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CONTROL OF THERMOREGULATION IN SPECIES

BACHELOR THESIS

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Abstract

Termoregulácia zahŕňa procesy riadenia telesnej teploty, v dôsledku čoho je teplota udržiavaná v relatívne stálom rozmedzí. Je to veľmi dôležité pre mnohé chemické procesy, ktoré sa odohrávajú v organizme.

Existuje mnoho mechanizmov termoregulácie. Vo všeobecnosti sa rozdeľujú živočíchy na ektotermné a endotermné. Endotermné zvieratá sú cicavce a vtáky. Tieto zvieratá majú vyššiu metabolickú rýchlosť ako ektotermné. Je to preto, lebo počas metabolických procesov sa tvorí teplo a endotermné živočíchy môžu regulovať telesnú teplotu reguláciou metabolickej rýchlosti. Zvýšená metabolická rýchlosť u endotermných živočíchov znamená, že ich spôsoby termoregulácie sú energeticky náročnejšie ako u ektotermných živočíchov.

Prenos tepla medzi zvieraťom a vonkajším prostredím sa uskutočňuje štyrmi mechanizmami: kondukciou, konvekciou, radiáciou a evaporáciou.

Kondukcia je prenos tepla pomocou pevných látok alebo tekutín bez pohybu. Konvekcia je prenos tepla pomocou média, ktoré sa pohybuje, napr. pohybujúca sa tekutina. Radiácia sa uskutočňuje medzi zvieraťom a prostredím. Absorbovaná energia sa premieňa na teplo na povrchu objektu. Zviera emituje teplo radiáciou.

Hlavné mechanizmy, ktorými sa stráca teplo sú evaporatívna a neevaporatívna strata tepla. Evaporatívna strata tepla sa uskutočňuje potením, zrýchleným povrchovým dýchaním alebo rýchlym pohybom membrán v hrdle pri otvorených ústach (napr. kormorány), kým neevaporatívne straty tepla sa uskutočňujú zmenami v izolácii, piloerekciou alebo zmenami postoja.

Triaška je termoregulačná odpoveď u homoiotermných zvierat. Odpoveď je ľahko spozorovateľná a zahŕňa rýchle sa opakujúce kontrakcie kostrových svalov. Tieto kontrakcie spôsobujú tvorbu tepla. Netrasová termogenéza zahŕňa hnedý tuk ako mechanizmus tvorby tepla.

U ektotermných živočíchov chýbajú autonómne termoregulačné mechanizmy typické pre endotermné organizmy. Avšak ektotermné organizmy majú istý spôsob regulácie telesnej teploty, ktorý spočíva vo vyhľadávaní prostredia, ktoré je pre nich vhodné. Tento spôsob vedie k tomu, že telesná teplota je stála za rôznych vonkajších podmienok. To je podstata tzv. termoregulácie chovaním.

Ak telesná teplota stúpa a zviera nie je schopné ju kompenzovať regulačnými mechanizmami, vyvíja sa hypertermia. Ak sa telesná teplota znižuje a zviera nie je schopné tento stav kompenzovať, vyvíja sa hypotermia.

Kľúčové slová: endotermia, ektotermia, termoregulácia, riadenie, telesná teplota

Abstract

Thermoregulation is a concept that refers to the process of regulating the body temperature in such a way that it is kept in a relatively constant range. This is very important, regarding the many chemical processes that happens in the body at any given time.

The thermoregulatory strategies in the world is many and diverse. The main division is between ectotherms and endotherms. Endotherm animals include mammals and birds. These animals have a higher metabolic rate than the ectotherms. This is because the metabolic processes produce heat, and the endotherms can regulate their body temperature by regulating the metabolic rate. The increased metabolic rate in endotherms means that their way of thermoregulating have a greater energy cost than the ectotherms strategy.

Heat transfer between the animal and the environment is happening through the four very distinct mechanisms: conduction, convection, radiation and evaporation. Conduction is the transfer of heat through a solid or a fluid, without movement. Convection is heat transfer through a medium that moves, for instance, fluid in flow is an example of heat transfer via convection. Radiation happens between the animal and the environment. Energy that is absorbed is converted into heat at the surface of the object. The animal will emit heat through radiation. The main mechanisms for heat loss include evaporative heat loss and non-evaporative heat loss. Evaporative heat loss happens through evaporation of sweat, or panting and gular fluttering etc. while non-evaporative heat loss happens through changes in insulation and piloerection, or through posture changes.

Shivering is a thermoregulatory response found in homeotherm animals. The response is rather remarkable, and involve the skeletal muscle performing rapid, repeated contractions. These contractions leads to heat production. The non-shivering thermogenesis include brown fat as a mechanism for thermoregulatory heat production.

In ectotherms, the autonomic mechanisms of thermoregulation seen in endotherms is lacking. However, the ectotherms do display some control over the body temperature by selecting thermal microhabitats that are appropriate for them. This behavior causes a body temperature that is stable under varying ambient temperatures. It is termed behavioural thermoregulation.

If the body temperature rises, and the animal is not able to compensate with its thermoregulatory mechanisms, it will lead to hyperthermia. If the body temperature decreases and the animal is not able to compensate, it will lead to hypothermia.

Key words: endothermy, ectothermy, thermoregulation, regulation, body temperature.

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List of abbreviations and symbols

a) ATP - Adenosine-5'-triphosphate

b) BMR- basal metabolic rate

c) CNS- Central Nervous system.

d) HSF- Heat Shock Factor

e) HSP- Heat Shock Protein

f) NST- Non-shivering thermogenesis

g) SMR- Standard Metabolic Rate

h) TNZ- Thermoneutral Zone

i) UCP-1 - Uncoupling Protein 1

1 Introduction

In this thesis, the goal has been to review the mechanisms of thermoregulation. This is the goal of the thesis because the thermoregulatory mechanisms in animals, whether they are endotherm or ectotherm, are basic mechanisms and foundation in many of the processes that happens in the body.

Thermoregulation is important because is a concept that refers to the process of regulating the body temperature in such a way that it is kept in a relatively constant range (Hill, et al., 2008). If the thermoregulation is insufficient, it will cause an increase or decrease in the body temperature of the animal. This would be unfortunate for the animal, because the body temperature influences the biochemical processes in the body. Increased body temperature can lead to hyperthermia if the animal is not able to compensate for the temperature. This can in worst-case scenario lead to denaturation of enzymes and death (Byers, 2012). On the other hand, if the body temperature is low, it can also affect the animal, and hypothermia develops. Hypothermia can easily occur during general anaesthesia with small animals, and it is then important to know the mechanisms behind the heat loss, so it can be prevented.

It is also important to know the mechanisms behind heat loss and stress from the point of view of animal welfare, and production. Endotherm animals kept at unsatisfactory temperatures will increase the metabolic rate to compensate for e.g. heat loss. Increased metabolic rate causes increased need for energy, and thus increased food consumption. That the energy is used for thermoregulatory mechanisms rather than production is uneconomic for the farmer.

Thermoregulation is an interesting topic, and it is important with knowledge about the foundations of the physiological regulation of body temperature, and the influence the ambient environment and temperature have on the animal and the thermoregulatory mechanisms.

2 The state of knowledge at home and abroad with respect to the field involving the theme of the study

2.1 What is thermoregulation

Thermoregulation is important for animals to keep the temperature in the body at a relatively constant range, because there are a number of chemical reactions going on in the body at any given time. These chemical reactions are sensitive to great changes in temperature, and if temperature gets too low, the metabolic processes are slowed and this will influence the functions of the body. This is because the temperature of the tissue is important for determining the functional properties of the constituents of the tissue, and the tissue. The tissue temperature affects whether the protein molecules in the tissue is high-preforming or low-performing molecular conformations. In addition, the tissue temperature influences biophysical processes in the body this include the rates of diffusion and osmosis. Temperature also influences the rate of biochemical processes and reactions (e.g. the optimal temperature of enzymes). The viscous state of cellular components is also one of the factors that is influenced by temperature, as the phospholipid layer of the cell membrane will adapt different properties in different temperatures. If the body temperature decreases only with 4 degrees centigrade (from a normal temperature of 38 °C to 34°C) animals will become unable to regulate their own body temperature. If the temperature continues to decrease, the animal will suffer from cardiac fibrillation and death when the body temperature reaches 29° to 27°C. Increase of body temperature is also unfavourable, as temperatures; over 45 °C will damage the brain (Cunningham, 2007).

2.2 Chemical changes

In biological membranes, lipid components may be as much as 25-50% of the dry weight of the membrane. The physical properties of the lipid components, and therefore the biological membranes, are markedly influenced by temperature. Normally the lipids consist in a “liquid crystal”-state that is intermediate between a material that is highly fluid, and a structure that is rather rigid. The balance can be easily disrupted by changes in the thermal environment. Disruption in the structural state of the lipids, causes changes in the viscosity of the membranes of the cell. Changes in the membrane functions can be very severe, and even cause heat death. Especially in very sensitive sites, such as the synapses, any malfunction will produce immediate behavioural effects (Wilmer, et al., 2005).

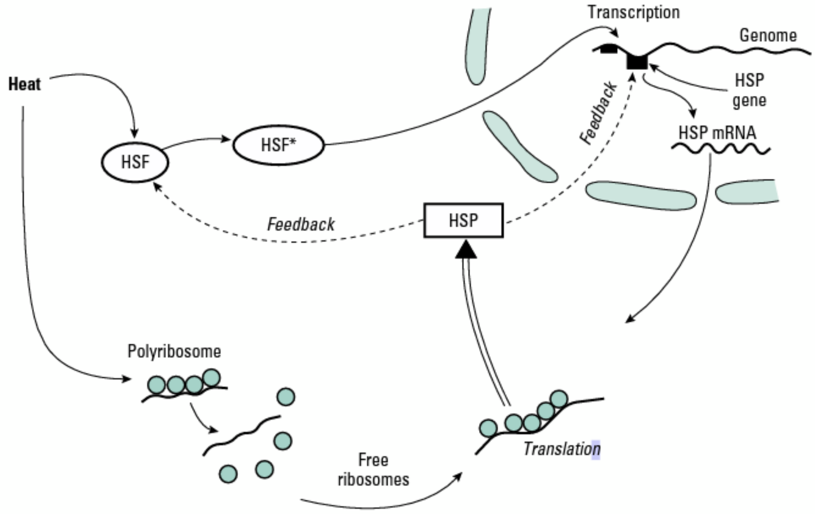
The induction on certain proteins that have a protective effect, is another effect of temperature at the biochemical level. These proteins are commonly called Heat Shock Proteins (HSP) or more generally stress proteins. These proteins have been proved to play a key role in regulation of protein folding and the coping mechanisms for proteins that have been affected by heat or other stresses. The HSP was a major field of interest during the 1980s and 1990s. The HSP are divided into several families based on their size in molecular weight. They are also divided into what proteins that are most common in the different organisms. In animals, the rather large HSP families dominate (HSP60, HSP70, HSP90, HSP100 and Lon), but in plants the smaller HSPs are more common than the large (this include HSP10, HSP27 and ubiquitin). HSPs seem to have little change in structure across the different kingdoms, and their functions are also highly conservative. They are induced by natural changes such as hypoxia, hyperoxia, osmotic shock, and change in pH. But they can also be induced by stress of a less natural nature such as the presence of alcohols, ionizing radiation, heavy metals, toxins and free radicals. Later they can bring the organism *cross tolerance*. This means that after the protein has been induced in relation to a particular stress, it will make the organism more tolerant for other types of stress (Wilmer, et al., 2005).

The introduction of HSP manifestation in relation to temperature is related to the normal thermal regime of the organism. Species that are from a warm environment will have a substantially higher threshold temperature before the response is expressed, than organisms from a cold environment. The concentration of the HSPs induced will also differ significantly between the different tissues within one single individual. The ability to synthetize HSPs is in large part correlated with the thermal tolerance in the organism. This is evident in all animal taxa (Wilmer, et al., 2005).

The mechanisms behind the action of HSPs are now understood as a kind of “molecular chaperonage”. Proteins are normally folded in to their tertiary structure after the synthesis, this tertiary structure is important for the function of the protein. If the proteins are exposed to various kinds of stress, they can respond by unfolding the tertiary structure. The tertiary structure can also be unfolded as a response to natural reactions in the cell, such as transport across membranes. If the protein first is unfolded it is a chance for it to refold wrongly, and thus be at risk of interacting with other cellular components, or other unfolded proteins, and this way make them useless. By recognizing the binding sites in the exposed side groups on the unfolded protein, the molecular chaperones limit the interactions to other cellular components, and unfolded proteins, and stabilizes the unfolded state of the protein. When it is appropriate, the chaperone molecule releases the protein, and lets it refold correctly, the protein is then free to resume its normal function. HSP is the primary molecular chaperones that are synthetized in reaction to stress that causes unfolding of protein. In some cases, HSP from different families can collaborate as co-chaperones (Wilmer, et al., 2005).

A cytoplasmic detector named *heat shock factor* (HSF) regulates regulation of heat shock response. Until the shock occurs, the HSF exists as a monomer. After the shock, the monomers are trimerized into an active trimeric form and is moved into the nucleus of the cell. Here it binds to the promoter site for the HSP genes, and thus the transcription of these proteins are initiated. The HSP70 family have a negative feedback interaction with the HSF by inhibiting the trimerization. This way, the HSF monomer and the unfolded protein is competing for interaction with the HSF. If there is an excess of unfolded proteins, the HSP70 will stabilize these, and the HSF is free to trimerize and increase the concentration of HSP. An overview of this process can be seen in ***figure 1*** (Wilmer, et al., 2005).

Figure no. 1, A model for regulatory systems during heat shock



Source: Wilmer, et al., 2005

2.3 Physical changes

The biological processes in the body generally display a temperature effect over two phases. The first phase is a consequence of the rates of the enzymatic processes in the body, increasing with the increased temperature. The rate of the enzymatic reactions increases with the increase of temperature, but only to a certain point (Wilmer, et al., 2005).

The second phase is when the temperature has risen to such a degree that the speed of the enzymatic reactions has reached its peak, and is starting to subside. Under normal circumstances, this temperature range is rarely experienced. The temperature at this level has a destructive effect, and therefore the rate of activity is starting to decrease.

For all enzymes and enzymatic processes there is an optimal temperature, when this temperature is surpassed, the rate of activity rapidly decreases, and denaturation and destructive effect on the enzyme occurs (Wilmer, et al., 2005).

The mortal body temperature for most body systems is around 43-45 °C, at this temperature the enzyme systems starts to denature (Reece, 2004).

2.4 Definition Homeotherm and Poikilotherm

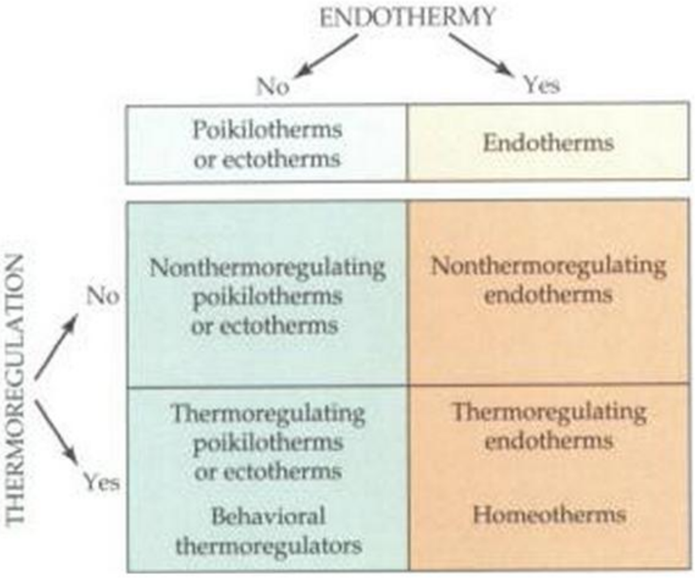
There are several different strategies for regulating the body temperature. Some animal's main strategy is to use metabolic heat to warm the tissues in the body. The organisms that use this strategy is termed *endotherms* as their heat is generated from inside. Endotherm organisms are divided in to two groups, the ones that perform thermoregulation and the ones that does not. The thermoregulating endotherms includes a group of animals that are classified as homeotherms. These organisms thermoregulate by physiological means, and not just by behaviour. Mammals and birds are examples of homeotherm animals (Cunningham, 2007).

On the other hand, you have the animals that are not endotherms, these are referred to as *ectotherms* or also *poikilotherms* as their body temperature is decided by the external environment and may be variable. Poikilotherms are also divided into one group that perform thermoregulation, and one group that does not. The poikilotherm organisms that practice thermoregulation does this by behaviour, this means that they move to environments that are favourable for keeping their body temperature stable (Cunningham, 2007).

Some animals also adopt different relationships to the environment at different times. This include for instance the hibernating animals. These are homeotherms when they are not hibernating, but when they hibernate they adapt neither thermoregulation nor endothermy (Cunningham, 2007).

In ***figure 2****,* is showed that animals may fall into four categories of thermal relations. These categories depends on whether the animal display endothermy, and if it displays thermoregulation (Hill, 2008).

Figure no. 2, Four categories of thermal relations



Source: Hill, 2008..

2.5 Homeotherm thermoregulation

Homeotherms are as earlier mentioned, organisms that practice thermoregulation by physical means and not only by behaviour. They do use behavioural methods to regulate the temperature, but are not limited to only this, as they can modify heat loss and conservation by physiological means (Reece, 2004). Homeotherms have a higher metabolic rate than the poikilotherms and this cause a production of heat that is 7 to 10 times greater than that in the poikilotherms. The high level of heat produced by metabolism makes it possible for the homeotherm organism to be more or less independent on the external or ambient temperature, compared to the poikilotherm (Reece, 2004). Under many circumstances the principal way the homeotherms thermoregulate, is by adjusting how rapidly they produce and retain the metabolic heat produced in the body by the various chemical processes (Hill, et al., 2008).

Since they evolved for some 70 million years ago, the homeotherms have been very successful. Their strategy of keeping a high metabolic rate for thermoregulation needs a very high energy intake (Reece, 2004). This means that the food requirements for homeotherm animals and birds is greatly increased compared to poikilotherm animals like reptiles and fish of the same size as the homeotherms (Hill, et al., 2008).

2.6 Metabolic heat

Heat inputs to the animal body comes in the form of heat from metabolic processes that goes on continually in the body. During all stages in the metabolic process, will the food ingested produce heat (Hill, et al., 2008). This is because both the energy that is ingested and the energy that is stored in the body is oxidized and yields chemical energy in the form of adenosine triphosphate (ATP), or as creatinine phosphate, this is the only form of energy the body and the animal system can utilize (Reece, 2004). The end products of the oxidation are various nitrogenous compounds such as urea or uric acid, but also hydrogen, and the oxides if carbon. Protein compounds are incompletely oxidised, and their loss from the body in excretory form represents a loss of energy from the system, this is also applies for the energy used for the synthesis of the proteins (Reece, 2004). The energy derived from ATP is used to internal work, such as maintaining active-transport systems, and muscle contraction. The energy that is used for the internal work in the system will ultimately end up as heat. Some of the heat that is derived from doing this kind of work will end up outside the body (Reece, 2004). In ***table 1***, there is an overview of the average range of the rectal temperature in some domesticated animals.

Table no. 1, Rectal temperature of domestic animals,

Animal	*Average (°C)*	*Range (°C)*
Stallion	37.6	37.2-38.1
Mare	37.8	37.3-38.2
Donkey	37.4	36.4-38.4
Camel	37.5	34.2-40.7
Beef cow	38.3	36.7-39.1
Dairy Cow	38.6	38.0-39.3
Sheep	39.1	38.3-39.9
Goat	39.1	38.5-39.7
Pig	39.2	38.7-39.8
Dog	38.9	37.9-39.9
Cat	38.6	38.1-39.2
Rabbit	39.5	38.6-40.1
Chicken (daylight)	41.7	40.6-43.0

Source: Reece, 2004

2.7 Basal metabolic rate

Heat produced by the body is related to the metabolic rate, because the basal metabolic rate is necessary for maintaining cell functions (Hill, et al., 2008).

The concept basal metabolic rate is an animal’s metabolic rate with some parameters. The basal metabolic rate must be determined while the animal is resting and fasting in its thermoneutral zone (TNZ). The thermoneutral zone has a lower-critical temperature and a higher-critical temperature. These are the highest and lowest ambient temperatures in the thermoneutral zones. The higher-critical temperature and the lower-critical temperatures are dependent on species (Hill, et al., 2008). Within the thermoneutral zone, the animal will keep its metabolic rate constant, but if the temperatures start to decrease below the lower-critical zone, the metabolic rate will start to increase in a linear way to the decrease in temperature, and with a higher metabolic rate follows higher body temperature (Wilmer, et al., 2005).

The tissues in endotherm animals have a much higher number of mitochondria and also much higher activity of mitochondrial enzymes than what is found in ectoderms in the same size. When the animal is active, it is generally the muscles that are the main heat source for the body. The muscles can in an active state elevate the metabolic rate 10-fold. If the endotherm animal (especially relevant in mammal and birds) is resting, thoracic and abdominal organs supplies most of the heat, they supply as much as three-fourths of the heat in the body of the resting animal (Wilmer, et al., 2005). It is also possible that the endotherm animals have a different kind of mitochondria, it is believed that the mitochondria in endotherms carry out oxidative phosphorylation that is always partially uncoupled, and this causes more heat to be released for a given level of ATP generation. The thermoregulatory mechanisms practised in endotherm animals are extremely expensive, and a large amount of energy that could have been used for growth and reproduction is used for thermoregulatory purposes. Thermoregulatory heat is actually the single largest component in the energy budget in homeotherm (Wilmer, et al., 2005).

The basal metabolic rate of an endotherm animal, is best compared with the standard metabolic rate (SMR) of a poikilotherm. SMR must be measured to a specific body temperature in a resting and fasting poikilotherm (Hill, et al., 2008). The most thorough recent analyses of resting metabolic rate in vertebrates shows that for small- to medium-sized vertebrates (body mass 50–1000 g), the resting metabolic rate of a typical bird can be approximately 15 times higher than that of a reptile, and for a typical mammal the factor is about 12 (Clarke, et al. 2010).

2.8 Heat transfer between environment and animal

In addition to making heat internally through metabolism, the animals also exchange heat with the environment and the surroundings. The heat transfer between animal and environment is made possible by four very distinct mechanism. These include convection, conduction, thermal radiation and evaporation as seen in ***figure 3*** (Hill, et al., 2008). A third way of heat loss considers excretion of faeces and urine that leaves the animal at body temperature (Reece, 2009).

The heat transfer mechanisms will always apply to the animal, as it can gain heat by one mechanism while losing heat through another. The mechanisms follows distinct laws, and can simultaneously operate in different directions. It is important that they are not simply lumped together, but each mechanism needs to be analysed on its own. Only after they all have been analysed on their own can the effects be summed together and the full effect of the heat-transfer mechanisms on the animal can be determined (Hill, et al., 2008).

Naturally, if the body temperature of the animal is to stay constant, the sum of all the heat gained and all the heat lost through all the heat transfer mechanisms must be equal (Hill, et al., 2008). For instance, if an animal is gaining heat from its surroundings and environment by the means of conduction and thermal radiation in addition to metabolic heat, it might be losing heat through evaporation and convection. If the body temperature of the animal is to stay stable, the amount of heat input per unit of time must be equal to the amount of heat lost per unit of time (Hill, et al., 2008).

2.8.1 Conduction

Conduction is the movement of heat from higher temperatures to lower temperatures. The heat is transferred through either solids or fluids without movement of molecules (Reece, 2004). Conduction and convection is often discussed together because they both have in common that when heat moves through a material or substance by either mechanism, the atoms and molecules of the substance participates in the heat transfer (Hill, et al., 2008).

A common example of conduction is the heating of a block of copper, the principle applies for all types of or solids and fluids without movement (e.g. stone and the ground), but say you are heating one side of a cupper block; you will soon notice that the temperature on the other side of the block is also increasing. The heat is moving through the block and appears on the other side, even if there is no macroscopic motion in the block. The heat is moving through the block by strictly anatomic-molecular interactions. If the atoms or molecules on one side of the block is agitated, they agitate the atoms that is further inside the substance by colliding into them; this causes the agitation to travel through the whole block (Hill, et al., 2008).

The rate of heat transfer from one side to the other side of an object can be determined by the formula:

$$H_{conduction} = k\frac{T_1 - T_2}{d}$$

Here *d* is the thickness of the block that the heat has to move through, T_1 is the temperature of on one side of the block, and T_2 is the temperature on the other side of the block. K is a constant, and H is the rate of conduction. The ratio $(T_1\text{-}T_2)/d$ is known as the *thermal gradient.* As seen in the equation, if the temperature difference on the two sides of the block is increased, the rate of conduction will also increase. An increase of the thickness of the block (*d*) will slow the rate of conduction through the block, as the agitation of the molecules must continue over a larger area (Hill, et al., 2008).

The coefficient *k* is dependent on the material the block is consisting of. Some materials transfer heat really well, while others conduct heat very poorly. Air is one material that conducts heat very poorly, and is therefore a very good insulator. If the material conducts heat poorly, we say that it has a low *thermal conductivity*, and a low value of K (Hill, et al., 2008). Water has a conductivity that is about 20 times higher than air, this means that water leads heat better than air, and thus has a higher K value.

The amount of the heat transferred is proportional to the size of the thermal gradient. If the skin temperature of the animal is equal to the temperature of the ambient air or water, conduction will not occur, and there will be no heat exchange (Reece, 2004). As earlier mentioned, the air has a low K value, and it conducts heat poorly. This makes air a good insulator if it is trapped against the skin. Fat is another material with poor conductive properties. Marine mammals commonly use fat as an insulating layer in the subcutis. This subcutaneous layer with low conductive properties reduces the heat transfer to the skin by conduction (Reece, 2004).

2.8.2 Convection

As earlier mentioned, conduction is the movement of heat through either solids or fluids *without* movement of molecules. Convection on the other hand is transfer of heat through a material or substance *with* macroscopic motion of the substance (Hill, et al., 2008). For convection to happen, fluid in flow is required (Hill, et al., 2008). The movement of the fluid or gas that is in contact with the skin causes the loss or gain of heat (Reece, 2004). This is because if a current of fluid or wind is present, the macroscopic motion in the material carries the heat from one place to another. This transfer of heat from one place to another through movement of the material is convection (Hill, et al., 2008).

Heat transfer by convection is much faster than with conduction, and that is one of the critical differences between the two. If a horizontal surface is 10°C warmer than the surroundings, and the air is moving by a speed of 4.5m/s, the heat transfer by convection will be 70 times faster than if the air is motionless. This is why wind greatly increases the thermal stress on a cold day (Hill, et al., 2008).

During heat transfer through convection the rate of the transfer depends on the temperature difference between the surface of the material and the moving fluid or air (Hill, et al., 2008).

The rate of convective heat loss can be calculated by the following formula:

$$H_{convection} = h_c(T_S - T_A)$$

Only if the surface temperature (T_S) exceeds the ambient air temperature (T_A) will the animal lose heat by convection. If the ambient temperature is higher than the surface temperature, the animal will gain heat by convection. The convection coefficient (h_c) depends on many factors. These include the shape of the body parts of the animal, their orientation to the wind, and the speed of the wind (Hill, et al., 2008).

Many of the body parts in animals is shaped cylindrically, this is true for e.g. limbs and torso. The rate of heat transfer increases as the diameter of the cylindrical shaped limb decreases. This physical law explains why the body parts like fingers (small diameter), is very vulnerable. They are easily cooled in cold environment (Hill, et al., 2008).

Water or air that is associated with transfer of heat by convection changes density. This causes it to move under the influence of gravity. This known as free convection. On the other hand, you also have forced convection; this is the loss of heat by convection that is caused by a wind or the motion of water. Convection can cause a heat loss of such an amount that it results in hypothermia. Wind chill includes both the air temperature and the wind velocity (Reece, 2004).

2.8.2.1 Heat Transfer in the Body

Heat transfer in the body is achieved by the combination of two mechanisms. There is the movement of heat from hotter tissues to cooler tissues through conduction, but on the other hand, also blood distributes heat through the body. This is a form of convective heat transfer; it is also the main method of distributing heat through the body (Reece, 2004)

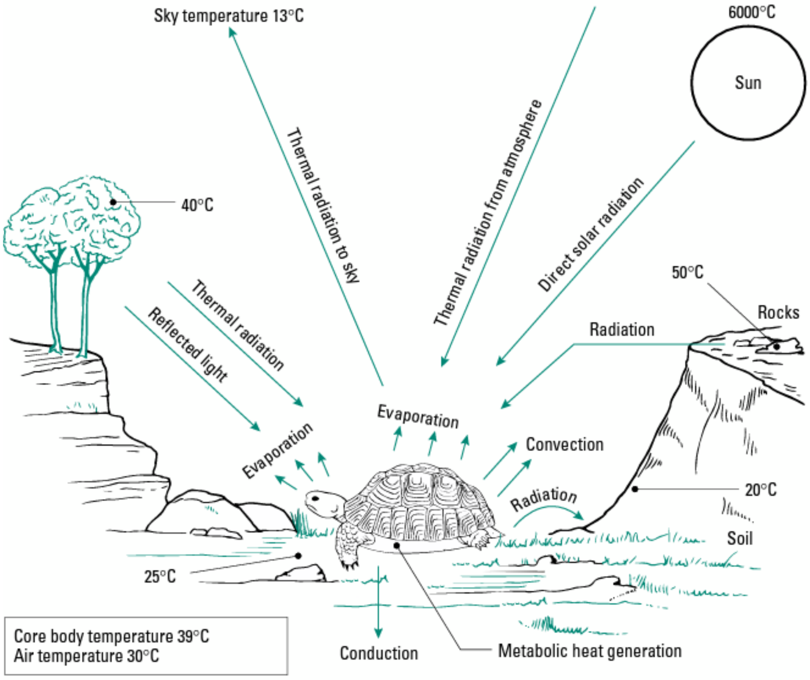
2.8.3 Thermal Radiation

Thermal radiation often ranks as one of the quantitatively dominant mechanism of heat exchange with the environment for terrestrial animals. Even though it is one of the most important mechanisms for heat exchange, it tends to be one of the least understood mechanisms. Everyone is familiar with radiant heating by the sun, but this is actually only one of the thermal radiation mechanisms (***Figure 3***). Thermal radiation is a heat transfer mechanism that is ubiquitous (Hill, et al., 2008).

That all objects emit electromagnetic radiation is the first important fact to recognize in the study of thermal-radiation heat transfer. If you consider a wall, it will emit electromagnetic radiation that is reflection of light. The light originates from a light bulb (or the sun) and then the wall reflects the light. The wall is also the original source of additional electromagnetic radiation; it emits radiation at infrared wavelengths that is invisible for the human eye. It travels with the speed of light and is unimpeded by intervening air until it hits a solid surface. This solid surface might for instance be an animal body, where the radiation is then absorbed. Simultaneously as the animal body receives the radiation, it emits its own electromagnetic radiation, some of which strikes the wall (Hill, et al., 2008).

This way, the animal body and the wall can exchange heat without being in contact with each other. The wall and the solid surface of the animal body does not need to be in especially close proximity, in fact they can actually be far apart. This is because any two objects that are separated only by air, undergo thermal-radiation heat exchange at the speed of light (Hill, et al., 2008).

Figure no. 3, The thermal exchange between a terrestrial animal and its environment



Source: Wilmer, et al., 2005

One of the key principles of thermal-radiation physics is that the surface temperature (T_S) of the object influences the range of wavelengths emitted by the object. If the surface temperature increases the wavelengths becomes shorter (Hill, et al., 2008). When electromagnetic radiation strikes an object, the radiant energy might pass through the object, it might be absorbed or reflected. The portions of the energy that is absorbed, reflected and transmitted is dependent on the properties of the surface of the object, and is wavelength-specific (Hill, et al., 2008).

The total rate of radiation emitted from an object is dependent on the relative surface area and the emissivity of the surface. Emissivity is a dimensionless constant that apply for any material and is related to the familiar concept of colour. The emissivity of a surface will vary for different wavelengths. This is what gives rise to perceived colour. If an object occurs red, this is because the material has high reflectivity and low emissivity of the seen red light (Wilmer, et al., 2005).

Energy that is absorbed is converted into heat at the surface of the object, e.g. the surface of the animal body. This can be experienced every day when our skin is warmed by radiant energy from the sun or from the embers of fire (Hill, et al., 2008).

Objects with temperatures that are on the biological range can be calculated to emit radiant energy in the range of 300-500m^{-2}. This is a very low emission if you compare it to hot bodies such as an electric heating element, or a light bulb, but it is a substantial heat loss in relation to the energy production from metabolism. For a resting animal of 10 kg and about 1m^2 of radiating surface, the emissive heat loss would be 300-500W, while the heat production through metabolic processes would be only around 20W. Of course, an animal like this would also gain heat through radiation from the components in the environment. Solar irradiance to the earth can if it is perpendicular to the earth's surface, exceed 1000W m^{-2}, this is much higher than the metabolic heat production of typical animals. The surfaces that are surrounding the animal (vegetation, rocks and soil) and have a similar temperature, will also radiate heat to the animal at roughly the same rate as the animal is emitting heat (Wilmer, et al., 2005).

2.9 Evaporative heat loss

Evaporative loss of water is an excellent way if dissipating heat; the latent heat of the vaporization of water is 2500 J/g at 0°C, and is still 2400 J/g at 40°C. The rate of evaporation is not only depending on the surface temperature, but also depending on the difference in water vapour density between the animal's surface and the environment. The surface resistance to lose water also influences the rate (Wilmer, et al., 2005).

For animals and birds faced with high environmental or metabolic (e.g. from exercise) heat loads, the active facilitation through evaporation is the ultimate line of defence. If heat accumulates to excessive levels and other thermoregulatory measures fail to stop the accumulation, active evaporative cooling becomes the only way to balance the heat gain and loss. The loss of water during evaporative cooling can dehydrate an animal if water to replace the lost water is not easily accessible. This is an probable explanation for why animals that live in environments where water is hard to find, employ other defences against overheating before they turn to evaporative cooling (Hill, et al., 2008).

There are various ways of achieving evaporative heat loss, this is because different kinds of body fluids can be used. Some reptiles and insects regurgitate gut fluids or urinate over their own surfaces to achieve heat loss by evaporation of the fluids. Nectar-feeding animals like butterflies and bees can regurgitate nectar or saliva onto their tongues and wave the droplet about to gain a cooling effect, this strategy is also known as tongue lashing (Wilmer, et al., 2005). The three major mechanisms of active evaporation that is known is: sweating, panting and gular fluttering (Hill, et al., 2008).

Sweating and panting is the two most obvious mechanisms used by mammals and birds for heat loss. Sweating is done from special glands at various points all over the body surface, and by panting the animal lose water from the respiratory surfaces by breathing rapidly through the mouth. These two different mechanisms involve supplementary Cutaneous Evaporative Water Loss (CEWL) and supplementary Respiratory Evaporative Water Loss (REWL). Most species has adopted to only one of these two different avenues of evaporative heat loss, but some species can switch between alternative mechanisms. It is not clear why some animals prefer one mechanism to the other, as they both need about the same amount of heat for evaporation. It is known that sweating is virtually exclusive to mammals, but something similar to sweating happens in some few species of frogs and in some insects such as cicadas. Some CEWL is reported in heat stressed birds, because epinephrine causes increased blood flow to the skin.

Smaller animals are at a disadvantage when they sweat because they have a high surface area to volume ratio. This is because heat load is proportional to body surface area and the water available for evaporation and cooling is proportional to the body volume. Small mammals therefore do not normally sweat because of the danger of dehydration. Panting is therefore more common in mammalian herbivores and nearly all carnivores. Panting is also found in all birds, as they lack sweat glands (Wilmer, et al., 2005).

2.9.1 Sweating

Sweating is an important thermoregulating mechanism, but not all sweat glands have a thermoregulating function. Some glands such as the ones in the axillary region of humans are odour-producing glands. Another example is the glands at the footpads of the dog, they are associated with increasing tactile sensitivity and the frictional resistance.

Humans are known to have a very well-developed mechanism for heat loss through cutaneous evaporation, but also other animals, particularly the larger species such as horses and cattle have evaporative heat loss through sweating as an important strategy for heat loss. In contrast to the sweat glands in humans, the large mammals like equines and bovines have apocrine sweat glands that are controlled by adrenergic nerve fibres (Reece, 2004).

There is two sweat gland systems, and they are fundamentally different from each other. The first sweat gland system includes ducts that open into the hair follicle, and are controlled by adrenergic fibres. The other system consists of ducts that opens up into the surface of the skin, after passing through the epidermis in a spiralling fashion that are controlled by the cholinergic part of the autonomic nervous system. When comparing these two cutaneous glands, it is obvious that they both can be used for thermoregulation (Reece, 2004).

The canine have an interesting alternative function of the sweat glands; the cholinergic footpad glands can increase the frictional resistance. The adrenergic glands that are found on the general body are identified with production of odour. These glands are comparative to the glands found in the axillary regions of humans. The odour is generated by bacteria that lives in the skin and utilize the sebaceous secretion and skin debris to produce compounds that are released in the air by evaporation. In ***table 2*** the types of sweat glands the various species of domestic animals have and their putative function can be seen (Reece, 2004).

Table 2, the types of sweat glands and their putative function in domestic mammals and humans.

Species	*Site*	*Type*	*Control*	*Function*
Dog	Footpad	Eccrine	Cholinergic	Frictional Resistance
	Skin	Apocrine	Adrenergic(α?)	Pheromone?
Cow	Skin	Apocrine	Adrenergic (α)	Thermoregulation
Sheep	Skin	Apocrine	Adrenergic (α)	Thermoregulation
Goat	Skin	Apocrine	Adrenergic (α)	Thermoregulation
Horse	Skin	Apocrine	Adrenergic (β_2)	Thermoregulation
Camel	Skin	Apocrine	Adrenergic (β_2)	Thermoregulation
Human	Skin	Eccrine	Cholinergic	Thermoregulation
	Axilla	Apocrine	Adrenergic(α?)	Pheromone?

Source: Reece, 2004

Even though the animal is not sweating, water loss occurs through the skin, but at a lower rate. This is termed transpirational water loss or insensible water loss. Sweating increases the rate of cutaneous evaporation by a factor of 50 or more by wetting the outer surface of the skin. The sweat is a saline solution and not pure water. The Na^+ and Cl^- concentration in sweat is lower than the concentration in blood plasma, and during acclimation to warmer weather conditions, the salinity of the sweat becomes reduced. Even if the salinity is reduced during acclimation, prolonged sweating will cause severe depletion of the body's Na and Cl reserves. Many animals does not sweat. Rodents, rabbits, hares lack integumentary sweat glands. Dogs and pigs does have sweat glands, but the secretion rates of the glands are so low that evaporative heat loss through sweating plays little or no role in the thermoregulation. Birds dos not sweat at all (Hill, et al., 2008).

Secretion from the sweat glands is activated by the sympathetic nervous system (Hill, et al., 2008).

The different innervations, especially with respect to the adrenergic nervous system, and the fact that the receptors may be either a α or a β_2 have implications or *the use of autonomic drugs*, whether they be agonists or antagonists. In bovines, caprines, and ovines α-receptors are found, while β_2 is found in equines and camelids. In equines the use of β- adrenergic agonists, and especially β_2 agonists, will stimulate sweating. General β-adrenergic blocking agents such as propranolol as well as specific β_2-adrenergic blocking agents will prevent sweating and may lead to hyperthermia during hot ambient conditions or following exercise as sweating is the main mechanism for heat loss in equines.

As a general rule regarding the evaporative heat loss mechanisms used by domestic animals, you can say that sweating is more important for the larger animals such as equines and bovines, while panting is more important for the smaller species such as sheep and dogs (Reece, 2004).

2.9.2 Panting

Panting is a common response to heat stress in birds and mammals. The increased breathing rate causes an increased rate of evaporation from the warm, moist membranes that lines the respiratory tract. The increased rate of evaporation causes a higher rate of evaporative cooling. In some species, the number of breaths per minute (respiratory frequency) increases progressively as the heat stress increases. Other species have a normal breathing frequency until there is an abrupt change at the onset of panting, and the rate of panting is independent of the level of heat stress (Hill, et al., 2008).

Dogs use the last mechanism. If the environmental temperature is cold, dogs have a breathing rate at about 10 to 40 breaths per minute. When they pant, the breathing rate jumps abruptly to 200 or more breaths per minute.

Analysis shows that if the animal has a stepwise change in breathing frequency, less muscular work is needed to pant. This is because the animals with stepwise change in frequency often pant at the resonant frequency of their thoracic respiratory structures. This means that less muscular work has to be done because the thorax has an essential tendency to “vibrate” between the inspiration and expiration positions at that frequency. Less muscular work means that less metabolic heat is produced (Hill, et al., 2008).

Panting also has certain advantages compared to sweating. One example is that no salts are lost from the body because of panting. This is because the evaporation occurs within the body and only pure water is evaporated. Another example of the advantage of panting is that panting forcibly drives air saturated with water vapour away from the evaporative surface. This makes the evaporation at the surface more effective.

There are also liabilities with using panting in comparison to sweating. The production of metabolic heat to drive the muscular work is one example. Another liability is the possibility of respiratory alkalosis. Respiratory alkalosis is an elevation of the pH of the body fluids as a result of excessive removal of carbon dioxide. During regular breathing (not panting), the respiratory rate is regulated so that the rate of which carbon dioxide is voided is in balance with the metabolic production of carbon dioxide. During panting there is a possibility of carbon dioxide being carried away by the breath faster than it is produced. This is because the breathing rate is increased for thermal control, instead of being governed by metabolic needs. If carbon dioxide is carried away faster than it is produced, the carbon dioxide concentration in the blood will fall. This causes the H+ concentration to fall. As the following reaction shifts to the left.

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^-$$

The decrease in H+ causes a rise in pH. This causes alkalosis, which can be deleterious for the body, because many cellular processes and enzymes are very sensitive to changes in pH (Hill, et al., 2008).

From extensive research, it has been learned that little or no alkalosis develops during panting in many of the mammalian and avian species that apply panting as regulative mechanism for heat control. These animals restrict the increased air movements during panting to their upper airways, and thus there is no exchange of carbon dioxide between the air and the blood. The membranes used for respiratory exchange in the deep lungs receive about the same rate of air when the animal is panting as when it is breathing normally, and this way the animal avoids alkalosis. By contrast, when there is extreme heat stress, resting but panting animals can often develop severe alkalosis. Superior tolerance to alkalosis has even been developed in some panting species (Hill, et al., 2008).

2.9.3 Gular Fluttering

Gular fluttering is a mechanism for evaporative cooling where the bird rapidly vibrate the gular area while holding their mouth open. The gular area is the floor of the mouth cavity and the process of gular fluttering is driven by the flexing of the hyoid apparatus. It promotes increased heat loss by increasing the flow of air over the moist and vascular oral membranes. The fluttering usually occurs with consistent frequencies. The frequency is apparently matched to the resonant frequencies of the structures involved. The fluttering is often done simultaneously with panting (Hill, et al., 2008).

Gular fluttering shares several positive attributes with panting. Not only does it create a forced and vigorous airflow across an evaporative surface, it does also not cause salt losses. On the other hand, unlike panting gular fluttering cannot cause severe alkalosis in the animal. This is because fluttering only enhances oral airflow and CO2 is not exchanged between the blood and air over the membranes. Thus fluttering will not cause changes in the blood plasma pH.

The movements in used in gular fluttering require less work than the ones in panting. This causes less heat production for increasing the evaporative heat loss (Hill, et al., 2008).

2.9.4 Wallowing

An additional thermoregulating and protecting strategy is wallowing. Wallowing is seen in many African mammal species such as buffalo, rhinoceros, warthog and elephant. These animas frequently engage in wallowing, and purposely covers their skin with mud from shallow freshwater habitat, when doing this they acquires and maintains a protective cover of mud that is beneficial for these largely hairless mammals. The mud layer is beneficial since it protects against sunburn, helps to disinfect wounds and traps parasites such as ticks or fleas (Vanshoenwinkel, et al., 2011).

2.9.5 Saliva Spreading

Saliva spreading is another way of evaporative heat loss. It is often seen in rodents and marsupials. When they are under heat stress, they spread saliva on their tail, limbs, chest and other body parts. On furred regions of the body, saliva spreading is a relative inefficient use of body water. This is because the evaporative surface (the outer surface of the fur) is insulated from the living tissues of the body. However, for many rodents saliva spreading is the only way to increase evaporative heat loss, and it is used in heat-stress emergencies (Hill, et al., 2008).

2.10 Noneveaporative heat loss

Mammals and birds employ several mechanisms with the goal of thermoregulating mechanically. This include their way of modulating resistance to dry heat transfer through insulation. They employ many distinct physiological mechanisms that are predominant for thermoregulation within the thermoneutral zone (Hill, et al., 2008).

2.10.1 Insulation

Sometimes a rather unlikely response is seen in some animals. Some animals in hot environments partially raise their dorsal fur or plumage. This reaction is seen as the temperature exceeds the body temperature in the animal. The reaction causes a thicker insulating layer that reduces conduction, convection and radiation in to the body, this way the heat uptake is reduced. This explains why some of the animals that are typically found in desert areas (like camels, sheep and ostriches) have a surprisingly dense pelage (Wilmer, et al., 2005).

2.10.2 Piloerection

One way to vary insulation is to erect or compress hairs or feathers. When the temperature is in the lower part of the thermoneutral zone the hairs or feathers is erected to a greater degree. The hairs are allowed to lie flat against the skin or held upright by the contraction or relaxation of the small arrector muscles; *mm. errectores pilorum.* The relaxation or contraction is controlled by the sympathetic nervous system. In mammals, these responses are termed pilomotor responses, while in birds they are termed ptilomotor responses. When the temperature reaches the lower level of the thermoneutral zone and the hairs or feathers are erected. When the pelage or plumage is fluffed, it will trap a relative thick layer of air around the animal. This air is motionless and insulating, as it increases the resistance to heat transfer through the pelage or plumage (Hill, et al., 2008).

If the temperature exceeds the animal’s body temperature, the animal can reverse any piloerection by flattening the fur or plumage and reduce the trapped air layer (Wilmer, et al., 2005).

Wetting the insulating fur or plumage by a brief immersion is even more effective than reversed piloerection. This is often employed by birds and mammals in hot weather. When the insulating fur or plumage is immersed, two effects are achieved: first there is heat loss by evaporation as mentioned earlier, but the evaporation is supplemented by an increased heat loss because the conductance of the wet surface is greatly enhanced. This is because the trapped water is a better conductor than air, and the layer is compressed in to a reduced thickness because of the water (Wilmer, et al., 2005).

2.10.3 Posture

In relation to the ambient temperatures, the animals can also change its posture to alter the amount of body surface exposed to the ambient conditions (Hill, et al., 2008).

At temperatures at the lower area of the thermoneutral zone, the animals can behaviourally reduce the surface area by adjusting their posture. This is achieved by trying to have the smallest surface area for the given volume (the animal’s volume). This is often done by bringing the limbs as close as possible to the body. On the other hand, if the temperature in the thermoneutral zone increases towards the upper limit, the animal will change posture to allow for the maximal surface for heat exchange. To do this, the animal extends its limbs (Reece, 2004).

There may be additional possibilities for cooling for the animal that involve exposing or erecting parts of the body that can act as radiators. This can be areas such as the ears, which have a large surface area, are thin and vascularized. This makes it possible to lose heat quickly from the peripheral blood supply. By pointing the warm parts of the body towards a cool part of the sky, there can be a particularly effective cooling. Small mammals can sit in the shade and point their noses or ears at the sky, away from the sun.

A group behaviour mechanism for containing heat is huddling. This is a very widespread phenomenon in terrestrial animals, and is found in many different habitats, from the extreme habitats of polar animals to young birds and mammals (Wilmer, et al., 2005).

Huddling is used by mammals and birds to reduce heat loss, especially through a reduction of their body surfaces that are exposed to cold. The reduction in heat loss will consequently allow a reduction in the metabolic rate of the animals. It is estimated that reduction in cold-exposed body surface area for huddling rodents ranges from 29 to 39%. When animals huddle, the ambient temperature surrounding each of the individual animal will increases due to the combined heat loss of all the animals. This will cause the temperature gradient between the body and the local environment to be reduced. Huddling will therefore allow individuals to experience ambient temperatures closer to or within the animals own thermoneutral zone (Gilbert, et al., 2010).

In addition to reduced body surface exposed to cold, and increased ambient temperature, a third mechanism that explains energy savings, relies on adjustments in body temperature of huddling animals. Most mammals and birds that huddle will maintain a higher and more constant body temperature than their isolated counterparts. This suggests that huddling functions as a warming mechanism. This is probably because of the reduction in heat loss. Some species are also known to lower their body temperature when they huddle. This will allow them to maximize the energy saved, by reducing the metabolic heat production further. Great snow geese goslings reduces their body temperature by 0.8◦C during huddling (Gilbert, et al., 2010).

For birds typical changes of posture is to tuck their heads beneath their body feathers, or squat so that their legs become enclosed in their ventral plumage if the ambient temperature is low. If the ambient temperature is high, many birds hold their wings away from their body (Hill, et al., 2008).

2.11 Shivering

Shivering is a thermoregulatory response found in homeotherm animals. The response is rather remarkable, and involve that the skeletal muscle perform rapid, repeated contractions. These contractions leads to heat production, through the inefficiency of ATP utilization. A central neuronal mechanism drives this involuntary thermoregulatory response. The central neuronal response is triggered by physiological stimuli, such as; exposure to a cold environment or the reception of pyrogenic immune signals by the brain during infection, and the aim of the response is to increase the thermogenesis (Nakamura, et al., 2011).

Within the structure of central thermoregulation, neurons in the preoptic area in the hypothalamus play a central role by receiving and integrating information peripheral temperatures, that are sensed by peripheral receptors (e.g. cutaneous), and also local brain temperatures. The preoptic area then provides the appropriate command signals to peripheral thermoregulatory effectors.

There are identified thermosensory pathways from the skin thermoreceptors to the preoptic area that mediates feedforward signalling required to stimulate rapid thermoregulatory responses, including shivering, if there is changes in the ambient temperature. There is separate pathways for transmitting cold and warm sensory signals from the skin (Nakamura, et al., 2011).

Skeletal muscle is normally used to produced movement and posture, but is also used by shivering thermogenesis to produce heat, (Morrison, et al., 2008). Skeletal muscle can contract in two patterns. When the muscle is used for locomotion for instance to move a limb, there is a synchronized contraction of all the motor units of the muscle. If there is shivering, all the motor units of the muscle will contract at more or less random intervals. During locomotion, the antagonistic muscles contract alternately, but during shivering, the antagonistic muscles will be activated simultaneously, and this causes shivering (Hill, et al., 2008).

2.12 Nonshivering Thermogenesis

Thermogenic mechanisms are normally classified as either *facultative* or *obligatory*. The *obligatory thermogenesis* is represented by energy being released as heat because of the activities of the organs and the cells in the body. The majority of this heat is provided by the basal metabolic rate. As earlier mentioned represents the basal metabolic rate (BMR) the minimal amount of energy that the body has to expend, if it wants to maintain the vital processes (Silvestri, et al., 2005). *Facultative thermogenesis* represents the additional heat that is produced in the event that the ambient temperature is changing, or also if there is a change in diet. A particular crucial element in the thermal physiology is the non-shivering thermogenesis (NST) (Silvestri, et al., 2005).

Non-shivering thermogenesis is very important because it

1) Provides heat that is needed for the thermal homeostasis.
2) During cold acclimatisation, it almost completely replaces shivering as the major source of metabolic heat production.
3) NST can act as an energy buffer during periods of overeating. Thereby it may reduce the metabolic effect and participate in the regulation of weight gain (Silvestri, et al., 2005).

2.12.1 Brown Fat

For small mammals and new-borns, the non-shivering thermogenesis in brown fat is the main mechanism for thermoregulatory heat production. During acclimatisation to colder ambient temperature, the sympathetic stimulation will trigger recruitment of brown adipose tissue by hyperplasia. This involves proliferation and differentiation of the precursor cells, and also hypertrophy of mature brown adipocytes. Hallmarks for the thermogenic recruitment process is the mitochondrial biogenesis and the increased synthesis of the uncoupling protein 1 (UCP-1). During cold acclimatisation, there is a great increase in mitochondrial protein content, and this recruits a large capacity for oxidative phosphorylation. However, in brown adipocytes, the UCP-1 causes increased proton leakage across the inner mitochondrial membranes. This causes the proton motive force to dissipate as heat, instead of synthesising ATP (Klingenspor, 2003).

Prolonged exposure to temperatures considered cold for the animal rises the non-shivering thermogenesis capacity by increasing the number of brown adipocytes and the amount of brown adipose tissue. Studies on cold-acclimated animals, shows that the brown adipose tissue may dissipate power of 300-400 W kg^{-1}. This means that it contributes to more than ~60-70% of the total non-shivering thermogenesis (Klingenspor, 2003).

The morphological traits of the brown adipose tissue, is very suitable for its function. It has dense vascularization, this ensures a sufficient supply of oxygen and metabolic substrates. The direct sympathetic supply to the brown adipocytes mediates the central control of the non-shivering thermogenesis. Brown adipocytes are also rich in mitochondria, with multiple invaginations of the inner membrane or the crista. It is in these mitochondria the earlier mentioned uncoupling protein 1 (UCP-1) is found (Klingenspor, 2003).

Thermogenesis can occur to a greater or lesser extent in nearly all tissues. This is because the heat production is a by-product of the inefficient mitochondrial ATP production and utilization. The sympathetic stimulation of the brown adipose tissue, happens under cold conditions, but brown adipose tissue is not the only tissues stimulated by CNS to produce heat under cold conditions. The CNS thermoregulatory networks can stimulate thermogenesis in response to a cold environment, to a fall in core body temperature, or to the presence of pyrogenic cytokines in hart and skeletal muscle in addition to brown adipose tissue (Morrison, et al., 2008).

Regulation of the level of thermogenesis in brown adipose tissue is done by sympathetic nerve activity as earlier mentioned, but also release of noradrenaline and β3-adrenergic receptor binding to brown adipocytes. These regulate both the activity of lipases that provide the immediate fuel molecules for the mitochondria in brown adipocytes, and also the level of expression of UCP-1 in the mitochondria of brown adipocytes (Morrison, et al., 2008).

Noradrenaline is released by sympathetic nerve fibres in brown adipose tissue, and it binds with different level of affinity to several α and β-adrenergic receptor isoforms that are expressed in brown adipocytes. The stimulation of brown adipose tissue hyperplasia is through β1-adrenergic receptors while the lipolytic and thermogenic action is primarily mediated by β3-adrenergic receptors (Klingenspor, 2003).

The brown adipose tissue has been developed as cold defence. It is an essential thermoregulatory effector in small mammals, rodents and infant humans. Their large surface area to body mass ratio suggests that the basal metabolism alone would not yield sufficient hear to maintain a stable body temperature in cold environments. The sites of brown adipose tissue depots in adult humans are very similar to those found in rodents: a large brown adipose tissue pad near the scapulae and shoulders and then individual pads on top of each sympathetic ganglion. There is also brown adipose tissue surrounding the adrenal glands and kidneys (Morrison, et al., 2008).

2.13 Regional Heterothermy

Regional heterothermy can be very beneficent for some animals living in cold environments. Some of the body’s appendages such as legs, tail and ear pinnae are potentially major sites for heat loss. They present a particular thermal challenge for the animal. If the animal lets the appendage cool, it will limit the heat lost across the appendage. This cause less temperature difference between the appendage, and the ambient temperature, and thus the driving force for hear loss from the appendage is lost. This type of regional heterotrophy is in fact very common. During low ambient temperature, the appendages can have a tissue temperature that is often 10-35°C lower than the animal’s core temperature (Hill, et al., 2008).

2.14 Torpor and Hibernation

Many mammalian and avian species allow their body temperatures to fall in a controlled manner, this controlled fall in body temperature only happens under certain circumstances. This phenomenon is in general term called controlled hypothermia. Hypothermia is a state of unusually low body temperature, and when it is termed controlled hypothermia, it is because the animal orchestrates the entry into and exit from the hypothermia, instead of being forced. The best-known types of controlled hypothermia include hibernation, estivation and daily torpor. In all these, the animals allow their body temperature to near ambient temperature within species-specific range of ambient temperatures. It is indicated that hibernation, estivation and daily torpor are all different manifestations of one single physiological process. The difference between these manifestations is the season of occurrence and the length or duration (Hill, et al., 2008).

Hibernation is the animal allowing the body temperature to fall close to the ambient temperature for several days or longer during the winter season. If this happens during the summer, it is considered *estivation*. Daily torpor is found at any season, and it occurs when the animal permits its body temperature to fall close to the ambient temperature for only a part of each day. The torpor is usually occurring several days in a row. The manifestation of torpor, hibernation and estivation permits the animal to escape the energy demands of homeothermy (Hill, et al., 2008).

The animals that are able to go into hibernation, estivation or daily torpor, is in fact able to switch back and forth between two thermal worlds that are very different. When they function as homeotherms they get all the benefits of homeothermy, like being independent of the external environment, but they also have to pay the price of high energy needs. When the animals suspends the homeothermy, they take on many attributes that are associated with poikilotherms. This includes the tissues being subjected to varying temperatures, but they have low energy needs. The amount of energy saved by controlled hypothermia depends on the duration of the hypothermia and the ambient temperature at which hypothermia occurs (Hill, et al., 2008).

The term *torpor* can be used to specify the period in hibernation that is characterized by supressed metabolic rate and body temperature. The term is often used instead of hibernation as hibernation happens only during the winter season and lasts for several months. The torpor seen during hibernation is distinct from the daily torpor displayed by a variety of small mammals. Torpor is functionally distinguished from hypothermia, because there is a metabolic suppression before the fall in core body temperature.

Hibernation is as earlier mentioned controlled hypothermia that lasts for several days or longer during the winter season. The torpor state is interrupted by brief, spontaneous arousals that occur at regular intervals. These arousals lasts for approximately one day, and the animals spontaneously return to high euthermic body temperature (35-37°C) that falls to the normal range of diurnal body temperature that is observed in the animal’s active season. Based on body temperature changes and the metabolic rate, the hibernation can be divided into separate stages (Drew, et al., 2007).

This include:

- The stage of entry when both the metabolic rate and the body temperature decreases.
- The steady-state torpor when the metabolic rate and the body temperature remains at minimum. This stage is defined by the gradient between body temperature and the ambient temperature.
- The arousal episodes (also known as interbout arousal), when there is an increase of metabolic rate and body temperature with short periods of interbout euthermy.

The torpor state during the hibernation period is not a result of exigency or lack of energy, rather it is adaptive, reversible and highly regulated because the animals can spontaneously rewarm to euthermia within hours in the absence of applied exogenous heat. Torpor defines the lower limit of mammalian metabolism through these highly regulated processes. It is also associated with an altered state of consciousness that is distinct from wakefulness, sleep, or coma (Drew, et al., 2007).

Metabolic rate depression is, for many animals, an important strategy for survival. The biochemical mechanisms that regulate the transitions to and from the hypometabolic state are reversible. Studies of these biochemical mechanisms identify that there are principles of regulatory control that are conserved across phylogenetic lines and that they are broadly applied to the control of multiple cell functions. One such mechanism is reversible protein phosphorylation. Reversible protein phosphorylation is known to contribute to the suppression of protein synthesis, to ion channel arrest, and to the regulation of fuel metabolism during hypometabolism (Storey, et al., 2004).

There is a clear adaptive value of the suppression of metabolic rate when feeding opportunities are inadequate or sporadic, and fat reserves are limited. All hibernators studied to date arouse periodically and does not exploit the energy saving of torpor to the maximum. The arousals account for over 75% of the total energy required for hibernation (Thomas, 1997).

The short arousals can last up to 48 hours. There is evidence that indicates that metabolic suppression during torpor is achieved through synergistic effects of both temperature independent (active) and temperature dependent (passive) processes that contribute to decrease the demand for oxygen. The size of the animal decides to which degree it depends on either passive or active depression of metabolic processes during the entrance or maintenance of torpor. In large hibernators (over 1000g) and in very small hibernators (under 100g), it is presumed that temperature independent processes are more involved, while there in middle-sized animals seems to be temperature dependent processes that are the determining factor for metabolic rate. Large animals actively supresses the metabolic demands during the repeated entry and torpid phases of hibernation. During the steady state torpor, the rates in oxygen consumption is not associated with changes in body temperature over a range of ambient temperatures above 0°C. One example is the artic ground squirrels, they will during the steady state of torpor, maintain constant and small rates of oxygen consumption despite difference of as much as 16°C in body temperature. Therefore, it appears that in large hibernators active (temperature independent) suppression of metabolic processes occurs both during entrance and in the torpid phase of the hibernation (Nathaniel, 2008).

During the entrance phase of the hibernation, the animals titrate brain energy demands to meet energy supply so that energy balance is maintained even though blood flow, glucose release and oxygen consumption is severely reduced. For the whole animal, the heart rate, oxygen consumption and respiratory rate are thought to drop drastically before a gradual decline in core body temperature. This gradual decline is probably to facilitate thermoregulatory fine-tuning that reduces the threshold for activity that is thermogenic and produces heat. After this, the metabolism declines and the animal seems to be out of thermal equilibrium and begins to cool off.

Hibernating animals use a variety if adaptive processes, which act in concert to protect the vital organs in the body, like the brain, during oxidative metabolism and pronounced fluctuations in blood flow. The effect is a balanced suppression of the energy demand and supply of the brain. This causes a new and steady hypometabolic state. During hibernation, the metabolic activity is believed to be actively suppressed. This is because the whole oxygen consumption, heart rate and respiratory rate in the animal first falls sharply, before there is a steady decline in core body temperature later (Nathaniel, 2008).

2.15 Colour and Colour change

Because coloration can affect radiative exchange, some animals can change the colour of their skin or cuticle. A few frog species and some lizards have the ability to do this. In lizards, the change is due to “iridophore” cells. In these cells, quite rapid thermally induced colour change arises when there is alterations in the packing between layers of reflective crystalline platelets inside the cells. The reflective crystalline platelets are cell organelles that contain crystals (Wilmer, et al., 2005).

The mechanism of colour change is best known in insects and crustaceans. The colour change include phase changes of lipid or other material within the cuticle. These phase changes tends to change the colour of the cuticle from a nearly black surface to a shiny almost metallic blue or green when the insect has an increased body temperature. This change can happen during a few minutes or over several hours (Wilmer, et al., 2005).

2.16 Fluctuations in Body Temperature

In homeotherm animals, the hypothalamic thermostat is able to keep a relatively constant body temperature even though there are great changes in the ambient temperature. However, it is also normal for the animals to have diurnal fluctuations in the controlled body temperature level. One example of this is for instance that the body temperature is lowest at the time of awakening and highest at the end of activity and before sleep (Reece, 2004). The diurnal changes are seen as changes in the mean body temperature.

Diurnal and nocturnal animals have their body temperature fluctuate in opposite directions relating to the hour of light or darkness.

There are also variations in the mean body temperature during the ovarian cycle. The variations follow the phases of the cycle, and this feature is well known and common in all mammalian species. At the time of the ovulation, the mean body temperature increases by 0.5-1°C. The mean temperature usually increases for 24 hours. The controlling factor in this process seems to be progesterone since the daily increase in temperature is synchronised with the rise in plasma progesterone levels at the ovulation, and the decrease in temperature with the decline in progesterone levels at the end of the cycle. If a conception occurs, the progesterone levels will remain elevated, and the same happens with the mean body temperature (Reece, 2004).

2.17 Poikilotherm Thermoregulation

As earlier mentioned, the animals that are not endotherms are referred to as *ectotherms* or also *poikilotherms.* This is because their body temperature is decided by the external environment and may be variable (Cunningham, 2007).

Environmental temperature is of key importance to all animals but since it links directly to their rate of metabolic processes and ultimately to growth and fitness it is especially important to ectotherms. A change in body temperature by only 1°C will alter the rate of many of the physiological processes by as much as 6–10% (Ward, et al., 2010).

Being a poikilotherm also includes having a variable body temperature. This is a characteristic most terrestrial ectotherms, and also many mammals and birds (when they are small), have in common (Clarke, et al., 2010).

As earlier mentioned, is the endotherm strategy of thermoregulation requiring more energy than the ectotherm, the energetic maintenance costs of ectotherms are more than 10 times lower than those of endotherms (Buckley, et al., 2012). Ectotherms can therefor survive without feeding for extended periods, buffering periods of low resource availability. This is in stark contrast to the most endotherms that have much more continuous feeding requirements (Shine, 2005).

2.17.1 Behaviour

The ectothermic vertebrate's thermoregulatory strategies are complex. The autonomic mechanisms of thermoregulation seen in endotherms is lacking in ectotherms, but the ectotherms do display some control over the body temperature by selecting thermal microhabitats that are appropriate for them. This behaviour causes a body temperature that is stable, even under varying ambient temperatures. This is termed behavioural thermoregulation.

Endotherm animals also use behavioural thermoregulation to keep a stable body temperature. When endotherms displays behavioural thermoregulation, it is often appearing before the animal have any physiological changes in response to the heat loss or gain (Lutterschmidt, et al., 2003).

As mentioned, ectothermic vertebrates rely primarily on behaviour to regulate their body temperature. Their behavioural thermoregulation mechanisms include strategies like changing between different microclimates, changing posture and orientation, burrowing and coordinating activity patterns with environmental temperature. One example of the last, is the nocturnal vertebrate. Although they are active when opportunities for precise behavioural thermoregulatory mechanisms are not available, studies have shown that these animals have diurnal behavioural thermoregulation within their retreat site. Several nocturnal gecko species perform postural changes during the day that allow them to thermoregulate. For instance can they raise their dorsal surface for contact with warm rocks overlying the retreat site (Lutterschmidt, 2003).

2.17.2 Physiological temperature control

Ectotherms have limited capability to control their body temperature physiologically, but when they do display physiological thermoregulation, it is often seen as modulation of the rate of heat loss or gain. Examples of this might be the moving blood between the periphery and the core of the animal. This moving results in changes in cooling and heating rates. The mechanisms of physiological temperature control in ectotherms also includes changes in the radiative properties of the animal's skin, metabolic rate, ventilation and evaporation rates, heart rate and blood flow (Lutterschmidt, 2003).

2.17.3 Tolerance of Freezing

Animals living in polar, temperate and alpine areas, are subjected to temperatures well below the freezing point either on a daily or yearly basis. During cold periods, the animals are posed to problems that include changes in membrane and protein structure.This is due to phase changes in the molecules, changes in electrolyte concentration and other solutes in the body fluids as well as changes in the metabolism. Ectothermic animals that are tolerant to cold can be divided into two groups. The division depends on which strategies the animals employs to survive during low temperatures (Ramløv, 2000).

The two groups include *freeze-tolerant animals*, that will survive formation of ice in their tissues, and *freeze-avoiding animals*. Freeze-avoiding animals can tolerate low temperatures but not the crystallization of the body fluids. The adaptions of freeze-avoiding animals are mainly directed towards avoidance or control of the formation of ice in their tissues. This can be accomplished by synthesis of low molecule weight cryoprotectants, ice nucleating agents and antifreeze proteins (Ramløv, 2000).

2.18 Recognition of Temperature changes

The detection of body temperature occur in several parts in the body in birds and mammals (Hill, et al., 2008). The temperature control centres receive information about the temperature through two different sets of temperature receptors; one set is warm receptors, the other is cold receptors. Both sets of temperature receptors, warm and cold, are located in the core if the body and in the skin (Reece, 2004). The core receptors can be found in the spinal cord and in the brain in the hypothalamus itself. In the skin, some areas have a particularly high density of cold receptors. The face is an area where the density of *cold* receptors is significantly higher than for instance the trunk area. Other areas of the skin can have higher density of *warm* receptors; this includes the lips and the nares. The skin of the scrotum is also an area with particularly high density of warm receptors, the receptors are important to keep the temperature within a normal range, which is around 0.5 to 1°C lower than the core temperature (Reece, 2004).

The cold and warm receptors use increased impulse frequency when they register temperature changes. Increased temperature causes increased frequency of firing in warm receptors, while cold receptors increase the frequency of firing if the temperature is decreasing (Reece, 2004).

The sensibility in the core and the skin receptors differ. The core receptors are as much as 5 to 10 times more sensitive than the skin receptors. Therefore, the core receptors are carefully monitoring and defending the core temperature. The skin receptors that are not as sensitive as the core receptors and are adapted to large fluctuations in temperature, are functioning as predictors. They predict fluctuations in the ambient temperature that can ultimately influence the core temperature (Reece, 2004).

Both the core and the skin receptors transmit their information to the hypothalamus (Reece, 2004). The hypothalamus is the principal control centre that processes the multiple sensory inputs and controls the thermoregulatory mechanisms (Hill, et al., 2008). The information from the temperature receptors is also transmitted to the level of consciousness. The animal can then receive the information from the receptors and recognise the changes in the core temperature. This makes it possible for the animal to perform the appropriate behavioural response to the temperature changes (Reece, 2004).

Species that thermoregulate by means of behaviour, animals like fish and lizards, must also have thermoregulatory control centres. These receive and process thermosensory information and coordinate the thermoregulatory processes, by orchestrating heat-producing and heat-voiding mechanism and thus stabilizing the body temperature (Hill, et al., 2008).

One interesting and important example of thermoregulation by behaviour is that lizards, amphibians and fish can perform so-called "behavioural fevers", if certain types of bacteria infect them, they moves to a warmer environment that give them a higher body temperature. The effector of this fever is thus the skeletal muscles that performs a modification of behaviour. If the poikilotherm is prevented from behaviourally elevating its body temperature when it suffers infection from bacteria, we can see that there is higher mortality and morbidity than in the individuals that are allowed to develop fever (Hill, et al., 2008).

If the behavioural response cannot keep the temperature constant, the physiological mechanisms such as cutaneous circulation changes, sweating, panting and shivering, will be invoked. The stronger the thermal stimulus is, the stronger the response will be. If the hypothalamus, spinal cord, or the scrotum is locally heated, they will activate all the heat loss mechanisms. The heat loss mechanisms will be activated to such an extent that the body temperature will fall (Reece, 2004).

2.19 Hyperthermia

For every 10°C increase in body temperature, the metabolic rate will double. This will again increase the heat production. This is called the *van't Hoff effect*. The result of this is increasing hyperthermia developing. The terms *heat stress* and *heat shock* is often synonymously used for the state following this, but there is an important distinction. Heat stress represents the early stages of hyperthermia where dehydration and hypovolemia is combined with a fall in vascular peripheral resistance associated with cutaneous vasodilation. This leads to hypotension. When the body temperature further increases (41-43°C), heat shock develops. Heat shock is in part caused by increased brain temperature and loss of the neural control of the thermoregulation.

Hyperthermic tissues have increased consumption of oxygen, but because of inadequate tissue perfusion, it cannot be provided with sufficient oxygen. This causes cell hypoxia, and consequent organ failure. At the end, denaturation of enzymes precedes death (Reece, 2004).

2.20 Hypothermia

Hypothermia is possible to classify as primary or secondary hypothermia. Primary hypothermia is typically a result of exposure to cold ambient temperatures, despite the body thermoregulating and producing heat as normal. Secondary hypothermia is classified as hypothermia resulting from changes in heat production. This may be because of illness, injury or drugs. Secondary hypothermia can understandably frequently cause morbidity and mortality in critically ill animals (Byers, 2012).

Hypothermia occurs when the core body temperature decreases below a certain point. After passing this critical point, the thermoregulation is impaired, and the animal will cease to shiver or seek heat. This is a characteristic response to the core temperature being low. Rather than peripheral vasoconstriction to protect the core of the animal, vasodilation predominates, and this causes the heat loss to continue. In addition to this, the heat production of the animal will decrease as the metabolic rate decreases. At the same time, will severe hypothermia depress the CNS and result in hypothalamus being less responsive to hypothermia. When the core temperature of the animal is further dropping, thermoregulation ceases (Byers, 2012).

Potential complications following hypothermia include cardiac effects. A common change seen is sinus bradycardia. In neonatal pigs, hypothermia is associated with markedly decreased contractility in the left ventricle, this leads to a reduced cardiac output and impaired diastolic relaxation. Also pulmonary effects are seen during hypothermia. If the hypothermia is severe, it will cause a reduction in both the tidal volume and the respiratory rate. This is because the cellular metabolism is reduced and the carbon dioxide production is lowered. This will naturally affect the stimulation of respiration. This can cause the animal to hypoventilate and contribute to the development of acidosis.

Other effects of hypothermia include hypoglycaemia, coagulation abnormalities, induction of diuresis and reduction in glomerular filtration rate. The declining body temperature also contributes to neurological effects. The cerebral blood flow and the autoregulation will be negatively affected by the declining temperature. This is frequently resulting in mentation changes. For each degree celsius drop in body temperature, the cerebral metabolic rate and cerebral blood flow will decrease with about 5%. Severe hypothermia is associated with abnormal neurologic signs that range from depression to coma (Byers, 2012).

There are also severe immunological effects caused by hypothermia. As hypothermia leads to impaired oxygen delivery to tissues (e.g. because of vasoconstriction) it can cause reduced resistance to infection. This is because tissue hypoxia is associated with impaired oxidative killing by neutrophils. Decreased body temperature causes impaired chemotaxis, reduction in phagocytosis, and depression of the production of cytokines and antibodies.

General anaesthesia and surgery can easily cause both primary and secondary hypothermia. This is because incubated patients inhale cold and dry air, which is delivered straight to their lungs. During preparation of the patient, the surgical site is routinely aseptic treated and this promotes evaporative heat loss. The table surface is cold, and the open body cavities will cause heat loss through conduction and radiation, respectively (Byers, 2012).

Anaesthetic agents affects the thermoregulatory centre in hypothalamus in such a way that the thermoregulatory responses are not triggered until low temperatures are reached. Peripheral vasodilation is caused by directly inhibiting centrally mediated thermoregulatory vasoconstriction. Anaesthesia decreases the metabolic rate by 15 to 40%. In addition is muscular activity inhibited which causes a decreased heat production. Reducing and minimizing the duration of the surgical procedures and the anaesthetics may reduce the incidence of secondary hypothermia (Byers, 2012).

3 Goal of the study

The goal of this study was to collect the knowledge of the modes of thermoregulatory mechanisms in different species.

4 Methods of study

The methods of study and research used during the work with this thesis include the collection of information from literary sources and from relevant articles from scientific journals and textbooks, as the thesis is based on purely theoretical knowledge from already published works.

The information from literary sources is used in large extent in this presentation of the thermoregulatory mechanisms in species.

Simultaneously have articles published in journals, been used frequently as sources for information. These have been accessed through searches in several online libraries. The search for scientific articles have been an important part of the research method.

5 Discussion

During the work with this thesis, information and knowledge about the thermoregulatory mechanisms in animals, and the animal’s thermal relationship with the ambient environment has been collected. The regulatory processes for the internal temperature of the animal is constantly influenced by the external or ambient temperature. This is true whether the ambient temperature is in the thermoneutral zone of the animal, or at levels higher or lower than this.

The two thermoregulatory mechanisms furthest apart on the thermoregulatory scale is the mechanisms of the poikilotherms and the homeotherm animals, which symbolize two very different strategies for regulating temperature and maintain the metabolic rate.

5.1 Poikilotherm vs. homeotherm thermoregulation

Ectotherm body temperatures tend to follow environmental temperatures closely, but many ectotherms effectively thermoregulate behaviourally. If the body temperature decreases, many of the biochemical processes in the body will slow down. This includes the metabolism and the assimilation of energy. Endothermy is very costly energetically, endothermic vertebrates require much more energy than ectotherms of the same size. However, the endotherms have the advantage of high metabolic rates, which enable rapid regeneration of energy supplies, and this way gives them greater endurance. The higher body temperature of the endotherm can also confer additional performance advantages (Buckley, et al., 2012).

The physiological performance of the ectotherms is influenced strongly by body temperature. During studies of reptile energetics, it is common to measure the metabolic rate at more than one temperature. This way, one allows for calculating the within-species response to temperature (Clarke, et al., 2010).

Birds and living mammals are characterised by high body temperatures, insulation and many taxa that have high muscle power output. However, a variety of ectotherms has also evolved a capacity to use their metabolic heat or insulation to generate warm tissue. This include a range of insects, some teleost and chondrichthyan fishes and incubating pythons. It is typical in these animals, that only a part of the body is warmed, and this is often locomotor muscle. The warming is also often limited to specific times. This regional warming is in many cases associated with the need to generate high muscle power output. In swordfish, regional warming of the brain and eye is important for enhanced vision (Fritsches, et al., 2005). This is hinting at the intriguing possibility that an active predatory lifestyle benefits of a warm brain (Clarke, et al., 2010).

This local heating to produce high muscle power output shows that even though a warm body is needed for the highest levels of muscle power output, endothermy is not a prerequisite. The most important aspect of endothermy is that it allows sustained high aerobic muscle power output. Even though e.g. a reptile and a mammal can sprint at the same speed, the mammal is capable of a much greater aerobic endurance.

The ectothermic vertebrates inhabit a wide range of thermal niches. Reptiles are found well into cold-temperate and even subpolar regions, even though the highest diversity of snakes and lizards are found in tropical regions. Amphibians are also widely distributed. Some frogs overwinter and shows a tolerance of freezing, with as their extracellular fluids are frozen solid (Clarke, et al., 2010).

Endotherms keeps their body temperature stable to maintain all the biochemical processes in the body. The mechanisms for keeping the body temperature stable has been reviewed in this thesis and include mechanisms for heat loss and heat gain. The mechanisms used by endothermic animals to loose heat is divided into evaporative heat loss, and non-evaporative heat loss. Evaporative heat loss includes for instance sweating and panting, while non-evaporative heat loss include change in insulation, piloerection, posture changes. These mechanisms are used not only as methods of heat loss, but also for heat gain. Ectotherms also have mechanisms for temperature control. These includes changes in the radiative properties of the animal’s skin, metabolic rate, ventilation and evaporation rates, heart rate and blood flow (Lutterschmidt, et al., 2003).

The shivering and non-shivering thermogenesis is found in endotherms as a means of increasing body temperature. Shivering enhances the metabolic rate and thus increases the body temperature. Non-shivering thermogenesis is a not so acute effect of reduced body temperature, and include the recruitment of brown adipose tissue. In brown adipose tissue, there is an increased proton leakage across the inner mitochondrial membranes that causes the proton motive force to dissipate as heat instead of producing ATP (Klingenspor, 2003).

5.2 What happens if the compensatory mechanisms for thermoregulation is inefficient?

The production of heat in the animal is due to the various metabolic processes in the body. This is directly proportionate to the body mass of the animal. The smaller animals, such as e.g. companion animals or pets, are typically animals with a higher surface-area-to-body-mass ratio, this makes them very susceptible to heat loss.

This is especially important to remember during the general anaesthesia of small animals, as this is a situation where hypothermia can easily be caused, e.g. because anaesthetic agents affects the thermoregulatory centre in hypothalamus in such a way that the thermoregulatory responses are not triggered until low temperatures are reached. Anaesthesia also decreases the metabolic rate. It can be lowered by so much as 15 to 40%. In addition is muscular activity inhibited which causes a decreased heat production. Reducing and minimizing the duration of the surgical procedures and the anaesthetics may reduce the incidence of secondary hypothermia (Byers, 2012).

Sometimes the animals are not able to reduce their body temperature with the thermoregulatory mechanisms available.

When there is no non-evaporative heat loss, evaporative heat loss is the only remaining mechanisms of heat loss. This happens for instance if the air temperature equals the skin temperature. If this is occurring, the metabolic heat produced must be equal to the amount of heat lost by evaporative mechanism (Reece, 2004). If the air temperature is above the skin temperature, the animal will gain heat, and evaporative heat loss must increase to keep the animal in heat balance. Air movement in this case will increase the result of evaporative heat loss, but on the other hand, it will increase the heat gained by convection (Reece, 2004).

As earlier mentioned, if the body temperature increases, an increase in the metabolic rate will follow. For each degree centigrade the body temperature increases, the metabolic rate will increase by 10% (Reece, 2004). This will eventually cause hyperthermia if the animal is not able to find a way to reduce its body temperature.

Emergency therapy of hypothermia is directed towards restoration of blood volume, and cooling of the skin that is assisted by fanning of warm air, not cold, to help evaporation. If the patient is immersed in ice, this will often cause vasoconstriction and hamper heat removal. Brachycephalic dog breeds are more commonly prone to heat stroke because of their large and soft palate that obstructs the upper airway flow. This also reduces the area of the nasal turbinates and impairs the humidification of the air that is inspired (Reece, 2004).

6 Conclusion

Thermoregulation is important for animals to keep the temperature in the body at a relatively constant range, because there are a number of chemical reactions going on in the body at any given time (Cunningham, 2007).

Hypothermia during general anaesthesia does not only have negative consequences. Hypothermia causes great neurologic protection. Cooling provides significant protection for the brain and the spinal cord during periods of interrupted blood flow. Therefor is mild lowering of the body temperature sometimes used during surgical procedures (Frank, 2001).

On the other hand, is there also negative consequences of hypothermia that it is important to be aware of. Hypothermia includes both negative cardiac and pulmonary effects. Hypothermia can lead to a drop in the respiratory rate and the tidal volume, something that can lead to hypoventilation. Hypothermia gives immunological consequences, and can increase the chance of infection as it impairs the function of macrophages and neutrophils. Coagulation of blood is also affected by the change in body temperature (Byers, 2012).

Horses are animals that have a small surface-to-body-mass ratio, and have consequently a small surface area for dissipation of heat, this is combined with a high metabolic capacity. When horses are exercised only about 20% of the muscle cell metabolism is used for work, the remaining 80% becomes heat. The blood flow of the animal increases during internal body heating, and transfers the heat from the core to the surface of the skin. If the vasodilation is not sufficient, the horse will turn to evaporative heat loss, and sweating will start.

Horses that compete during the winter season is often clipped. This is to mobilize a more effective heat dissipation through evaporative loss during the exercise and prevent overheating of the animal. The removal of the winter coat allows for a more effective evaporation as the sweat is evaporated directly instead of wetting the fur (Wallsten, 2012).

7 Resumé

Termoregulácia je dôležitá pre zvieratá na to, aby udržiavala teplotu tela v relatívne úzkom rozmedzí, pretože chemické reakcie v organizme v danom čase a fyzickom stave bunkových lipidových membrán a rýchlosť enzymatických procesov je ovplyvnená zmenami v teplote (Cunningham, 2007). Existuje niekoľko mechanizmov pre reguláciu telesnej teploty. Niektoré zvieratá využívajú hlavne metabolické teplo na ohrievanie tkanív v organizme. Organizmy, ktoré využívajú tento mechanizmus sa nazývajú endotermné živočíchy, pretože ich teplo sa tvorí vo vnútri organizmu. Na druhej strane existujú ektotermné organizmy, ktoré sú tiež známe ako poikilotermné organizmy, lebo ich telesná teplota závisí od vonkajšieho prostredia a môže byť variabilná (Cunningham, 2007).

Teplo vstupuje do organizmu z metabolických procesov, ktoré sa odohrávajú v tele. Počas všetkých fáz metabolických procesov natrávená potrava vydáva teplo (Hill et al., 2008). Homeotermné organizmy majú väčšiu metabolickú rýchlosť ako poikilotermné (Reece, 2004). Za rôznych podmienok základným mechanizmom termoregulácie pre homeotermné organizmy je prispôsobenie sa zmenám v produkcii metabolického tepla (Hill et al., 2008).

Okrem tvorby tepla internou cestou pomocou metabolizmu, zvieratá vymieňajú teplo s prostredím a okolím. Prenos tepla medzi zvieraťom a prostredím sa uskutočňuje určitými mechanizmami. Medzi tieto mechanizmy patrí konvekcia, kondukcia, tepelná radiácia, evaporácia (Hill et al., 2008) a sekrécia výkalov a moču (Reece, 2009). Kondukcia je prenos tepla z miesta s vyššou teplotou na miesto s nižšou teplotou. Teplo sa prenáša pomocou pevných látok alebo tekutín bez pohybu molekúl (Reece, 2004). Konvekcia, na druhej strane, je prenos tepla cez materiál alebo látku s makroskopickým pohybom látky (Hill et al., 2008) a hocijaké dva objekty, ktoré sú oddelené len vzduchom podliehajú termálnej radiácii cez výmenu tepla rýchlosťou svetla (Hill et al., 2008).

Evaporatívna strata vody je excelentný spôsob uvoľňovania tepla. Rýchlosť evaporácie nezávisí len od povrchovej teploty, ale aj od rozdielov v hustote vodnej pary medzi povrchom zvieraťa a prostredím. Rezistencia povrchu strácať vodu tiež ovplyvňuje rýchlosť (Wilmer et al., 2005). Existujú tri hlavné mechanizmy aktívnej evaporácie: potenie, zrýchlené povrchové dýchanie alebo rýchle pohyby membrán v hrdle pri otvorených ústach (Hill et al., 2008). Potenie sa uskutočňuje zo špeciálnych žliaz nachádzajúcich sa v rôznych miestach na povrchu tela a zrýchleným dýchaním zviera stráca vodu z povrchu respiračných ciest cez otvorené ústa (Wilmer et al., 2005).

Cicavce a vtáky majú niekoľko mechanizmov na mechanickú termoreguláciu. Patrí sem modulovanie odolnosti voči prenosu suchého tepla izoláciou. Majú niekoľko fyziologických mechanizmov, ktoré sa uplatňujú pri termoregulácii v termoneutrálnej zóne (Hill et al., 2008). Jedným zo spôsobov izolácie je zježenie srsti (piloerekcia) alebo peria (ptiloererkcia) (Hill et al., 2008).

Vzhľadom na teplotu okolia, zvieratá tiež môžu meniť postoje s cieľom meniť veľkosť povrchu tela, ktorý je exponovaný k teplote okolia (Hill at al., 2008). Patrí sem krčenie sa, ak je teplota okolia nízka (Gilbert et al., 2010) a ďalšie možnosti zahŕňajú chladenie pre zvieratá, keď ležia natiahnuté na zemi a ich časti tela slúžia ako radiátory (Wilmer et al., 2005).

Triaška je termoregulačná odpoveď u homeotermných zvierat a sú to rýchle opakované kontrakcie kostrového svalstva. Tieto kontrakcie tvoria teplo (Nakamura et al., 2011). Ako časť netrasovej termogenézy, hlavným mechanizmom pre termoregulačnú produkciu tepla je hnedý tuk. V hnedých adipocytoch, UCP - 1 spôsobuje zvýšené uvoľnenie protónu cez vnútorné mitochondriálne membrány, čo vedie k protónovej hnacej sile vo forme tepla namiesto syntézy ATP (Klingenspor, 2003).

U mnohých cicavčích a vtáčích druhov dochádza ku kontrolovanému poklesu telesnej teploty. Takýto náhly pokles telesnej teploty sa uskutoční len za určitých podmienok a nazýva sa riadená hypotermia. Najznámejším typom riadenej hypotermie je hibernácia (Hill et al., 2008).

Ektotermné organizmy sa vyznačujú určitým riadením telesnej teploty tým, že si vyberajú mikroprostredie, ktoré je pre nich vhodné. Takéto správanie umožňuje udržiavať stálu telesnú teplotu aj za rôznych teplôt okolia. Ektotermné zvieratá, ktoré žijú v oblasti s nízkou teplotou prostredia potrebujú tolerovať chlad. Ektotermné organizmy, ktoré tolerujú teplo môžu byť rozdelené do dvoch skupín. Rozdelenie závisí od mechanizmu, ktoré zvieratá použijú na prežitie pri nízkych teplotách. Tieto skupiny zvierat sú tie, ktoré tolerujú tvorbu ľadu v tkanivách (*freeze - tolerant animals*) a tie, ktoré tvorbu ľadu v tkanivách netolerujú (*freeze – avoiding animals*). *Freeze - avoiding animals* môžu tolerovať nízke teploty, ale netolerujú kryštalizáciu vody v telesných tekutinách (Ramlov,2000).

Ak sa telesná teplota zvýši, metabolická rýchlosť sa zvýši a to zase zvýši produkciu tepla. Tento stav sa nazýva Hoffov efekt. Výsledkom tohto efektu je zvýšená hypertermia (Reece, 2004).

Hypotermiu je možné rozdeliť na primárnu a sekundárnu. Primárna hypotermia typickým dôsledkom chladným vonkajším teplotám, pričom tvorba tepla a termoregulácia sú v norme. Sekundárna hypotermia vzniká v dôsledku porúch produkcie tepla v dôsledku choroby alebo poranenia.

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