulance of the horse and the rate of non-evaporative heat loss, the deep body temperature (No. 1), the skin and coat temperature (Nos. 5-9), the air temperature (Nos. 10 and 11), and the radiant temperature of the enclosure (No. 15) were measured.

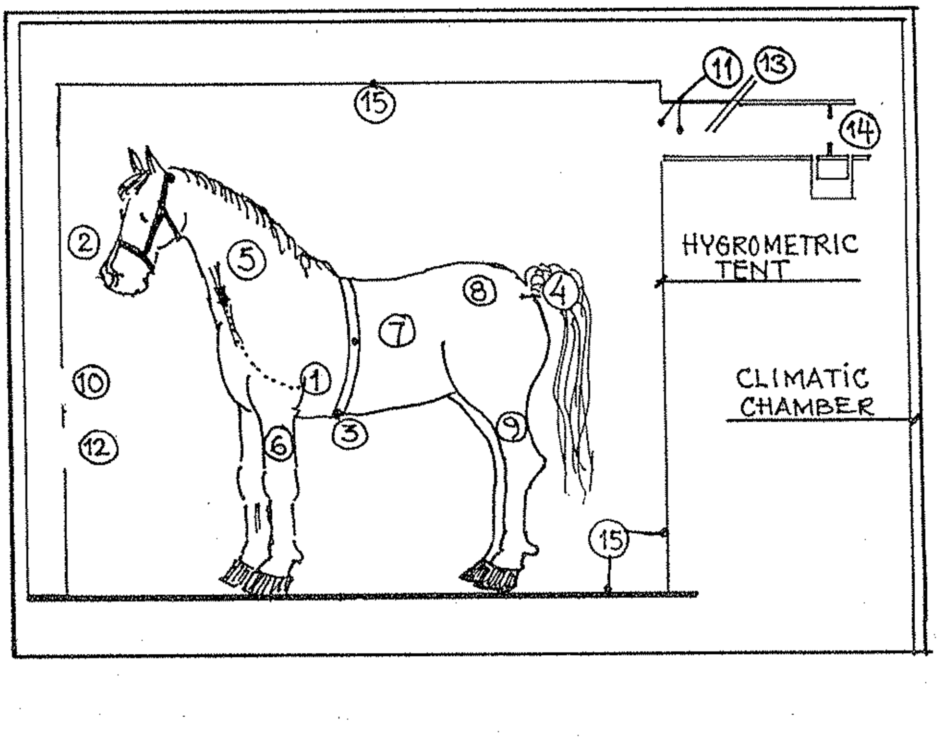


Figure 14. The interior of the climatic chamber with the horse and the measuring equipment. The numbers refer to the parameter measured and equipment presented in Table 2.

Table 2. The table presents the parameters measured, the measuring equipment used in the experiment, with the rated accuracy. The numbers in the first column relate to the illustration of the interior of climatic chamber, Figure 14.

No.	Measured parameter	Equipment	Rated accuracy
1.	Body core temperature	Thermistor-tip catheter (7F, 1.25 m, Swan-Ganz, Edwards lab., Santa Ana, CA, USA)	
2.	Respiration rate	Capnograph (Engström eliza mc CO_2 analyzer, Gambro inc., Stockholm, Sweden)	
3.	Heart rate	Electrocardiogram (Siemens-Elema AB, Sweden)	
4.	Rectal temperature	Thermistors (Fenwal Electronics/ADP, Milford, MA, USA)	±0.2°C
5.	Skin and coat temperature on the neck	Thermistor, see No. 4	±0.2°C
6.	Skin and coat temperature on the forearm	Thermistor, see No. 4	±0.2°C
7.	Skin and coat temperature on the barrel	Thermistor, see No. 4	±0.2°C
8.	Skin and coat temperature on the rump	Thermistor, see No. 4	±0.2°C
9.	Skin and coat temperature on the gaskin	Thermistor, see no. 4	±0.2°C
10.	Inlet air temperature	Thermistor, see No. 4	±0.2°C
11.	Outlet air temperature	Thermistor, see No. 4	±0.2°C
12.	Inlet air dew point temperature	Dew point hygrometer (Model 660, EG&G Environmental Equipment Division, Burlington, MA, USA)	±0.3°C with a dew point sensi-tivity of ±0.06°C
13.	Outlet air dew point temperature	Dew point hygrometer, see no. 12	
14.	Orifice for measuring airflow rate	Differential pressure sensor (Alexander Wiegand, Klingenberg, Germany)	±0.5 Pa
15.	Radiant temperature	Infrared thermometer (Everest Interscience Inc., Tustin, CA, USA)	±0.5°C

GENERAL DISCUSSION

The results are presented in detail in the accompanying Articles I to IV; where Article I deals with heat loss, Article II with thermal insulance, Article III with physiological responses and Article IV with climatic energy demand. The different means of heat loss are discussed in relation to a physiological parameter. The rate of non-evaporative heat loss is discussed in relation to thermal insulance. The respiratory rate is discussed in connection to the rate of evaporative heat loss. The total heat loss and the heart rate are discussed together. The concept of thermoneutrality and critical temperatures are discussed in relation to both heat loss and physiological parameter.

There is a discrepancy between the results in Article IV compared to Article I and II. In Article IV on clinatic energy demand the rate of non-evaporative heat loss was calculated with a Nusselt number for the whole body. However, in Article I and II, different equations were used for the trunk and the extremities to estimate Nusselt numbers. This is further discussed in Article I. Also, the term thermal resistance is used in a wrong way, since the thermal property of a layer is referred to and the proper term should be thermal insulance. The average lower critical temperature of 18°C in Article IV is too high. In further analysis of the results, a general LCT for these horses were approximated to 5°C. This development in interpreting the results relate to the altered approach to the calculations.

The results of studies on heat loss and heat balance can be of practical use in the management of horses. Some examples of practical implementation of the results are presented for the reader in the discussion. These examples are estimation of the lower critical temperature, the amount of extra feed an animal needs due to a cold thermal environment, the effect of heat loss on design of climatization systems in a barn and the effects on the heat balance of shearing or covering the horse with a rug.

Non-evaporative heat loss and thermal insulance

Thermal insulance describes the thermal property of an insulation layer. Figure 15 shows the effects on the thermal insulance of the peripheral tissue (M_{tissue}), the coat (M_{coat}) and the boundary layer of air (M_{air}). The result shows that the horse has the ability to regulate the thermal insulance of the peripheral tissue within certain limits as the ambient air temperature changes. The decreasing coat thermal insulance in warm ambient air temperature can be explained by the presence of a wet or moist coat, which conducts heat more easily and has a lower thermal insulance (Cena & Clark, 1979). The total thermal insulance is that of the tissue, coat and boundary layer acting in series (McArthur, 1981; McArthur, 1991). The total thermal insulance will determine the rate of non-evaporative heat loss according to the Equation 9, which derives from Equation 6:

$$q_{non\text{-}evap} = (T_{core} - T_{amb}) / M_{total} \quad (9)$$

where

$q_{non\text{-}evap}$	rate of non-evaporative heat loss	$[W\ m^{-2}]$
T_{core}	body core temperature	[°C]
T_{amb}	ambient temperature	[°C]
M_{total}	total thermal insulance	$[m^2\ K\ W^{-1}]$

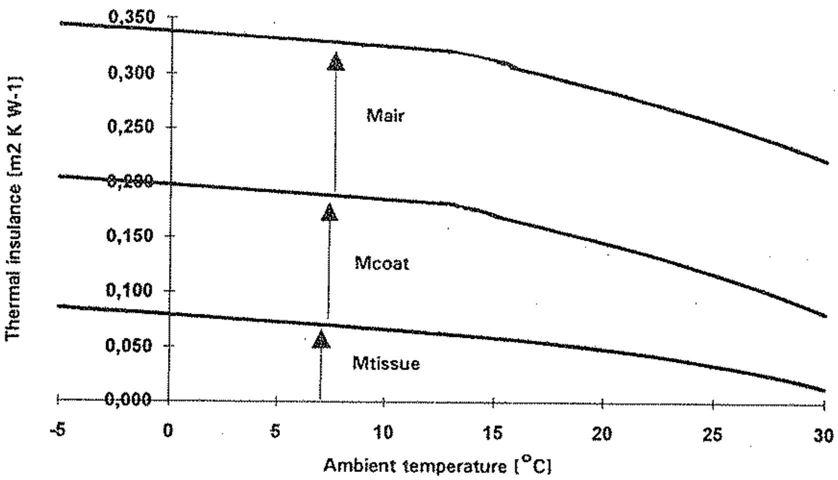


Figure 15. Diagram showing trends of the results of thermal insulance of peripheral tissue (M_{tissue}), coat (M_{coat}) and boundary layer of air (M_{air}).

The rate of non-evaporative heat loss can be estimated by using the total thermal insulance from Figure 15 and a notional temperature difference between the body core and the ambient air temperature. This result is presented in Figure 16, represented by the dotted line. In this case the body temperature varies from 37.2°C in air temperatures at and below 0°C and increases linearly to 38.2°C at an air temperature of 38°C. The dotted line shows the ability of the horse to dynamically regulate to some extent the rate of heat loss when the ambient temperature changes. However, the result, from Article I, of the rate of the non-evaporative heat loss, using a weighted average for the five measuring sites on the horse, is represented by the straight solid line (Figure 16). The difference of the two curves in Figure 16 can be explain if the individual results of the horses are viewed. The results of the individual horses show that several horses have a dented lines. However, the dented lines are slightly phase displaced, which resulted in a straight regression line.

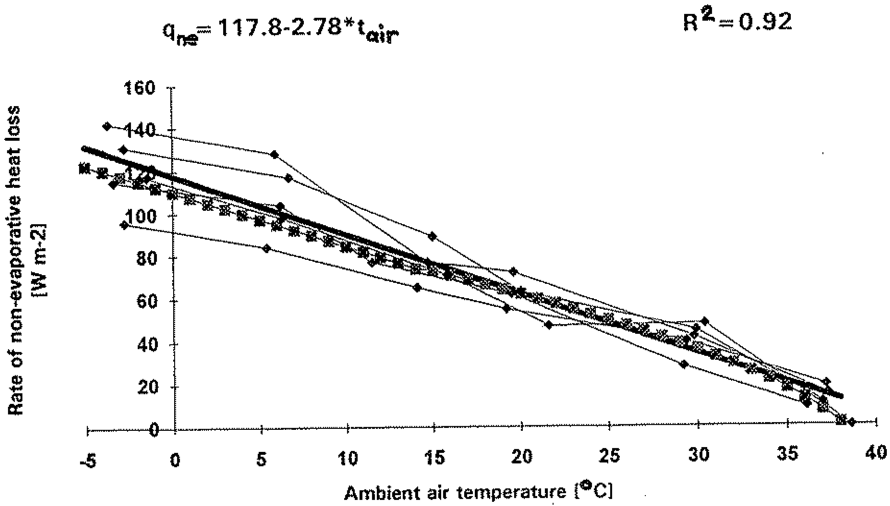


Figure 16. The result of the rate of the non-evaporative heat loss using a weighted average for the five measuring sites on the horse, represented by the straight solid line. The dotted line is the rate of non-evaporative heat loss estimated from the total thermal insulance in Figure 15.

The extra energy demand for a horse in cold environments can be estimated from the rate of non-evaporative heat loss. The climatic energy demand (CED) is defined by MacCormack & Bruce (1991) as the non-evaporative heat loss from an animal expressed in watts per square metre (W m^{-2}) of the surface area of the animal. The extra energy demand below the lower critical temperature can be estimated from the slope (2.78 W m^{-2} K^{-1}) of the increasing rate of non-evaporative heat loss in Figure 16. The amount of extra energy needed for a specific horse is found by multiplying surface area by CED and temperature difference below LCT. The climatic energy demand is further discussed in Article IV.

The slope of the straight solid regression line in Figure 16 is -2.78 $Wm^{-2}K^{-1}$, which when inversed corresponds to a total thermal insulance of 0.36 m^2 K W^{-1}. This total thermal insulance, estimated from the result of rate of non-evaporative heat loss in Article I, coincides with the total thermal insulance established in Article II, where the maximal tissue thermal insulance was estimated to 0.100 m^2 K W^{-1}, the coat thermal insulance was estimated to be 0.120 m^2 K $W^{-1}$and the thermal insulance of the boundary layer calculated as 0.140 m^2 K W^{-1}. The results of the tissue thermal insulance can be compared to that of cattle. The maximal tissue thermal insulance of a 500 kg cow can be estimated as 0.220 m^2KW^{-1} (Ehrlemark, 1988). Cattle can consequently withstand lower temperatures than horses. The lower thermal insulance of horses is of thermal advantage to a sweating animal and in comparison with cattle, horses have a better developed ability to sweat.

Evaporative heat loss

The rate of evaporative heat loss and the respiration rate are presented in the two diagrams in Figure 17. Both the parameters follow the same trend and increase in warm ambient air temperatures. The trend of the respiration rate starts to increase at an ambient air temperature of 16°C. The rate of evaporative heat loss shows a more pronounced increase.

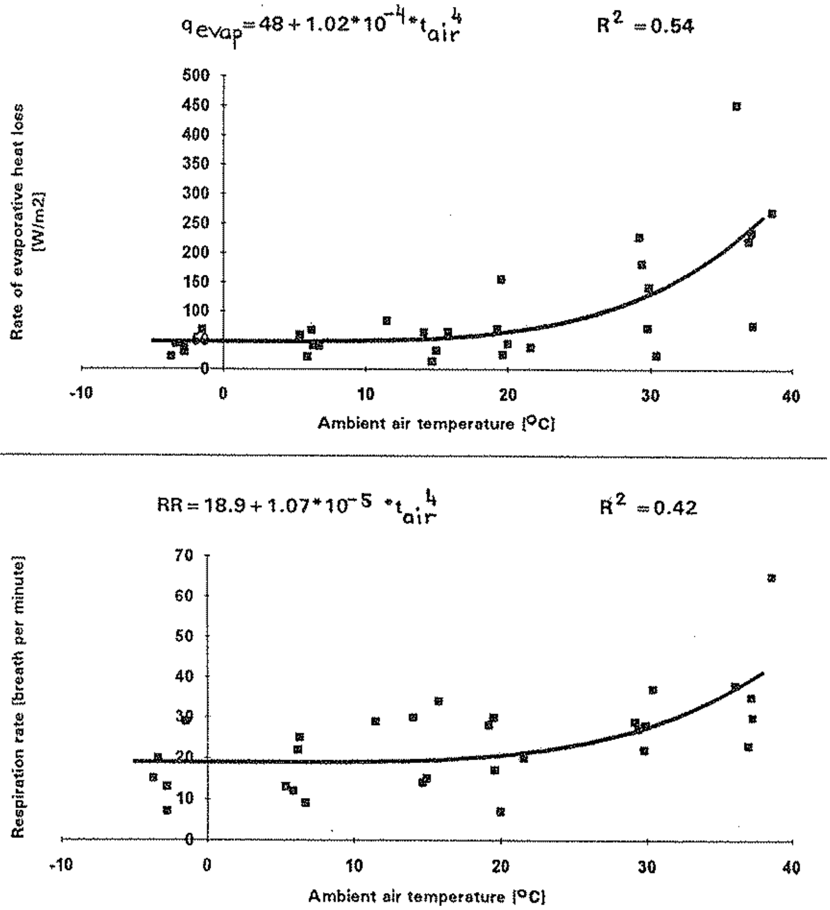


Figure 17. The rate of evaporative heat loss (upper diagram) and the respiration rate (lower diagram) plotted versus the ambient air temperature.

The respiratory rate versus the rate of evaporative heat loss is plotted in Figure 18. A stepwise linear regression was conducted to find the step-function presented. The interpretation of this diagram is that above the rate of evaporative heat loss of approxiately 100 W m^{-2}, the respiratory evaporative heat loss does not contribute any further to the increase in evaporative heat loss. However, respiration rate is used to change dynamically the rate of evaporative heat loss below this level of heat loss.

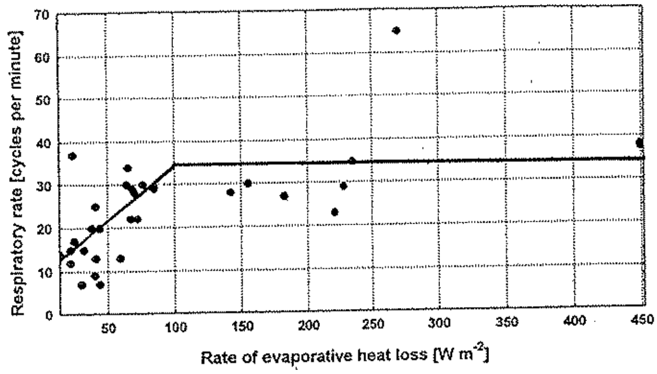


Figure 18. Respiratory rate plotted versus the rate of evaporative heat loss. Below the rate of evaporative heat loss of ≈100 W m^{-2} the respiratory rate changes dynamically, but above the break-point sweat will be solely responsible for the increase in rate of evaporative heat loss.

To test if the regulation of evaporative heat loss was related to both body core and skin temperature, the evaporative heat loss and the respiratory rate are plotted versus the difference between body core and skin temperature (Figure 19). This shows a step function in both cases. The evaporative heat loss will increase when the temperature difference is less than 6.6°C. The respiratory rate, on the other hand, will adjust to a steady state in a temperature difference smaller than 6.6°C and decrease linearly to a minimum value with a temperature difference greater than 6.6°C. A possible explanation for this may be that the energy metabolism of respiration will add to the heat load in a hot environment and sweating will therefore be more favourable for the total heat balance. Whittow & Findley (1968) showed an increase in oxygen uptake due to thermal panting in oxen. However, the respiratory rate of thermal panting in oxen is much higher (≈175 cycles per minute) as compared to the rates in horses.

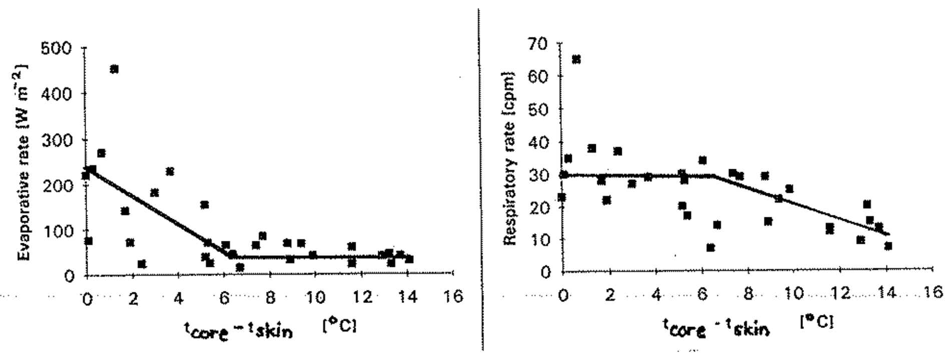


Figure 19. Rate of evaporative heat loss and respiratory rate are plotted versus the difference between body core and skin temperature. The diagrams show a break-point at the temperature difference of 6.6°C.

Sweating pattern

The trend of rate of evaporative heat loss represents the results of mean values for the last half hour of the experiment and gives no information about how the sweat is secreted. The pattern of sweating has been studied by Bligh (1967), Allen & Bligh (1969) and Johnson & Creed (1982). These studies argued that the horse has a fluctating sweating pattern. Figure 20 shows the results of the entire measurement period for horse 4 at 30°C. The results show a fluctating pattern, with an integrated average increase in rate of evaporative heat loss with time. This result agrees with the model in the thesis of Bligh (1967) concerning the process of secretion and discharge of sweat. Bligh (1967) states that the secretion of sweat is a myoepithelial expulsion that is super-imposed on a controlled secretory activity and is described by the illustration in Figure 21. This models the theoretical secretory pattern of a gland in which both sweat secretion and discharge are due to the activity of the secretory cells which function as a variable output pump controlled by a neural or humoral stimulus. The myoepithelium still contracts periodically, but has only a transient effect upon the rate of sweat discharge (Bligh, 1967).

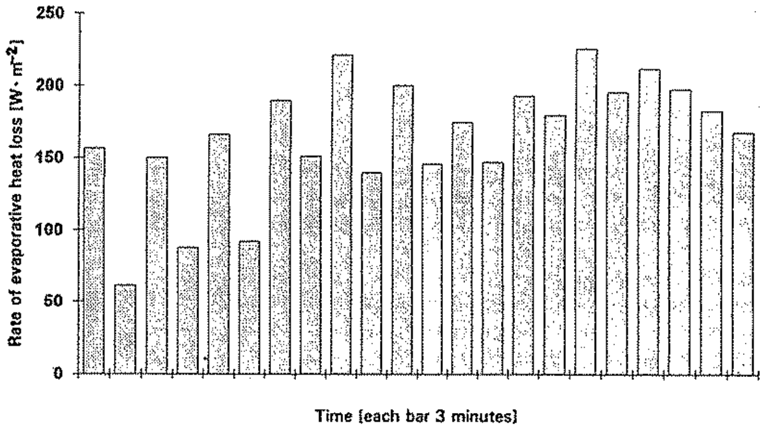


Figure 20. The sweating pattern of the entire measurement period for horse 4 in 30°C. Each bar represents a three minute period.

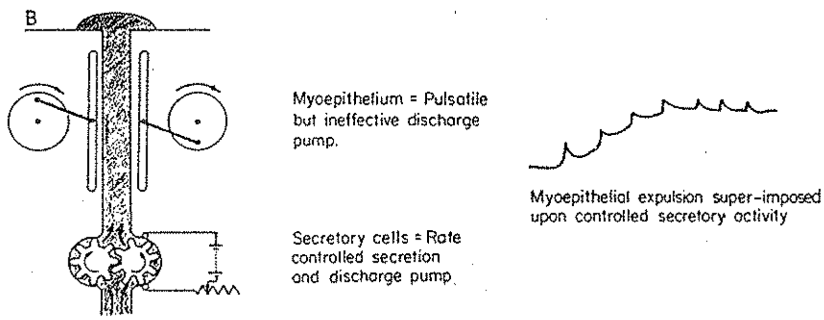


Figure 21. Illustration of Bligh's (1967) model, showing that the secretion of sweat as a myoepithelial expulsion super-imposed on a controlled secretory activity.

The result in Figure 20 is a practical application of the theoretical model of Bligh (1967) and measurements from the other horses showed the same trend in sweating pattern. It is interesting that the pattern can be seen even though the measurements are done with a hygrometric tent that measures both the respiratory and the cutaneous evaporative heat loss. However, at 30°C the cutaneous evaporative heat loss will be the major part. The time duration of a sweating cycle has to be taken into account. Johnson & Creed (1982) found a sweating cycle in horses to be one minute long. Each bar in the figure represents three minutes and will thus contain three sweating cycles, if the one-minute sweating cycle is valid for all horses. Since there is an odd number of cycles in one bar, this will either amplify or weaken the result.

Total heat loss and heart rate

The rate of total heat loss was calculated by summation of the rate of non-evaporative heat loss and the rate of evaporative heat loss. The trend for the rate of total heat loss is presented in Figure 22. The trend shows a slight increase at both ends of the range of ambient temperature studied. In ambient air temperatures below 5°C, the increase is due to an increase in non-evaporative heat loss. In ambient air temperatures above 25°C, the increase in total heat loss is due to the pronounced increase in evaporative heat loss. This pronounced increase of evaporative heat loss that exceeds that thermoneutral rate of total heat loss can be considered a short-term effect. If the horses were moved to a warmer environment, they would acclimatise to regain heat balance.

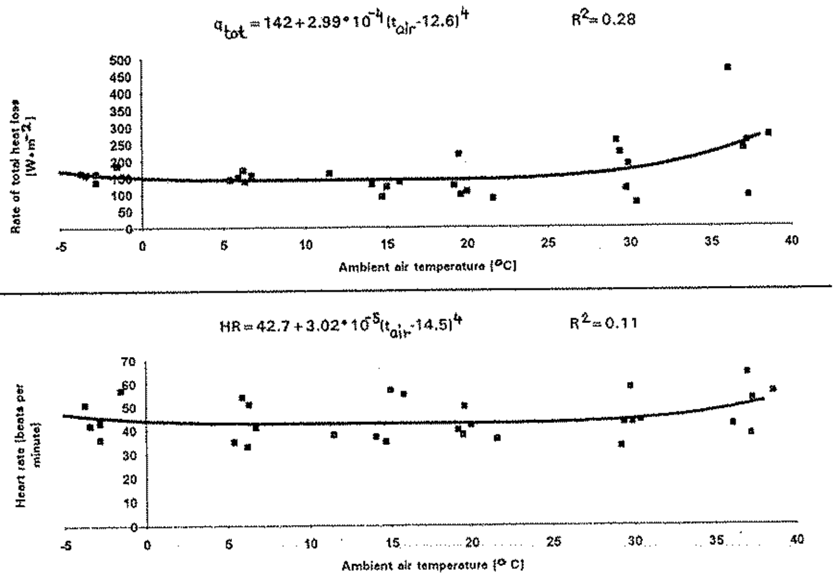


Figure 22. The trend for the rate of total heat loss (upper diagram) and heart rate (lower diagram) plotted versus the ambient temperature.

An interesting observation is that the trend of the heart rate follows the same trend as the total heat loss (Figure 22). In cold temperatures the horses were more active: eating hay, moving about and in some cases shivering, and the increased heart rate is probably due to this increased activity. This is indirectly caused by a need to produce heat, since the heat loss is greater than the thermoneutral heat production. The slight increase in heart rate in ambient air temperatures above 30°C can be explained by peripheral vasodilation to minimise the tissue thermal insulance. Cardiac output will increase to increase the blood flow when the peripheral resistance to blood flow decreases due to peripheral vasodilation. Heart rate can be used as a measurement of cardiac output in normovolemic horses.

Heat production

The heat production was estimated from the feed intake. The horses in the study were fed an amount equivalent to 170 W m^{-2} metabolisable energy per day. The ratio of heat production to metabolisable energy can be estimated from Equation 3; the ratio is 0.74. The heat production will then be 126 W m^{-2}. This agrees with the reference rate of heat production in Table 3 of 127 W m^{-2} for the Standardbreds.

Table 3. Body weight, estimated surface area and calculated rate heat production, estimated from a formula using the body weight and the surface area.

Parameter	Horse 1	Horse 2	Horse 3	Horse 4	Horse 5
Body weight [kg]	135	540	530	465	475
Estimated surface area [m^2]	2.2	5.4	5.3	4.8	4.9
Reference values of heat production estimated with the formula, Article IV: $P_{tot} = 6.1m^{0.75}$ [W]	242	683	674	611	621
Correponding rate of heat production [W m^{-2}]	111	126	127	127	127

The rate of total heat loss, 142 W m^{-2}, may be overestimated. The rate of non-evaporative heat loss is calculated from areas exposed to the environment. Surfaces on the horse, that face each other and have no net loss of radiation, are not considered. Let us make a calculation in Table 4 to exemplify this. The result of this example is that 16% of the surfaces had no net loss of non-evaporative heat. The steady state level of total heat loss, 142 W m^{-2}, could consequently be slightly too high, when comparing with the estimated rate of heat production of 127 W m^{-2}.

Table 4. Example of the effect of facing surfaces that would decrease the non-evaporative heat loss on a 500 kg horse with the estimated surface area of 5.1 m^2

Rate of total heat loss [$W m^{-2}$]	Rate of evap. heat loss [$W m^{-2}$]	Rate of non-evap. heat loss [$W m^{-2}$]	Non-evap. heat loss [W]
142	- 48	= 94	479
127	- 48	= 79	403
		Difference in non-evap. heat loss =	76
			which equals 16%

Critical temperatures and thermoneutral zone

A thermodiagram is drawn from the obtained results in this discussion and is presented in Figure 23. The input data, shown by the dotted lines:

1. The rate of non-evaporative heat loss based on the total thermal insulance and a notional temperature difference (the dotted line from Figure 16),
2. The regression line of the rate of evaporative heat loss and,
3. The rate of total heat loss is the sum of the above 1 and 2.

The minimal rate of total heat loss of 127 W m^{-2} corresponds with the heat production estimated from the feed intake and reference estimation of heat production.

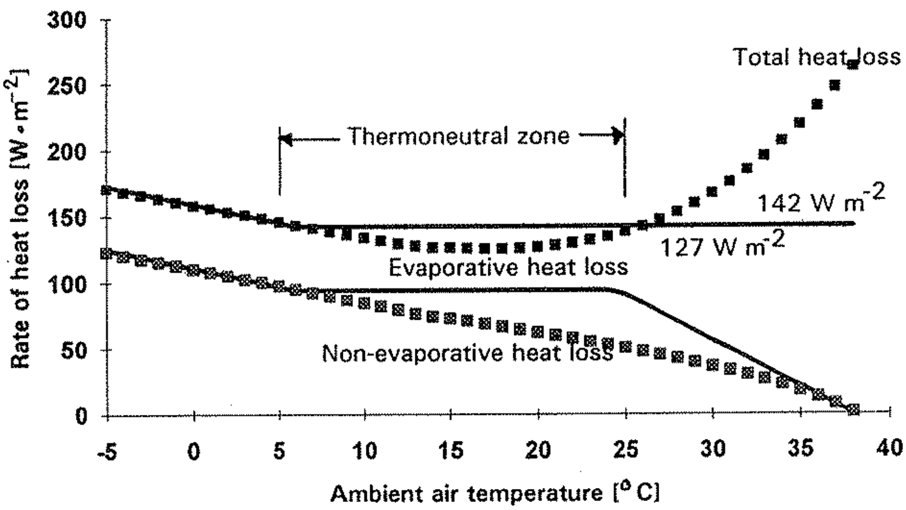


Figure 23. Relationship between heat loss and heat production. The dotted lines are results from the experiment and the solid lines represent a theoretical explanation.

In the figure the theoretical model of an animal's heat loss and heat balance is shown by the solid lines. The non-evaporative heat loss starts at 0 when the ambient temperature is equal to the body temperature and increases with the inverse of the minimal total thermal insulance (here 7 $Wm^{-2}K^{-1}$) as the ambient temperature decreases. The non-evaporative heat loss reaches a steady state level, which corresponds to the total heat production (plane of nutrition (Mount, 1979)) minus the minimal evaporative heat loss. At and below the lower critical temperature, the total thermal insulance is maximised and the non-evaporative heat loss increases with the inverse of the maximal total thermal insulance (here 2.78 $W\ m^{-2}\ K^{-1}$). The total heat production will show an equal increase in order to maintain the body temperature. However, the true nature of the pattern of heat loss and heat balance seems more refined, complex and dynamic than this theoretical model, since the dotted lines differ from the straight lines. Even so, this theroretical model can be used as a pedagogical tool for introduction to the heat balance and homeothermy of animals.

In Figure 23 the total heat loss shows an increase below 5°C and this temperature will be called the lower critical temperature. This lower critical temperature agrees with Young & Coote (1973) who found the lower critical temperature in young horses and indoor horses to be 0-5°C. The upper critical temperature might be defined in three differents ways, according to Mount (1973). The upper critical temperature is defined as the ambient temperature when

1. the metabolic rate increases,
2. the evaporative heat loss increases, or
3. the tissue thermal insulance is minimal.

These three temperatures will differ when viewing the results:

1. 25°C if the metabolic rate is considered to follow the total heat loss (Figure 22),
2. 20°C when the evaporative heat loss increases (Figure 17) and
3. 30°C when peripheral vasodilation is maximal (i.e. minimal thermal insulance of the tissue, Figure 15).

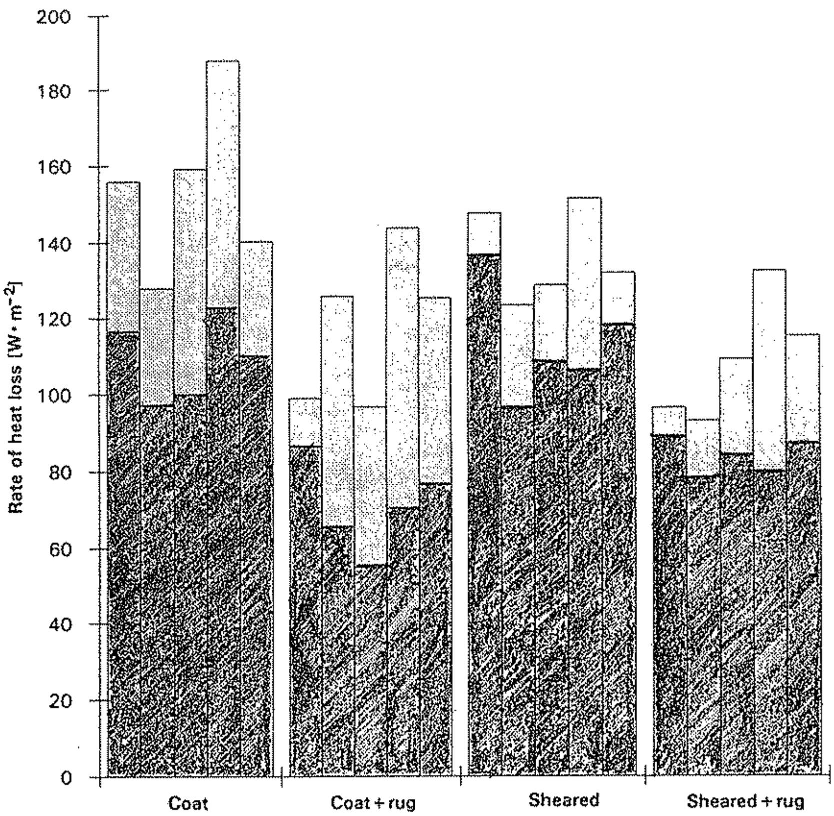
These exemples of different upper critical temperatures shows that it is hard to establish a uniform definition for the upper critical temperature. Webster (1991) argued that the upper critical temperature is not amenable to the construction of an absolute definition. Estimates of upper critical temperature vary according to whether heat stress is considered to be a problem of productivity or not and will differ depending on which physiological parameter one chooses, eg. heat production, respiratory rate or rectal temperature (Webster, 1991). The results show that sweating occurs before the tissue thermal insulance is minimal, which agrees with an analysis by McArthur (1987) of the data of Worstell & Brody (1953), confirming that the onset of sweating occurs before tissue resistance has reached the minimum value, so that control of heat loss by sweating and vasodilation occur together.

McBride *et al* (1983) defined the thermoneutral zone (TNZ) as related to minimal metabolic rate and concluded that the thermoneutral zone for the horses in the study was between -15°C and 10°C in still air conditions (Figure 4). Christopherson & Young (1986) defined the thermoneutral zone as the range of temperatures in which an animal maintains body temperature in the short term with little or no additional energy expenditure. In TNZ physical processes of heat transfer occur in the body to balance heat production, these responses being primarily variation of blood flow to the skin, piloerection, and postural changes. Based on the definition of Christopherson & Young (1986) a general thermoneutral zone for the horses in the present study can be estimated, from the range of steady state level of rate of total heat loss in Figure 22, to be in the range 5°C to 25°C. It is noticable that that steady state level of the heart rate (Figure 22) also reflects a thermoneutral zone of 5°C to 25°C. However there will be individual differences. The span of temperature in the thermoneutral zone was 25°C in the study of McBride *et al* (1983) and 20°C in the present study. According to Cena & Clark (1979), most homeotherms have a narrow thermoneutral zone and wider temperature ranges and lower critical temperature are associated with both greater insulation and size. The rather wide range in thermoneutral zone of horses is associated with being a a fairly well insulated large homeotherm.

The thermoneutral zone, the non-evaporative and evaporative heat loss, together with the design and construction of the building will affect the principle and design of a climatization system in a stable. The ambient air temperature in the stable should be regulated to fall within the thermoneutral zone so as to be thermally comfortable for the horse. During the winter season the ventilation rate is regulated to exhaust moisture and carbon dioxide. The non-evaporative heat loss from the horse in relation to heat loss through the building fabric and in the exhaust air is used to calculate the need for additional heating. The optimal set-point for the ambient air temperature in the stable during winter season is just above the lower critical temperature of the horse. The evaporative heat loss will then be minimal and the non-evaporative heat loss will contribute positively to the heat balance of the stable. Ventilation rate and extra heating will be minimised, which saves money. In the summer, the main purpose of ventilation will be to limit the temperature increase in the stable in relation to the outside ambient air temperature.

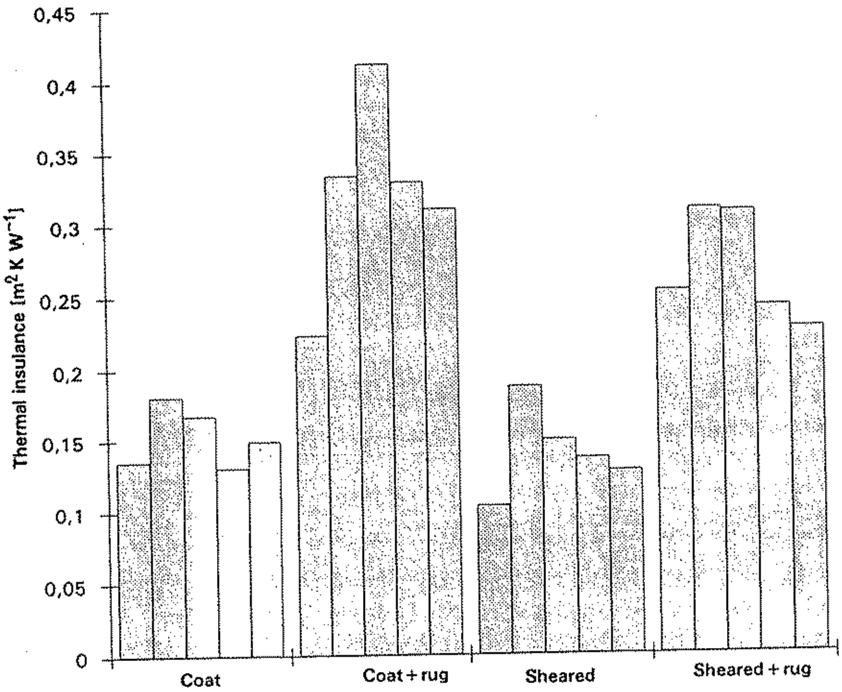
Altered insulation

Some additional measurements of the effects of altered insulation on the horses were made in the climatic chamber. The results of the rates of heat loss are shown in Figure 24 and the thermal insulance of the tissue and coat are presented in Figure 25. As expected, the sheared horse with no rug had the lowest thermal insulance, followed by the control horse with coat and no rug, the sheared with rug and the intact coat with rug. The rate of total heat loss was significantly ($p<0.05$) lower for all the treatments as compared to the control. Also sheared horse with rug was significantly lower than sheared horse without a rug. I had expected the sheared horse without a rug to have a higher rate of total heat loss as compared to the control. However despite a marginally higher rate of non-evaporative heat loss for the sheared horse, it was compensated by a decrease in the rate of evaporative heat loss. The rug was found to lower the rate of non-evaporative heat loss, since the rate of non-evaporative heat loss was significantly ($p<0.05$) different between the treatments without rug compared to treatments with rug. A sheared horse with a rug had the lowest total heat loss and will manage well during the winter. A sheared horse will dry off faster after it has been wet. This is an advantage not only for the heat balance but also for grooming the horse. The sheared horses had a lower rate of evaporative heat loss. This is preferable for the total climatization situation of the stable in the wintertime. A lesser volume of moisture will be added to the stable air, which results in lesser ventiation rates for moisture balance and consequently lower ventilation rates and lesser need for extra heating.



MEAN:	Coat	Coat + rug	Sheared	Sheared + rug
TOTAL	155	118	137	109
EVAP.	46	47	26	27
NON-EVAP.	109	71	111	82

Figure 24. The diagram shows rates of heat loss from the effects of shearing and covering. The average rates of total, evaporative and non-evaporative heat loss are enumerated below the diagram.



MEAN: 0.152 0.321 0.140 0.267

Figure 25. Results on the thermal insulance of the tissue and coat from the effects of shearing and covering.

Behaviour and size

The horse uses its behaviour to regulate its heat balance. According to Cymbaluk & Christison (1990) these behaviours can be seeking shade or shelter, temporary changes in activity, postural changes and regulation of feed intake. I'd like to exempliy and discuss how different behaviour can related to regulation of heat production and heat loss. A change in posture to limit the exposed area within the body, or standing close together in the herd will decrease the non-evaporative heat loss, since the amount of non-evaporative heat loss for the whole horse is determined by both the rate of loss and the exposed area. Consequently, besides the rate of heat loss, the horse can manipulated the area exposed to control the amount of non-evaporative heat loss, since surface areas that have the same temperature and are facing each other will have no net radiant heat loss. Excessive gain of radiant heat can be avoided by seeking shade; conversely heat can be gained by exposing a large area on a cold but sunny day. Shelter seeking can protect the animal from wind (convective heat loss), radiant heat loss to a clear sky and from precipitation (evaporative heat loss). Temporary changes in activity and regulating the feed intake will affect the heat production. Increased activity and feed intake will increase heat production. In warm environments, activity and feed intake decrease and the opposite occurs in cold environments. This was in fact observed during my experiments. I also made other observations and reflections about individual differences in handling heat load in warm and hot conditions. The horse with the lowest evaporative rate was the Shetland pony, which had the largest surface area in relation to body weight. Consequently, it can dissipate a relatively larger proportion of non-evaporative heat and it does not have to depend on evaporation as much as a heavier horse. The two horses with the highest evaporative rates were the Standardbreds that were considered to have the most temper and to be of an active type of horse. It was one of the most active Standardbred that had the very high respiratory rate of 65 cycles per minute. The main explanation is probably not the activity level, but the fact that the ambient temperature was higher than the body core temperature and the horse was heat stressed.

DESCRIPTIVE MODEL

In research today, there is a goal to minimise the use of live animals and to use non-living models instead. MacCormack & Bruce (1991) measured rate of non-evaporative heat loss at 120 W m^{-2} on a non-living model built in a horizontal barrel placed outdoors during the Scottish winter. The results from both these studies are in agreement with the results in the present study, measured on live horses. Therefore, it seems possible in the future to use non-living models to measure enviromental effects due to different climates. Non-living models together with basic information on the thermal properties of the horse may in the future be used in computer simulations to estimate heat balance and thermal comfort of horses.

System analysis and computer simulation are means of modelling dynamic processes like thermoregulation. However, it is important to understand that reality differs from our limited perception and interpretation of it. The view of reality that we get through our senses and by measurements and studies is not the same as reality itself (Gustafsson *et al*, 1982). This is a statement with which it is easy to agree when working with biological systems. The body and its regulating mechanisms is far more refined and dynamic than can be described by a simulation model. A simulation model can only describe what happens to a system during specific limited conditions. The model presented in Figure 26 describes the parameters of the heat balance in the horse and its regulating mechanisms. It can be considered as a summarizing illustration of the thermoregulatory system. From this, it is as yet premature to construct a program for computer simulation, but it can serve as a basis for further work. More information input is needed to create a valid simulation. In my future research, I would like to accept the challenge to construct a simulation model which illustrates the thermoregulatory response of a horse in different thermal environments and levels of activity.

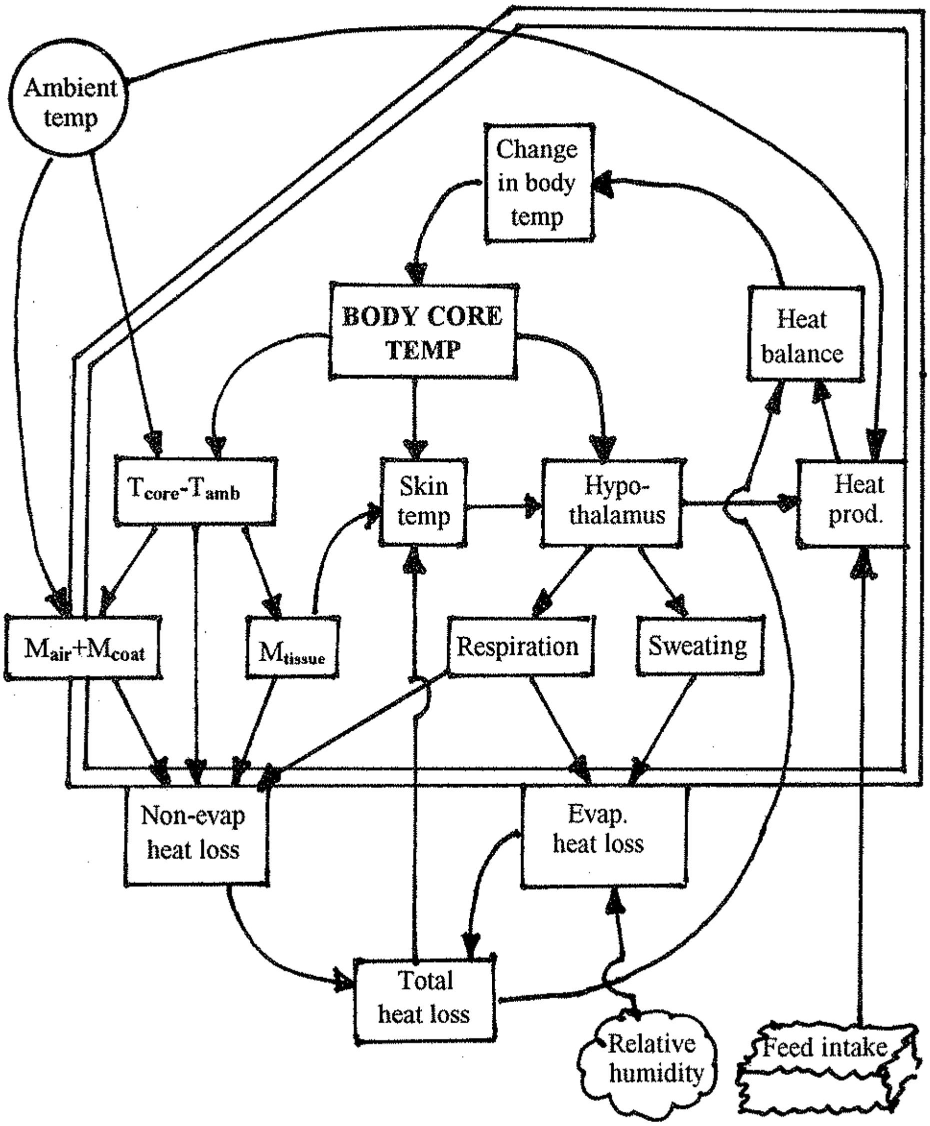


Figure 26. Schematic diagram of the model describing the parameters of heat balance in the horse and associated regulating mechanisms.

The following assumptions are made in the descriptive model in Figure 26 and will serve as explanations to the illustration:

- Heat production depends on both the feed intake and the ambient temperature. A period of internal heat production, e.g. shivering, adds to heat production, if the actual value of the integrated temperature in the hypothalamus is too low as compared to the set-point.
- The tissue thermal insulance, M_{tissue}, depends on both the body core temperature and the ambient temperature (Guyton, 1991).
- The rate of non-evaporative heat loss depends on the total thermal insulance and the temperature difference between the body core and the environment.
- The hypothalamus integrates signals from the skin temperature receptors and the receptors of body core temperature. The integrated value is compared to a set-point and initiates heat-producing responses or active increase in heat dissipation by increase of evaporative heat loss.
- The temperature difference between the body core and the skin is equal to the tissue thermal insulance times the total heat loss.
- The change in heat storage will affect the body core temperature.

This descriptive model shows the complexity of the thermoregulatory system and illustrates connection between different mechanisms. To penetrate and understand the model the reader is advised to follow different pathways in the model guided by the comments above. Further explainations are not meaningful, but try learning by doing.

SUMMARISING CONCLUSIONS

The horse could maintain a normal body core temperature despite an acute and brief change in ambient temperature. No effect on the heart rate was noticed.

The horses in this study was found to fairly well insulated with a maximal thermal insulance estimated to 0.360 m^2 K W^{-1}, divided into thermal insulance of tissue estimated to 0.100 m^2 K W^{-1}, of the coat 0.120 m^2 K W^{-1} and of the boundary layer 0.140 m^2 K W^{-1}. Compared to reference values of tissue thermal insulance in cattle, these horses had about half the tissue thermal insulance and can consequently not withstand as low temperatures as cattle. The horse was found to be able to regulated the tissue thermal insulance, which is a physiological function to adjust the rate of non-evaporative heat loss.

The climatic energy demand was found to be 2.78 W m^{-2} per degrees Celsius below the lower critical temperature. This equivalent to an extra daily ration of approximately 0.15 kg of hay per degree Celsius below the lower critical temperature.

When the non-evaporative heat loss was limited by increasing ambient air temperatures, the horses showed a good ability to dissipate evaporative heat by increased respiratory rate and by sweating in order to maintain heat balance. The trend of the respiratory rate was found to follow the trend of the rate of evaporative heat loss. In moderate ambient air temperature the respiratory rate was used to dynamically regulated the rate of evaporative heat loss. In high ambient air temperatures sweating was the main mean of evaporative heat loss. The sweating pattern, found in this study, was a practical application of the theoretical model of Bligh (1967). Both body core and skin temperature were found to be related to the regulation of the evaporative heat loss.

The thermoneutral zone, defined as the range of temperatures in which an animal maintains body temperature in the short term with little or no additional energy expenditure, was estimated in general for these horse to range from 5°C to 25°C. It was exemplified that the upper critical temperature is hard to define and varied in the examples to be, 20°C, 25°C or 30°C, depending on definition. From the discussion on upper critical temperature, it was concluded that onset of sweating occurred before tissue insulance had reached the minimum value, so that control of heat loss by sweating and vasodilation occurred together

An altered insulation by shearing and covering was studied. In the winter season it can be of advantage to shear horses that are exercised and trained for competitions, since according to Cena & Clark (1979) hairlessness is an advantage in facilitating sweating, which can be of importance for the exercising horse. Also the managing of the horse is facilitated and one might speculate in a faster recovery after exercise. It is of advantage for the climate in the stable with sheared horses in the winter season. Then the ventilation rates are controlled to exhaust moisure and carbon dioxide. A decreased evaporative heat loss like in the sheared horses is an advantage, since the ventilation rates can be keep down. The increased non-evaporative heat loss in the sheared horses will be favourable for the climate, since heat from the horses will keep the indoor temperature up. It is important to point out that a sheared horse needs a rug or complementary feeding to ensure that it can remain body core temperature.

Future reseach

In the progress of this study I have come across problems and new questions that needs further investigations. Since the respiratory rate was found to be an important parameter, further investigation of breathing strategies and regulation of respiration in hot climate is needed. An important and central issue in reseach of thermoregulation and heat balance is the surface area of the horse. Already a study dealing with measuring and estimating the surface area of horses is going on. After studying standing horses, I'd like to accept the challenge to work with thermoregulation of the exercising horse during exercise but also in the recovery phase. A interesting question, often raised by horse trainers, is if shearing will increase the performing capacity of the horse. A parallel aim for my future reseach is to develop a simulation model for short-term thermoregulatory responses in horses and include the aspects of exercising in different thermal environments.

FROM HYPOTHESIS TO SYNTHESIS

The hypothesis is that the thermoregulatory system and strategies of the physiological functions are evolved to cope with, and will reflect, situations associated with the fundamental living conditions and natural behaviour of the horse. This means that the thermoregulatory system of the horse is evolved to maintain an almost constant body core temperature despites changes in the thermal environment within a fairly wide range. The thermoregulatory system is also evolved to dissipate an exerise-induced heat load from a flight.

The fundamental living conditions of horses are to live in herds on the steppe, to graze for the most part of the day, and to flee in case of danger. What thermal situations do they need to be able to handle? On the steppe, temperature and radiation can vary greatly between day and night. In case of flight the horse has to dissipate the exercise-induced heat load so as to restore the set-point body temperature.

The horse was found to have a good ability to sweat, which it has evolved to handle the exercised-induced heat load. The tissue thermal insulance is an evolutionary compromise to provide insulation in cold temperature but not be too high since a lower tissue thermal insulance is of thermal advantage to a sweating animal. Since horses are evolved to eat for most of the day, they will compensate for the heat loss due to a somewhat lower thermal insulance with a constant and even feed intake. The coat being a thin insulating layer of hair is probably the best physical compromise for allowing the skin to lose heat by evaporation whilst providing protection from heavy solar loads (MacFarlane, 1964; McArthur, 1987). Some hair coat is also desirable to reduce heat loss at night (McArthur & Clark, 1987). The fact that horses live in a herd is an advantage since it enables the herd members to protect and help each other to handle different thermal environments.

The interesting phenomenon with horses is that their thermoregulatory responses are evolved to handle both cold and hot environments. This is reflected in the worldwide distribution of horses. I conclude that my hypothesis has become a synthesis that the thermoregulatory responses of the horse are evolved for a species that lives in a herd and flees in case of danger and is born to live free on the steppe.

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