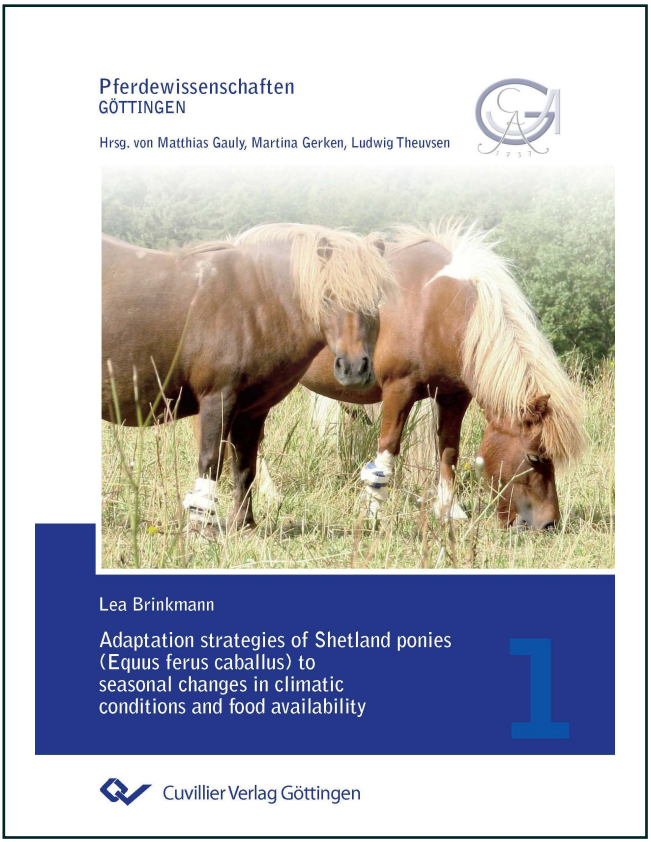
Lea Brinkmann (Autor)

Adaptation strategies of Shetland ponies (Equus ferus caballus) to seasonal changes in climatic conditions and food availability



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CHAPTER 1

INTRODUCTION

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INTRODUCTION

An increasing number of domesticated horses are kept in outdoor group housing systems. These systems are ascribed to allow the performance of the horses' natural behaviour patterns. However, in Central Europe ambient temperatures can easily range from -25 °C to +35 °C over the course of the year, thus exposing animals to extreme environmental conditions. Horses need to adapt to the varying external effects by changes in physiological parameters, behaviour and metabolism to sustain their homeostasis (Arnold and Dudzinski, 1978). Wild horses are known to adapt by accumulation of body fat, reduced activity and a reduced metabolic rate (Scheibe and Streich, 2003; Arnold et al., 2006; Berger et al., 2006), while domesticated horses may have a reduced adaptive capacity so that especially in winter the environmental conditions can result in health problems. Little information is available on the adaptation of domestic horses under such conditions. Furthermore, there is limited knowledge if the extensive outdoor housing can be described as an appropriate housing system for horses.

Adaptation is a widely used term that describes the modification processes during the evolution, the ontogenesis and the actual genesis as well as the resulting modification of body structure, physiology and behaviour. Behavioural adaptation is based on genetics, learning, formation of memory, memory and tradition creation (Gattermann, 2006). The adaptation ability of domesticated horses may be reduced as the transfer of the animal to the human household represents a manipulation of the natural selection. The human being changed the animals' environment in such a manner that the struggle for existence, decisive for natural selection, lost importance. Furthermore, the animal was modified by zootechnical measures. The artificial selection by humans resulted in changes of body structure, organic functions and behaviour (Scheunert and Trautmann, 1987). Nevertheless, behaviour patterns that were carried over from the ancestors but lost their function or their primary role still exist as behavioural relicts (Bogner and Grauvogl, 1984). In general, domesticated horses are gentler, less aggressive and have reduced sensual performance (Zeitler-Feicht, 2001).

Domestic horses can be subdivided in three subcategories: ponies, cold-blooded horses and warm-blooded horses. The cold-blooded horses are massive, heavy, short built and have a high compactness index (Langlois, 1994; Zeitler-Feicht, 2001).

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Warm-blooded horses are high, long-limbed and slender with long extremities (Langlois, 1994) and show less body weight than the cold-blooded horses (Zeitler-Feicht, 2001). In contrary ponies have the tendency for restricted growth, round shape, short extremities and opulent mane and tail hair. Their hair coat is longer and they have more undercoat especially in winter. For this reason they are suited for loose housing. Ponies also have a high feed conversion and tend towards adiposity (Zeitler-Feicht, 2001).

Thermoregulation as adaptive mechanism in endothermic animals

Under extensive housing conditions, among the different adaptive mechanisms, thermoregulation is of special importance for horses. Their body temperature needs to be kept in narrow limits to ensure the reactivity and to sustain the function of the brain. This chapter will focus on their thermoregulatory mechanisms.

The horse belongs to the homoeothermic animals. These animals possess a highly developed temperature regulation and are able to keep their metabolic rate and body temperature relatively constant with changing environmental temperatures (Crompton et al., 1978; Bianca, 1979; Ousey et al., 1992; Singer, 2007). This enables these animals to sustain a constant metabolic rate and reactivity in the vital organs over a wide climatic range. The price for that are a four- to eightfold increased specific energy demand and the need for continuous substrate supply (Else and Hulbert, 1981; Singer, 2007).

The body of homoeothermic animals can be subdivided in the body shell and the body core. The temperature of the body core (organs, thoracic- and abdominal cavity, brain) is kept relatively constant by thermoregulatory mechanisms, the body shell temperature lies below the core temperature and varies depending on thermoregulatory needs. The body shell is composed by the skin, hypoderm and temporary by the muscles and extremities. There are high topographical temperature differences in the body shell. Horses distal limb temperatures can be reduced to 1.7 °C (Palmer, 1983), whereas the skin of the torso shows high temperatures with only slight fluctuations (Scheunert and Trautmann, 1987; Penzlin, 1991; Schmidt-Nielsen, 1997).

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As changes in heat loss due to changes in ambient temperature, humidity and wind speed and heat production e.g. by activity and feed consumption may occur quickly, the body needs to possess efficient mechanisms for the control of heat loss and heat production (Scheunert and Trautmann, 1987). Reactions regarding thermal variations can be functional, structural or ethological (Bianca, 1977). Functional and structural changes can be characterised as physiological temperature regulation (Wollenweber, 2007). A survey on physiological, chemical and behavioural mechanisms of thermoregulation is given in Tab. 1.

Tab. 1 Physical, chemical and behavioural measures of thermoregulation (Wittke, 1972).

Climate	Measures for temperature regulation		
	Autonomic regulation		Behavioural regulation
	Physical	Chemical	
Heat	Increased blood circulation of the skin	Decrease in heat production	e.g. Searching for shade, wetting with water
	Panting, Sweating		Reduction in activity and food consumption
Cold	Reduced blood circulation of the skin	Increase in heat production	e.g. Grouping (collective temperature regulation),
	Piloerection		searching for wind shadow

Surface receptors in the skin as well as thermoreceptors in the body core submit continuously terminal impulses to the hypothalamus (Hensel, 1966) where the received information is compared with an internal `set-point`. The hypothalamus determines if the body temperature is too cold, too hot or if the temperature is appropriate (Sjaastad et al., 2003). If the body temperature deviates from the `set-point`, different thermoregulatory mechanisms are implemented (Hensel, 1966).
Body heat, generated by metabolic waste heat, must equal the heat loss to sustain homoeothermic (Scheunert and Trautmann, 1987; Schmidt-Nielsen, 1997).

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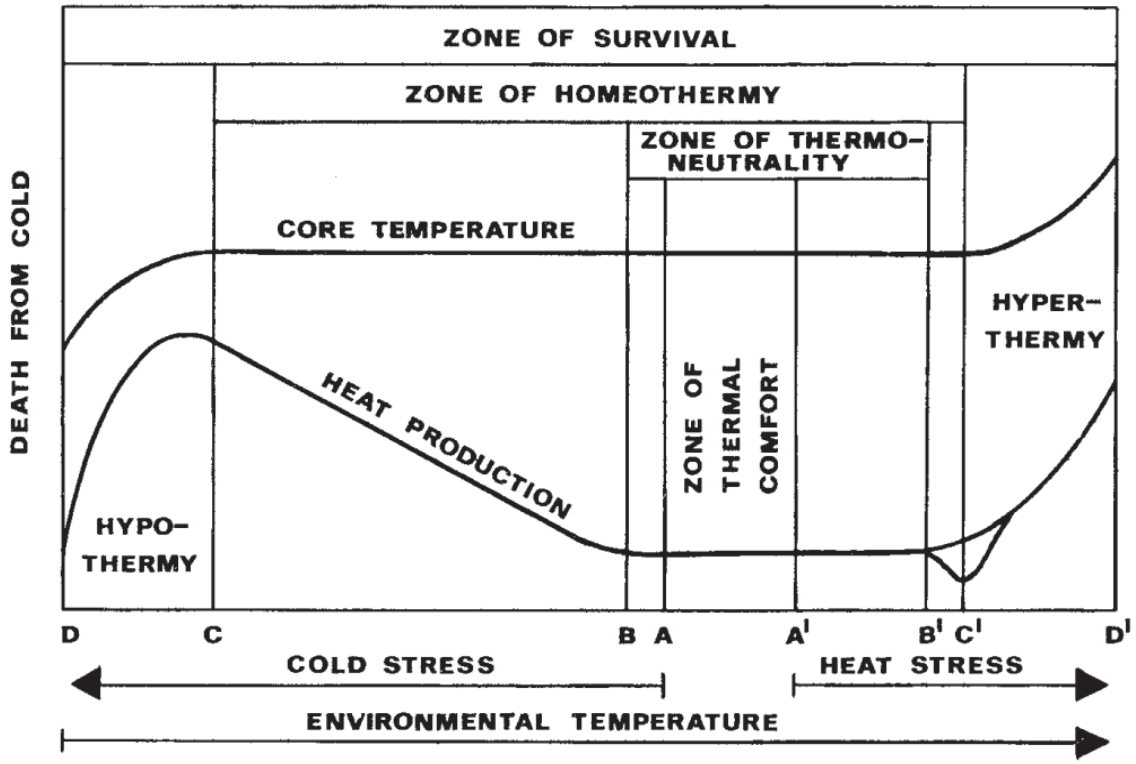

Fig. 1 Schematically illustration of the thermoneutral zone and the critical temperatures after Bianca (1968).

Bianca (1968) schematically outlined the reaction of the homoeothermic animal to changes in the ambient temperature (Fig.1). The thermoneutral zone (B - B`) is the temperature zone in which the generated heat from the basal metabolic rate is sufficient to keep the body temperature constant without larger thermoregulatory mechanisms (Bianca, 1979; Scheunert and Trautmann, 1987). For horses there are highly variable data for this temperature zone. McBride (1985) states -15 to 10 °C, Clarke (1987) 10 to 30 °C while Morgan (1997a) found a temperature zone of 5 to 25 °C. However, these specifications present guideline values that can be influenced by factors like humidity, wind speed, precipitation and radiation (Schrader, 2009). If the ambient temperature decreases below a certain limit, the lower critical temperature (B), more heat is required to compensate the heat losses and therefore the metabolic rate is increased (Schmidt-Nielsen, 1997). Above the upper critical temperature (B`) the metabolic rate and likewise the heat loss increases due to sweating and panting. If the heat loss mechanisms become insufficient in hot and humid conditions, the body temperature increases until death of heat occurs at body temperatures of 43-44

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°C, primarily because of denaturation of certain enzymes and regulatory proteins (Sjaastad et al., 2003). On the other hand death of cold may occur when the heat production in the body cannot compensate the heat losses due to extreme low temperatures (Bianca, 1971) or insufficient feed supply.
Therefore, the seasonal feed shortage in the temperate zone in the winter months is standing in contrast to the higher thermoregulatory energy demand in winter. The homoeothermic animals adapted to this dilemma by migration, the creation of feed cache, higher body insulation or the reduction of heat loss by decreasing the body temperature and hibernation (Bligh, 1998; Singer, 2007).

Ethological/behavioural thermoregulation

Changes in the animals' behaviour are important thermoregulatory mechanisms (Hetem et al., 2007). The main function of the behavioural thermoregulation is the minimization or prevention of heat loss (Bianca, 1977). Behavioural thermoregulation can be divided in heat producing and heat retraining mechanisms (Autio, 2008) and means the selection of an environment and activity that reduces the thermal stress. Behavioural thermoregulation requires less energy than thermoregulation by sweating or by burning calories to maintain the core body temperature (Houpt, 2005). Therefore, it is initiated before physiological thermoregulation occurs (Bianca, 1977).

In a cold environment the main mechanisms of the behavioural thermoregulation are the reduction of the relative body surface (Bianca, 1977), shelter- and comfort seeking (Hetem et al., 2007) and turning the smallest surface towards the wind (Boyd and Houpt, 1994). A reduction of the morphological body surface is not possible but a reduction of the freely exposed, heat dissipating surface by grouping and standing close to each other is possible (Bianca, 1979; Langlois, 1994). The time spent lying is reduced (Duncan, 1985) to avoid heat loss to the ground via conduction. The animal seeks shelter and comfort in warmer, sunny microclimates and weather shielded areas (Bianca, 1979) such as trees, bushes, and lower elevations (Zeeb, 1994). Furthermore, horses reduce their locomotor activity to preserve energy reserves and increase the time spent grazing to maximise their energy intake as caloric needs are greater in the cold (Duncan, 1980; 1985; Berger et al., 1999; 2006).

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During hot weather horses search for cool, humid soil (Bianca, 1979) and breezy locations (Zeeb, 1994). They avoid direct solar radiation by standing in the shade (Crowell-Davis, 1994) and moisten the body surface with water to cool the body by evaporation (Bianca, 1977). Additionally, the horses decrease their activity and feed intake to reduce the metabolic heat production (Bianca, 1977; 1979).

Physiological and chemical thermoregulation

The physiological thermoregulation comprises structural as well as functional mechanisms. The structural modifications involve vasoconstriction and vasodilatation, increase of the coat density and coat length as well as piloerection (erection of the guard hair) (Kolb, 1967). If the body core temperature of the animal is elevated, the tone of the muscle cells in the arterioles decreases and as consequence the cutaneous blood flow and skin temperature increases. This vasodilation therefore raises the heat loss from the body since this is dependent on the temperature gradient between the skin and the environment. Vasoconstriction occurs during exposure of the animal to a cold environment. The sympathetic nervous system controls the constriction of the vessels that supply the cutaneous tissues, especially the ears and the extremities with blood. The blood flow in the dermis diminishes and the heat transfer is reduced. At a temperature around 0 °C vasodilation occurs by sudden opening of the vessels to permit intermitted warming of the skin (Radostits et al., 2005). Vasoconstriction was observed by several authors in horses held under cold conditions (Palmer, 1983; Mogg and Pollitt, 1992; Morgan, 1997b).

The horses' hair coat density and length is dependent on the ambient temperature, photoperiod and horse breed (Kooistra and Ginther, 1975; Cymbaluk, 1990; Zeitler-Feicht, 2001) and it serves to create a static air layer above the skin (Penzlin, 1991) to reduce the heat loss. Cold-blooded horses and ponies have a higher coat density and length than Arabians and Thoroughbreds (Mills and McDonnell, 2005). Zeitler-Feicht (2001) describes a more dense short hair and a rough guard hair in ponies. However, cold housed horses do not inevitably grow a thick winter coat when they are adequately fed (McBride et al., 1985).

Each guard hair follicle has a muscle, called piloerector muscle *(arrector pili)*, which is located in the outer layer of the dermis and attached to the hair bulb. An increase

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in the impulse frequency of the sympathetic nerves causes contraction of the muscle. Thereby the hair is erected and the distance between the skin and the tip of the hairs increases. This increases the thickness of the air layer between the hairs used for body insulation (Sjaastad et al., 2003). Ousey (1992) showed an increase of the coat depth by 0.3 to 1.4 cm in foals and Young and Coote (1973) reported of a 20-30% higher hair coat depth in adult horses. Piloerection on different parts of the body can have various effects. A complete piloerection on the dorsal surfaces actually might increase the heat loss since warm air rises, while piloerection on the ventral surfaces conserves heat (Davenport, 1992).

Nearly all mentioned structural mechanisms serve to reduce the heat loss. The heat dissipation under a hot environment is mainly induced by functional thermoregulation. The animals' body heat can be dissipated by radiation, conduction, convection and transpiration (Fig. 2).

Radiation

Warm bodies exchange heat with cooler bodies by radiation (Langlois, 1994). The heat dissipated by radiation is dependent on the temperature difference between the body surface and the environment (Scheunert and Trautmann, 1987). In general, the animal's body has a higher temperature than the environment and therefore looses heat (Langlois, 1994). Horses can reduce the heat loss trough radiation by reducing the skin temperature. On the contrary, the increase in skin temperature by increased peripheral blood circulation results in a higher heat loss by radiation (Scheunert and Trautmann, 1987). The cooling by radiation may be high at night during cold winter month (Cymbaluk and Christison, 1989), but horses can reduce the heat loss by standing close to each other and by seeking shelter (Bligh, 1998; Mejdell and Boe, 2005).

Conduction

Conductive heat loss takes place by the direct contact with objects and is likewise dependent on the temperature gradient between the animals and the environment (Langlois, 1994). In a standing position the horse is only loosing small amounts of heat by conduction, while during lying this heat loss can be remarkable (Clark, 1994). In summer horses will therefore seek for cooler soil to lie down. Wet body- or/and lying surfaces will enhance the heat loss by conduction as water has a high thermal

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conductivity (Autio, 2008). Thus, in winter horses reduce the lying times on the cold and humid soil to minimize heat loss (Duncan, 1985; Langlois, 1994).

Convection

Convection is the heat transfer via moving air or water and depends on the temperature gradient. If the body temperature is higher than the ambient temperature, the air that is in contact with the skin will be heated by conduction. The heated air ascents and is replaced by cooler air (Sjaastad et al., 2003). This free convection elevates with decreasing temperatures (McArthur, 1991) but is of limited significance for the horse as it is equipped with a fur. Forced convection due to wind is of greater importance (Sjaastad et al., 2003). To minimize heat loss in winter horses are seeking for wind protected areas. In summer during high temperatures they are looking for windy places to enhance this type of heat loss (Zeeb, 1994). Convection also occurs within the body. This means that the heat generated in the muscles and organs is transferred to the skin by the blood (Vogel, 2006).

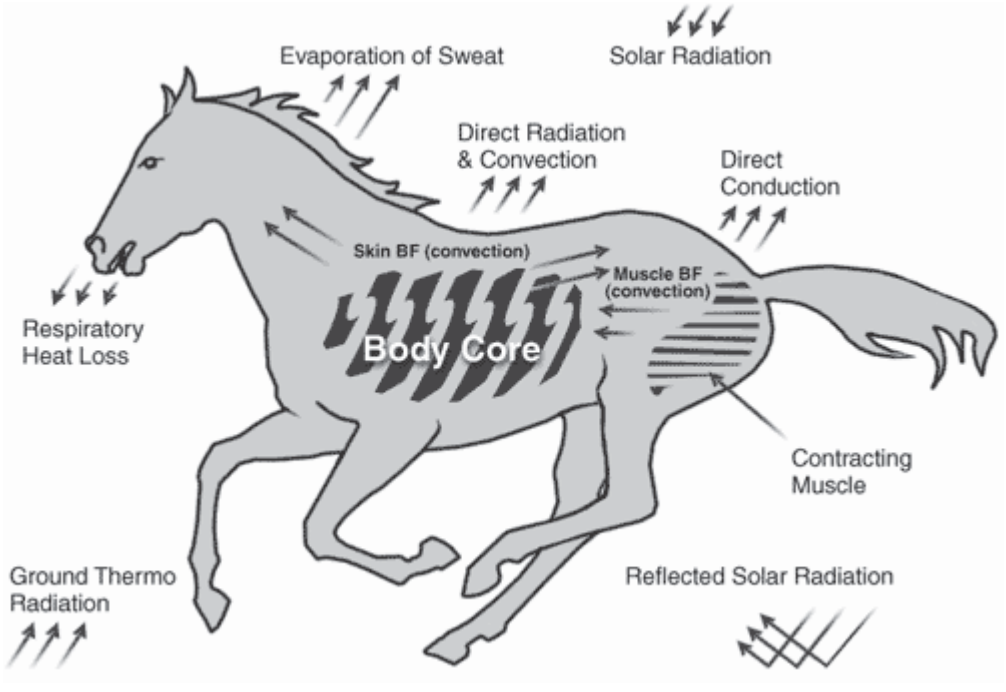

Fig. 2 Functional mechanisms of heat dissipation to the environment and heat gain by the environment in the horse (BF: blood flow) (Wood, 2009).

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Evaporation

The evaporation is the most efficient way to loose body heat under hot conditions (Scheunert and Trautmann, 1987) and is associated with the loss of water vapour from the respiration system and the skin (Clark, 1994). There are 2430 kJ detracted by the evaporation of one litre water on the body surface (Scheunert and Trautmann, 1987). With high ambient temperatures the heat loss via evaporation in horses increases while the loss by non-evaporative mechanisms decreases. However, evaporation depends on the difference in water vapour pressure between the skin and the ambient air and the amount of exhaled air (Morgan et al., 1997).

Small amounts of water that diffuses continuously trough the skin and evaporates are described as insensible evaporation. This water loss cannot be controlled as water molecules diffuse continuously through the skin. At low ambient temperatures the insensible evaporation stays almost constant and accounts for 20% of the entire heat loss (Morgan, 1996). The sensible evaporation includes panting, sweating and salivation whereupon sweating is of higher importance for horses (Scheunert and Trautmann, 1987; von Engelhardt and Breves, 2000) even if water is also lost by respiration.

Chemical thermoregulation

In the homoeothermic animal there are three chemical mechanisms to generate heat which all depend on the metabolic reactions involved in synthesis and breakdown of ATP (Langlois, 1994). These three ways are the basal metabolic rate, the shivering thermogenesis and the non-shivering thermogenesis (Cannon and Nedergaard, 2004). The basal metabolic rate is the rate of energy metabolism measured of a resting, awake, fasting animal in the thermoneutral zone. Thus, the basal metabolic rate is needed to maintain cell and organ functions (Bligh, 1998). Sixty percent of the body's heat production during rest is produced by heart, liver, kidneys and brain (Sjaastad et al., 2003); the remaining heat is generated by muscles, skin and skeleton (Autio, 2008). The metabolic rate rises with hormonal factors and muscular contraction (Irvine, 1967; Langlois, 1994).

The shivering thermogenesis refers to involuntary tonic and rhythmic contraction of both flexor and extensor at the same time and occurs as a reflex (Scheunert and Trautmann, 1987; Langlois, 1994). Though shivering is usually an acute response to abrupt cold exposure (Cannon and Nedergaard, 2004; Radostits et al., 2005) and

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increases the heat production of the animal to about four times of the basal metabolic rate (McArthur, 1991). However, the shivering thermogenesis increases the blood circulation in the extremities and results in an elevated heat loss and energy demand (von Engelhardt and Breves, 2000). Shivering was shown by Irvine (1967), McBride (1985), Morgan (1997a) and Morgan et al. (1997) in mature horses, by Mejdell and Boe (2005) for Icelandic horses and by Ousey et al. (1992) for pony foals exposed to cold temperatures.

The non-shivering thermogenesis via brown adipose tissue is more economical (Kolb, 1967). It is a very particular process that enables the brown adipose tissue to produce heat. Energy, released by the oxidation of glucose and fat, is directly dissipated as heat instead of being synthesized to ATP (Langlois, 1994). Brown adipose tissue exists in small body sized mammalian species (Dawkins and Hull, 1964; Foster and Frydman, 1978), but also in newborns of larger species (calves, lambs) (Alexander et al., 1975; Symonds et al., 1992). However, in the foal, there is no evidence of any brown adipose tissue stores (Acworth, 2003). Adult larger mammals lack brown adipose tissues (von Engelhardt and Breves, 2000). Thus, this thermogenesis is irrelevant for juvenile and adult horses.

Torpor and hibernation: a specific thermoregulatory and metabolic adaptation

In cold winters the energy demand of the animals to maintain a high body temperature is high while the vegetation which provides the primary energy supply is scarce in temperate regions (Bligh, 1998). Especially small animals have high metabolic rates that would increase further at low ambient temperature and become too expensive when feed is rare (Schmidt-Nielsen, 1997). A solution to solve this problem is to let the body temperature fall towards the environmental temperature (Bligh, 1998) and reduce the energy expenditure (French, 1982) by entering daily torpor or hibernation. It is assumed is that hibernation is more related to the seasonal feed shortage than to direct cold stress (Bligh, 1998). Furthermore, hibernation and torpor are well-regulated physiological states and not comparable with temperature reduction in cold-blooded animals (Schmidt-Nielsen, 1997).

Torpor and hibernation are characterized by the controlled reduction of body temperature and metabolic rate (Bligh, 1998; Geiser, 2004) together with other

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physiological functions like heart rate and respiration rate (Schmidt-Nielsen, 1997). Nevertheless, it has to be differentiated between prolonged torpor or hibernation in hibernators and daily torpor in daily heterotherms (Geiser, 2004). Hibernation usually begins in autumn and lasts until spring (Heldmaier et al., 2004), however, it consists of a sequence of torpor bouts. These bouts, lasting for several days or weeks, are interrupted by periodic rewarming and normothermic periods with durations of mainly less than a day (Twente et al., 1977; French, 1982; Heldmaier et al., 2004). Hibernating animals, usually weighing between 10 – 1000 g, can reduce their body temperature by more than 35 °C (Kayser, 1961). The entire mass range of hibernators is about 5 g to 80 kg. However, reductions of the body temperature below 10 °C are restricted to species with a body weight of less than 10 kg (Geiser, 2004). Many hibernators increase their body fat content before entering the hibernation and refuse to hibernate when fat reserves are not adequate (Geiser, 2004).

Daily torpor of daily heterotherms always lasts less than a day and is interrupted by daily foraging and feeding (Geiser, 2004). Both the metabolic rate and the body temperature are maintained at a higher rate (MacMillen, 1965; Morhardt, 1970; Geiser and Ruf, 1995). The daily torpor is less seasonal than hibernation but mainly occurs in winter times (Kortner and Geiser, 2000a). Furthermore, no extensive fattening is exhibited by daily heterotherms so that they enter torpor with low body weights (Kortner and Geiser, 2000b) and the main energy supply remains consumed feed rather than body fat (Geiser, 2004).

Apart from hibernation and daily torpor many other tachymetabolic heterotherms undergo periods of hypometabolism, whereas an alleviated form can be observed regularly during the circadian rhythm (Heldmaier et al., 2004). Comparable rhythms in body temperature variation were also observed in horses with decreasing body temperatures during the night and highest temperatures in the late evening. The range of deviation in horses was 1 °C (Piccione et al., 2002) being in the range of 0.5 – 2 °C stated for other species (Heldmaier et al., 2004).

Hypometabolism as a strategy to cope with feed shortage under winter conditions was expected to be absent in large mammals. Instead fattening, increased insulation and reduced locomotor activity were assumed to be sufficient to withstand the winter (Arnold et al., 2006). Despite this, large mammals may also show short phases of deeper hypometabolism with only small changes in body temperature because of their low thermal conductance and high thermal inertia due to the large body size

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(Heldmaier et al., 2004). A nocturnal hypometabolism was already detected in red deer (*Cervus elaphus*) (Arnold et al., 2004), moose (*Alces alces*) (Renecker and Hudson, 1985), ibex (*Capra ibex ibex*) (Signer et al., 2011), and Przewalski horses (*Equus ferus przewalski*) (Arnold et al., 2006)

Specific physiological changes in the horse

Generally, there is little information available concerning the adaptation of horses to cold ambient temperature and especially concerning the adaptation to long term heat stress without physical activity of the animal.
In the following, a review is given on the specific physiological changes described for horses exposed to high or low ambient temperatures.

Rectaltemperature / Skintemperature

The measurement of the rectal temperature is suited to evaluate the body core temperature that is specified in adult horses as 37.5 – 38.0 °C (Langlois, 1994; Knickel et al., 2002; Hines, 2004). Foals have a slightly higher body temperature of 37.5 – 38.5 °C (Kolb, 1967; Knickel et al., 2002). It is considered that deviations of more than 1 °C of normothermia leads to discomfort, and that a decrease of more than 10 °C or an increase of more than 5 °C is fatal (Langlois, 1994).
Exposing the horse to a hot environment results in an increasing rectal temperature (Honstein and Monty, 1977; Ott, 2005). Likewise the skin temperature raises (Honstein and Monty, 1977) as the blood circulation of the body periphery increases by vasodilation. The temperature difference between skin and environment becomes greater and the heat dissipation by radiation and conduction increases (Scheunert and Trautmann, 1987). Short-term exposure (1 hour) of horses to ambient temperatures of -3 to 37 °C did not lead to changes in the rectal temperature (Morgan, 1997).
Decreasing ambient temperatures did not result in a uniform development of the rectal temperature. In neonates the rectal temperature remained constant during exposure to cold for several hours (Ousey et al., 1992), however, cold-habituated

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yearlings showed a lowered rectal temperature of 0.4 °C (Cymbaluk and Christison, 1993).

Heart rate

There is variable Information concerning changes of the heart rate under different climatic conditions. According to Cymbaluk and Christison (1993) yearlings did not change their heart rate with lower ambient temperatures. Likewise Morgan (1997a) found no effect of a cold environment on the heart rate in adult horses. Similar results were shown by Art and Lekeux (1988) for ponies. On the contrary, Ousey (1992) reported increasing heart rates in foals with ambient temperature falling below 20 °C. According to Arnold et al. (2006) a long-term exposure of Przewalski horses to a cold environment led to decreased heart rates.
An increase in cardiac output was shown by McConaghy (1996) for ponies at ambient temperatures of 41 °C. At ambient temperatures above the thermoneutral zone the increasing blood circulation of the skin (Scheunert and Trautmann, 1987) requires a higher cardiac output per minute so that the cardiac output as well as the heart rate increases with increasing ambient temperature (Kolb, 1967). However, Morgan (1997a) as well as Art and Lekeux (1988) found no change of the heart rate with higher ambient temperatures.

Respiration rate

With higher ambient temperatures the heat loss via evaporation needs to increase, since the temperature gradient between the skin and the environment is lowered and the non-evaporative heat loss is reduced. Not only the heat loss by sweating increases but likewise the heat loss from the respiratory system rises (Morgan, 1997a). With a higher in- and exhalation the amount of water lost and with it the amount of heat that can be dissipated increases. Few data is available for changes in respiration rate of horses under changing environmental conditions. Art and Lekeux (1988) as well as Honstein (1977) observed no changes in the breathing pattern of ponies and horses with changes in ambient temperature and humidity. On the contrary Morgan (1997a) found increased respiration rates for horses exposed to temperatures above 20 °C for one hour. Ousey (1992) described increasing

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respiration quotients for foals with decreasing temperatures and Cymbaluk and Christison (1993) showed a reduction of 27% in the respiration rate in yearlings under cold environment exposure.

Blood parameters

Different blood parameters exhibit changes at extreme ambient temperatures that can be attributed to thermoregulation. However, only little information regarding changes in blood parameters of horses exposed to high and low ambient temperatures is available.

The thyroid gland produces the hormones thyroxin and triiodthyronine which are responsible for the basal metabolic activity. When these hormones are increasingly produced and released to the blood, the metabolic rate increases (Scheunert and Trautmann, 1987) Thus, the metabolic intensity can be determined by their concentration in the blood (Mejdell and Boe, 2005). High and low ambient temperatures lead to changes in the thyroid gland activity. With high ambient temperature less thyroxin is released to the blood to reduce the metabolic heat production. A cold environment leads to an increased thyroid gland activity with increased thyroxin concentrations in the blood and an increased heat production (Thompson, 1973; Penzlin, 1991). Irvine (1967) showed an increase in the thyroxin secretion rate of horses during adaptation and housing in a cold environment. In addition, Floris (1990) found effects of the season on the triiodthyronine concentration. Despite this, Mejdell and Boe (2005) could not detect an effect of ambient temperature on serum thyroxin concentration. Equal findings were reported by McBride (1985) for thyroxin and triiodthyronine. According to Sjaastad (2003) changes in the thyroid hormones secretion do not occur instantly after acute cold exposure since the thyroid gland needs to increase size before a higher secretion level is reached. Therefore, prolonged cold exposure is needed to increase thyroid hormone release.

During cold winter weather the energy available by feed consumption may not be sufficient and body fat is mobilized to cover the energy demand. Blood lipid concentrations can therefore change with temperature changes as monitored by Floris (1990). Likewise Ott (2005) reported an altered rate of glucose and lipid metabolism.

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High environmental temperatures led to higher concentrations of total protein and urea nitrogen as well as adrenalin. The total protein and urea nitrogen concentrations decreased under low ambient temperatures (Floris et al., 1990; Ott, 2005).

Sweating

The heat loss via evaporation is the most effective heat loss mechanism under hot temperatures for the horse (Morgan et al., 1997). It has been suggested that when temperatures and humidity is high, evaporative heat loss is difficult (McCutcheon and Geor, 1996). At high ambient temperatures the amount of sweat lost by the horse increases (Ott, 2005). At 20 to 25 °C no or little cutaneous water vapour loss was recognized by Allen and Bligh (1969) while Johnson and Creed (1982) found a water vapour loss of 61 – 94 g/m^2 per hour at these temperatures. At temperatures of 45 °C the losses were distinctly higher with 306 – 1210 g/m^2 per hour. Though, fluctuating rates in sweat output of the horse were observed with increasing temperatures (Allen and Bligh, 1969; Johnson and Creed, 1982), whereas initial sweating occurs as pulses with a frequency of one pulse per minute, followed by a continuous emission of sweat (Johnson and Creed, 1982).

The sweat of the horse is unusual as it contains high concentrations of glycoproteins that reduces the surface tension and helps the sweat spread along the hair. Thus, a greater surface is formed helping to increase the evaporation and heat loss (Marlin, 2008; Kennedy, 2011). Furthermore, the proteins lead to foam formation preventing sweat from dripping down, because every lost drop of sweat is lost for thermoregulation. Additionally the foam formation increases the reflection of solar radiation.

With decreasing ambient temperatures the evaporative heat loss looses importance and other ways of heat dissipation become significant (Morgan et al., 1997).

The described changes in the physiological parameters due to exposure to heat usually decline after a few days since the animal acclimatize to the higher temperatures (Ott, 2005), e.g. by a reduction of the metabolic heat production and feed intake (Bianca, 1977).

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Scope of thesis

The number of robust horses held in year round extensive outdoor housing systems increases continuously, thus exposing the animals to extreme environmental conditions. Wild horses are known to adapt to changing environmental conditions, e.g. by the accumulation of body fat, changes in activity or even a reduction in metabolic rate. It is the question if domesticated horses have the ability to adapt to the extreme climatic conditions as they are usually selected for high performance, short hair length and a less compact body stature. Extensive outdoor housing of horses is also associated with a restricted control over animals, especially in winter. Particular the body condition of ponies is difficult to assess and can result in inadequate feed supply that may cause health problems in the animals. This impairment of the animals' health has financial consequences caused by the therapy as well as ethological consequences by the impaired welfare.

Ten Shetland ponies were housed under semi-extensive conditions over a one year period. In summer the animals were kept on pasture with access to shelter, in winter the ponies were housed on a paddock with an adjacent stable. The effect of possible feed shortage in extensive horse keeping systems on animal health was simulated by feed restriction of five animals in winter.

The aim of this thesis was to investigate seasonal adaptive changes in locomotor activity, resting behaviour, physiological and blood parameters as well as in total body water and total water intake. The changes in the parameters can be used to draw conclusions on the adaptation capacity of these animals and to evaluate if the year round semi-extensive housing meets welfare requirements of the horses.

The more detailed aims of the study were:

- To determine the diurnal and circadian rhythm of activity and resting behaviour and to observe changes in the adaptation capacity of metabolic rate, body temperature regulation and resting heart rate in horses kept under semi-extensive conditions (Chapter 2).
- To observe whether the recorded data suggests the existence of hypometabolism in larger domestic mammals such as the horse (Chapter 2).
- To estimate seasonal adaptive changes of hormones and metabolites in the horse under semi-extensive conditions and during feed restriction (Chapter 3).

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- To compile equilibration times measured for the isotopes Deuterium, Tritium and ^{18}O in animal studies and to identify impacts upon it (Chapter 4).
- To identify factors influencing the total water intake and the total body water in horses under semi-extensive housing conditions and to evaluate a prediction equation for total body water based on the isotope dilution technique (Chapter 5).
- To compare the adaptation mechanisms in the horse found in the present studies with strategies found in other domestic herbivores such as sheep, goats and cattle (Chapter 6).
- To evaluate if the semi-extensive outdoor housing leads to impairment of the animal welfare or if this housing system can be assessed as adequate for horses (Chapter 6).

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