ADAPTIVE THERMOREGULATION IN DIFFERENT SPECIES OF ANIMALS

Biochemistry and Physiology

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The lowest temperature on Earth has been reported to happen in Antarctica, while the highest one, in geothermal springs has reached over 350°C (Knut-Schmid Nielsen, 1990). The most amazing adaptations can take place at extreme temperatures: survival in inactive states, freezing, However, temperatures not only vary geographically but also within a given region, temperatures can change drastically between seasons or within a given day.

We will first briefly review the effects temperature has biochemically and physiologically on animals and then proceed to describe how different species of animals cope with temperature changes using different strategies.

Temperature can be defined as a measure of the molecular motion (Lehninger 1965). There is usually a limit beyond which an organism's biochemical processes and tissues are deeply affected and even damaged. Enzymes are also dependent on temperature changes, so their activity can be altered by them as well as the activities of their substrate and the intracellular department they act on. If the temperature changes persist, protein synthesis and degradation can also be altered, sometimes this leads to differential gene expression in order to create different isozymes (that are synthesised according to the temperature of the environment) (Prosser et al, 1952).

On the cellular level, the membrane is kept in its usual fluid state thanks to homeoviscous adaptation that promotes a variation of the fatty acids composition in the lipids. Even though the cell membrane constituents are the most directly affected by temperature changes, other cell constituents can also be influenced negatively, like microtubuline, for instance (cold-labile in mammals). Finally, temperature also induces the formation of HSPs (Heat Shock Proteins), molecular chaperones that induce thermotolerance.

Physiologically, organisms can be affected both by low and high temperatures. Animals that are able to survive low temperatures usually face the problem of the possibility of having their contained water frozen. Some animals present freeze-tolerance, which allows them to survive ice formation in their bodies. This is quite typical in many invertebrates (insects, gastropods, nematodes). Other animals (like marine fish) directly avoid freezing: they are freeze-intolerant. They possess antifreeze compounds. Freeze tolerance can be quite a cheap strategy that is very suited for organisms living in very cold areas, whereas freeze-intolerance is better suited for more variable climates. Regarding high temperatures, animals usually show an upper critical temperature, which, if surpassed, can affect metabolical pathways, membrane structures and tissues (Hoar, 1966).

Before going any further, it would be important to remember that the thermal balance of an animal is determined by metabolic heat production and the temperature changes produced by evaporation (only for animals living in the air), radiation, convection and conduction (given by layers of fat, hair, fur, …) (Knut Schmidt-Nielsen, 1990). To maintain the body's temperature, heat production should equal heat loss.

We will now analyse briefly the animal patterns of body temperature. The earliest terms used to separate these patterns were simply "warm-blooded" and "cold-blooded animals". Then the terms poikiloterm and homeoterm were applied to animals according to the constancy of their body temperature (Hoar, 1966). Today we use the terms "endothermic" and "ectothermic" animals, referring to the heat sources they use. Ectotherms depend mostly on external heat sources (mainly the sun), while endotherms depend basically on their inner metabolical heat.

It is obviously very important for animals to look for strategies to keep warm. Endotherms have a higher mitochondrial concentration in their tissues, which enables them to produce more metabolic heat than ectotherms. Their mitochondria are also different; their uncoupled oxidative phosphorilation enables them to produce four to eight times more heat than ectotherms. Their temperature varies with activity: in birds and mammals, thoracic and abdominal organs produce most of the inner heat, but during intense activity, they can produce ten times as much heat (Willmer et al., 2000).

Since heat is always produced by the body, its production takes lot of energy in endotherms, energy that cannot be used for other important functions such as growth and reproduction. It is crucial for these animals to remain within the thermoneutral zone, in which heat production will not vary. Heat production can be increased in three ways (Hoar, 1966). Firstly, voluntary muscular activity (physical exercise), used mainly by humans and even by certain insects that can fly for small distances just to keep their bodies hot. Secondly, shivering (all endotherms, some ectotherms), which is directly associated to the use of oxygen. Thirdly, there exists non-shivering thermogenesis (placental mammals, marsupials, some birds) (Stott, 1985). It occurs, for instance, in fat cells with many mitochondria, in very vascularised mammalian tissues (brown adipose tissue) (Svendsen, 1974).

Heat is produced mainly in the animal's organs, so it needs to be distributed in its whole body and be dissipated in accordance to the body's physiological needs. Thermoregulation by peripheral blood flow control is usually seen in large endothermic animals but is also present in small ectothermic animals like lizards and insects (Knut Schmidt-Nielsen, 1990).

There can also be countercurrent heat exchanges that act preserving the body heat and are found in the extremities of animals living in cold climates (legs or flippers of whales, seals, gulls, horns of ungulates, tails of beavers, etc). In this case, warm blood in the arterioles runs close to the venous return, which results in the appendage being always cool. This gives way to regional heterothermy, a thermal gradient along the extremity.

Another way of preserving heat gain is insulation. Mammals can change insulation intensity by pilo-erection, the angle of the hair being changed by muscles at its root. Birds can also lower their body temperature by pilo-erection (feather fluffing), having a better control of their feathers than that of mammals with their hairs. Birds also have an uropygial gland that lubricates their feathers. This prevents the feathers from getting wet and so ensures insulation (Hutchinson, 1954).

Aquatic mammals take the blood out of the body surface, an adipose layer in between the two. This is an internal insulation system.

To cope with heat loss during longer periods, mammals and birds produce thicker furs and feathers and aquatic mammals increase the thickness of their superficial fat (Bell, 1985).

While ectotherms are usually not able to vary their insulation, some insects have developed superficial hairs (bumblebees) or internal air sacs.

Animals also seek to adapt their temperature by looking for better environments. Small terrestrial animals can look for better microclimates: choice between sun and shade, hide-outs, nests (Prosser, 1952).

Reptiles and insects also like to bask in the sun, exposing through crests and sails as much surface as they are able to. Mammals also change postures, choosing to expose either fur or naked skin depending on their heat needs. Bees are able to share their body heat in their tight hive colonies. Tundra and polar bears huddle.

As we have analysed animals' strategies for keeping warm, we will analyse now other strategies that they use for keeping cool.

Keeping cool is usually less hard than conserving warmth. However, it all depends specifically on the animal's habitat and life habits.

Transient hyperthermia is used by large animals that live in areas where nights are very cold and by small animals living in cold hide-outs. In this way, these animals avoid having specific mechanisms to lose heat.

A way to lose heat for an animal can be to do exactly the opposite of what was mentioned a few lines above, that is to increase peripheral blood circulation (mammals, birds, reptiles). Other animals (mammals from hot climates, for instance and also birds) use a strategy called carotid rete: they have a heat exchanger device (cold blood network) running side by side to the blood network that supplies the brain (Hoar, 1966).

Animals can also regulate temperature loss by modifying the properties of the surfaces of their bodies. Humans can easily take clothes off, birds and furry animals flat their feathers and furs and sometimes can get them wet. Some animals living in very hot climates, like camels, increase the thickness of their furs, for, since their body temperature exceeds that of the air, they don't take in so much heat. Others, like lizards and a few frogs can also change their body colours (through reflective crystalling platelets located within their cells) so they can be cool (Willmer et al, 2000).

The best strategy for heat loss in the case of larger terrestrial animals is obviously evaporation. Birds and mammals develop it mainly by sweating (from glands located on the body surface) (Mount, 1965) and panting (breathing through their mouth, in order to lose water) (Hutchinson, 1954) (Findlay et al, 1950, 1954).

Here again, we can find different behaviours that try to maximize the body loss of heat (Brockway, 1965). Small endotherms and ectotherms try to find postures that minimize their exposure to the sun, while maximizing their exposure to the breeze (insects and lizards stilt).

Another common strategy to evade changing temperature is torpor or dormancy, an inactive state. This is common in freshwater fish, for instance, that stop feeding when they lack preys, or in amphibians and reptiles during harsh weather. Insects go through diapause, diminishing their activity and metabolism, even stopping their development. When day length changes, their neuroendocrine system send signs in different ways that cause them to look for shelter, accumulate reserves and sometimes spin a cocoon. Diapause is also broken neuroendocrinally, usually by another signal, this time sent from the brain to the prothoracic gland in insects, for example (Willmer et al, 2000).

Even though we have viewed it in relation to ectotherms, torpor also exists in endotherms. Mammals and some birds also exhibit this behaviour, lowering their metabolic activity and accumulating extra nutrients. Torpor is many times confused with "winter sleep", which is usually seen in larger animals like bears. Both states can be called "hibernation" (Prosser et al, 1952). To arise from torpor, each species has its own critical arousal temperature. In mammals, in the arousal, we see first a non shivering thermogenesis of the brown adipose tissue and then shivering, marking the "awakening" of the muscles.

Another way animals use to avoid temperature changes is migration, set on by low food resources and changing weather. Small invertebrates retreat into crevices in rocks or trees, freshwater invertebrates (frogs, turtles) go deeper into their streams and other animals like birds, migrate over long distances seeking new biomes (Hutchinson, 1954).

In order to control their body temperatures, animals must have thermal effectors that enable them to modify enzymes, alter thermal responses, and even change the behaviour of their whole body. In mammals and reptiles, the nervous system has thermostats ("cold receptors" and "warm receptors"), that is neurones that increase their firing below or over a certain temperature. These neurones are linked to other neurones that are the effectors of such physiological and behavioural effects like sweating, vasodilation (in high temperatures) or vasoconstriction and basking (in low temperatures). In vertebrates, especially in mammals, there are hormones (adrenaline, steroids) responsible for glycogen breakdown that increase metabolic rates. Thyroid hormones have the same effect in most endotherms and also in lizards, allowing them to increase their activity (Knut Schmidt-Nielsen, 1990).

Finally, we have seen the effect on temperature on animal bodies and the different strategies adopted by different species of animals to cope with temperature changes. Some authors (Willmer et al, 2000) have wondered why endotherms and many ectotherms (reptiles, insects) have settled for such high body temperatures. It is true that these help the animal to lose more heat in a controlled way. It allows more forceful muscle action and faster neurological and hormonal function, in other words a faster physiological response and more sophisticated behaviour. Evolution, then seems to be selecting for higher temperatures… but we must not forget that body temperatures are the result of a combination not only of evolutionary but also of biochemical, physiological and behavioural needs.

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