456 GENERAL ECOLOGY: ANIMAL PHYSIOLOGY

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Synopsis

Animal physiology is the study of how animals work and the biological processes essential for animal life, at levels of organisation from membranes to the whole animal. It is closely linked with anatomy and with basic physico-chemical laws that constrain living as well as non-living systems. Despite these constraints, there is a diversity of mechanisms and processes by which different animals work. The discipline of animal physiology is underpinned by the concept of homeostasis of the intra- and extra-cellular environments, neural and endocrine systems for homeostatic regulation, and the various physiological systems including ionic and osmotic balance, excretion, respiration, circulation, metabolism, digestion and temperature.

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456 General Ecology: Animal Physiology

Animal Physiology

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Animal Physiology

Animal physiology is the study of how animals work, and investigates the biological processes that occur for animal life to exist. These processes can be studied at various levels of organisation from membranes through to organelles, cells, organs, organ systems and to the whole animal. Animal physiology examines how biological processes function, how they operate under various environmental conditions, and how these processes are regulated and integrated. The study of animal physiology is closely linked with anatomy (i.e. the relationship of function with structure) and with the basic physical and chemical laws that constrain living as well as non-living systems. Although all animals must function within basic physical and chemical constraints, there is a diversity of mechanisms and processes by which different animals work. A comparative approach to animal physiology highlights underlying principles, and reveals diverse solutions to various environmental challenges. It can reveal similar solutions to a common problem, or modifications of a particular physiological system to function under diverse conditions. The discipline of animal physiology is diverse and here the major areas of research and investigation are outlined.

Homeostasis and Regulation

An important characteristic of animals is the ability to self-regulate the extracellular environment in which their cells are bathed and function. The extracellular environment is a buffer between the intracellular environment and the external environment of an animal, which consists of an aquatic or terrestrial environment in exchange with the atmosphere. These external environments can be highly variable with respect to their physical characteristics, which would affect the intracellular physiological processes necessary for animals to function. Therefore, some aspects of the intracellular environment of an animal are invariably kept different from their external environment. Consequently, an important role of homeostasis in animals is the regulation of aspects of the extracellular environment different from the external environment to provide an optimal internal environment in which the cells function.

Homeostasis is an underlying principle of animal physiology, and physiological systems are the means by which homeostasis is maintained. Homeostatic processes maintain the internal environment, although not all animals regulate all physiological variables to the same extent. Animals may conform with respect to some physiological variables, with the internal variable the same as for the external environment.

For both conformers and regulators, there is a range of environmental conditions over which the animal can survive. Beyond this range, conformers experience sufficient change in the internal environment that physiological processes no longer function effectively, and regulators can no longer regulate against the environmental gradient and their internal environment changes sufficiently to prevent normal physiological function.

Homeostasis does not necessarily require a regulatory mechanism. Equilibrium homeostasis and steady-state homeostasis are non-regulatory means by which an internal variable is kept constant *e.g.* a body fluid solute can remain relatively constant if the rate of excretion balances the rate of synthesis (Figure 1). Many other homeostatic mechanisms, however, require regulation to maintain constancy. Negative feedback control is the most common regulatory system whereby a change in a variable is detected by a sensor and then counteracted by a response from an effector organ that is opposite to the perturbation (Figure 1). Many physiological systems are controlled by several regulatory effectors, resulting in multiple control systems with greater overall precision of regulation. The nervous and endocrine systems are responsible for integrating physiological functions in an animal. They ensure that the physiological processes of different cells, tissues and organs occur in a controlled and co-ordinated manner, and result in whole-body homeostasis.

Nervous system

The nervous system integrates physiological functions and ensures that the physiological processes of different cells, tissues and organs occur in a controlled and co-ordinated manner, and result in whole-body regulation. It is responsible for co-ordinating rapid and precise responses to perturbations in the animal's internal and external environment by sensing changes in a physiological variable, integrating and interpreting the changes, and eliciting an effector response to counteract the change.

The nervous system consists of aggregations of two cell types, neurons that generate and conduct action potentials (a change in polarity of voltage across a cell membrane) and glial cells that are accessory cells which support and assist the function of neurons. Neurons can be classified as sensory (or afferent), inter (or internuncial) or motor (or efferent) and connect to one another, and to sensory or motor effector cells, via synapses (Figure 2). In primitive animals (and simple reflexes in complex animals) there is a direct connection between sensory and effector cells by a single motor neuron, resulting in a simple three cell sensory-motor circuit. However, in more advanced animals additional interneurons between the sensory and motor neurons allows for much greater complexity, permitting more complex integration and interpretation of sensory information, sophisticated motor control, and the development of complex behaviours.

The most primitive nervous systems are nerve nets; they occur in coelenterates and some flatworms. The development of cephalisation (a head region) led to the concentration of neurons at the anterior end of the animal, forming the brain, and nerve cords consisting of concentrated groups of neurons transmitting information to other regions of the body. The nervous system is most highly developed in vertebrate animals. Here the brain and spinal nerve cord form the central nervous system while the peripheral nervous system consists of many paired nerves that run from the spinal cord to the peripheral regions of the body. These transmit sensory information to the central nervous system and return motor commands to the peripheral effectors. The somatic nervous system innervates efferent organs under conscious control (*e.g.* skeletal muscle), while the autonomic nervous system innervates involuntary visceral organs (*e.g.* gut and heart).

Endocrine systems

Like the nervous system, the endocrine system regulates an animal's internal environment but it is a much slower control system. Chemical messengers (hormones) provide communication between sensory and effector cells. Hormone systems occur in all animals; they have become increasingly complex throughout evolutionary time compared to the basic neuron-endocrine systems of primitive animals. The endocrine system controls a wide range of physiological processes including reproduction, growth, development, metabolism and osmo- and iono-regulation. It can respond to short and long term variations in internal and external environments and is important for the maintenance of homeostasis. Neuro-endocrine systems consist of neural sensory and interpretive pathways but instead of directly innervating an effector organ there is release of a chemical messenger into the blood at a hemal organ. This chemical messenger is then distributed to peripheral target organs where it has an effector action.

Hormones are secreted by endocrine glands (and neurohormones by nerve cells) in response to perturbing stimuli, and are then transported via the circulatory system or diffuse through tissues to target organs and cells. Thus a key characteristic of hormones is that they exert their action at a distance from the site of their secretion. Hormones don't initiate any unique cellular activities; rather they modify the rates of existing activities. Hormones may have inhibitory or excitatory effects on target cells, usually by inducing or repressing enzyme activity within cells, although they may act on the nucleus to influence the expression of genes or influence the permeability of cells to solutes.

Historically, hormones were considered to be chemicals released from endocrine glands (glands of internal secretion in contrast to exocrine glands such as salivary, sweat and digestive glands that produce external secretions) but hormones may also be secreted by a variety of other tissues. Traditionally, hormones were considered to differ from neurotransmitters, which function only locally at the site of release (synapse) but this distinction is no longer so clear. Hormones function at very low concentration (*e.g.* 10^{-12} to 10^{-9} M). Target organs have specificity for particular hormones due to the properties of receptors that are either on the surface of the cell membrane or inside the cell. Receptors reversibly bind the hormones with high specificity and affinity. Water-soluble hormones are derivatives of amino acids (catecholamines, peptides, proteins) or fatty acids (eicosinoids). These interact with surface receptors that span the cell membrane. Often they trigger a secondary “messenger” inside the cell. In contrast, lipid-soluble hormones such as steroids (adrenocortical and gonadal steroids in vertebrates, ecdysones and juvenile hormones in invertebrates) and thyroid hormones usually pass through the cell membrane and interact with intracellular receptors. Some bind to membrane receptors which are then internalised. Many hormones that are transported in the circulatory system (in particular the lipid-soluble hormones) bind to a water-soluble carrier protein to aid transport.

Hormones are classified by the distance over which they travel to have their effect. Autocrine hormones affect the cell that secreted them. They react with receptors on their own surface to produce a response and are usually involved in cell division. Paracrine hormones act over a very short distance, diffusing through extracellular fluid to affect local tissues. Endocrine hormones affect distant organs and tissues. They are secreted into the circulatory system and are transported by the haemolymph or blood. Pheromones are an additional form of chemical communication that occurs between rather than within individuals. They are highly volatile compounds released into the external environment and detected in small concentrations by receptors (usually on the nasal epithelium of vertebrates or antenna of insects) of another individual. Pheromones function to synchronise and induce reproductive activity, and to define territorial boundaries.

Water and ion balance

Maintaining water and ionic balance is a fundamental physiological process for animals because animal cells can only function effectively over a specific, relatively constant range of body fluid composition. For unicellular animals, the intercellular environment is juxtaposed with the external environment. For multicellular animals, the extracellular space is a buffer between the intracellar and external environments. In all animals, the intracellular environment has a different ionic composition from the external environment. For some animals there are osmotic differences, but their intracellular and extracellular environments must have the same osmotic concentration to maintain constant cellular volume (but invariably they have different ionic concentrations). The challenges associated with maintaining osmotic and ionic homeostatis differ with the external environment of the animal, and so there are various strategies for animals to maintain fluid and ion balance.

Aquatic Environments: seawater

With respect to extracellular fluid, animals in marine environments either osmoconform (have the same osmotic concentration) to seawater (1000 mOsm; Figure 3) or osmoregulate at a lower osmotic concentration (usually 300 – 400 mOsm). In addition, they either ionoconform with extracellular fluid, having the same ionic composition as seawater, or they ionoregulate and maintain different ionic concentrations. Animals that conform to seawater do not have to overcome the problem of continual osmotic loss of body water to and gain of ions from the environment, but high ion concentrations adversely influence cellular metabolic processes. Most marine invertebrates osmoconform and ionoconform to seawater, but a few osmoregulate and ionoregulate. Hagfish are the only vertebrates to both osmo- and ionoconform.. Marine bony fish both osmo- and iono-regulate. Marine elasmobranchs osmoconform but ionoregulate at about 600 mOsm; urea and TMAO (trimethylamine oxide; which counteracts the negative effects of the urea on proteins) make up most of the osmostic gap between this and seawater (Figure 4).

Aquatic Environments: freshwater

Freshwater animals must both osmo- and ionoregulate as it is impossible to osmo- or iono-conform to such a dilute environment. Freshwater animals gain water by osmosis from their environment, and lose ions by diffusion. Excess water is eliminated as copious dilute urine and ions are obtained by active transport across the gills, skin or gut.

Terrestrial Environments:

Terrestrial environments are characterised by limited water availability, so dehydration is a major threat. Evaporative water loss (EWL) across the skin and respiratory tract is a major avenue of water loss by terrestrial animals. Water is also lost in faeces and urine. Water is gained in a terrestrial environment via drinking, as preformed water in food, and as metabolic water production. Water may also be absorbed across the body surface. Ions are gained from food and by drinking, and are excreted in urine and faeces and sometimes by salt glands.

Many invertebrates (e.g. molluscs, crustaceans) and amphibians are restricted to moist terrestrial habitats, at least when active, but many are more successful terrestrial animals because they have adaptations to minimise EWL. Arthropods have a chitinous exoskeleton, covered in a waxy cuticle that forms a barrier to evaporation. Birds, mammals and especially reptiles have a cornified epithelium that increases resistance to EWL (Fig 5). Insulating fur (mammals) or feathers (birds) is a further barrier. Nasal counter-current exchange of heat and water in the respiratory passages of reptiles, birds and mammals reduces respiratory EWL. Arthropods, birds and reptiles typically produce insoluble uric acid as their nitrogenous waste material, and the mixing of urine and faeces in their hindgut (where water is re-absorbed) minimises excretory water loss. Many desert reptiles and mammals survive without drinking, maintaining water balance with preformed and metabolic water alone. Most birds are able to travel long distances to obtain drinking water, although some can also survive without access to free water. Excess ions are lost by many reptiles and birds via cranial salt glands. Mammals do not have salt glands, and remove excess ions by producing urine that is hyperosmotic to blood (up to 9000 mOsm). Some birds are also able to produce hyperosmotic urine to excrete excess ions, but not to the same extent as mammals.

Excretion

Excretory organs are essential for maintaining iono- and osmo-homeostatis as they balance the gains and losses of water and solutes. They regulate the concentrations of ions and water in the body and play a vital role in excreting waste products including inorganic and organic solutes derived from the animal’s diet, metabolic processes or foreign materials, preventing these wastes from accumulating to toxic levels. Thus excretory organs must selectively retain or remove a range of solutes from the body.

Simple animals rely on diffusion and membrane transport systems to remove wastes. However, the evolution of larger and more complex animals necessitated specialised excretory organs. Although in most animals the integument is relatively impermeable to water and solutes, specific epithelial regions can be specialised for the regulation of particular solutes or water. Tubular excretory organs are more generalised than these epithelial organs, and occur in most multicellular animals. They evolved primarily for water and solute excretion, but in a terrestrial environment they also play a crucial role in eliminating nitrogenous wastes and osmo-concentrating urine in some species.

Four major organ systems are responsible for excretion in animals. The respiratory system (lungs or gills) removes CO_2, and gills also play a vital role in ammonia, carbonate and ion excretion, by both diffusion and active transport. The digestive system, in addition to eliminating undigested food, is also a site of ion and water absorption and excretion, and the vertebrate liver excretes bilirubin (derived from the breakdown of red blood cells). The integument and various glands of animals may have a primary or secondary excretory function *e.g.* water and ion uptake by the skin of amphibians, salt glands of reptiles and birds, rectal glands of elasmobranchs, and sweat glands of mammals.

Renal organs, including protonephridia, nephridia, Malpighian tubules and coelomoducts (e.g. the vertebrate kidney) consist of tubules that filter body fluids and then selectively secrete or reabsorb water, organic molecules and ions. The major functions of these excretory tubules are initial formation of excretory fluid, typically by filtration, then reabsorption of fluid and “useful” solutes and secretion of specific “waste” solutes. Only a few terrestrial animals are able to excrete urine that is more osmotically concentrated than their blood; the vertebrate kidney can excrete hypo-osmotic or iso-osmotic urine but only mammals and birds can excrete hyper-osmotic urine due to the counter-current multiplication role of the renal medulla.

Gas exchange

Most animals require oxygen to sustain their metabolic demands. Food is oxidised to produce ATP and carbon dioxide is produced as a waste product, so animals must obtain oxygen from their environment and release carbon dioxide back into the environment. Gas exchange between the internal and external environment in all animals occurs through passive diffusion. For small, simple animals, diffusion across the body surface is sufficient to meet their metabolic demands, However, an evolutionary trend amongst animals for increased size and metabolic rate requires specialised surface regions for specific functions such as gas exchange (as well as locomotion, feeding, digestion, sensory reception). So, a large body size and complexity necessitates specialised respiratory structures. Most respiratory structures require ventilation, the continual replacement of the external medium at the respiratory surface with fresh medium to maintain favourable concentration gradients for diffusion (Figure 6). Animals are classified as air and/or water breathers. The physical characteristics of these two media constrain the ventilatory mechanisms necessary to maintain gas exchange across the respiratory surface, and therefore the nature of the surface itself.

Aquatic animals have gills, evaginated and highly folded external surfaces, for gas exchange. Water is dense and viscous (compared to air) so unidirectional flow over the gill surface is preferable. This also means that gills can have a counter-current flow of external medium (water) and internal fluid (blood/haemolymph) for very efficient O_2 extraction by counter-current exchange (Figure 6). The O_2 concentration is also much lower for water (5-6 mL L^{-1}) than for air (210 mL L^{-1}) so a high efficiency of counter-current exchange is important. CO_2, however, is extremely soluble in water so its loss to the aquatic environment is not so problematic as O_2 uptake. Consequently aquatic animals generally have low body fluid CO_2 levels.

Terrestrial animals have an internalised respiratory structures, lungs or trachea, because avoiding desiccation is a major challenge. Moist externalised respiratory structures such as gills can have an excessively high EWL, but internalised structures have a lower EWL. Air is much less dense and viscous than water, and has a higher oxygen concentration, so lung ventilation by a tidal pool or cross-current system is not too inefficient or energetically restrictive. Lungs may be ventilated by positive pressure "buccal pumping", as in amphibians, or by negative pressure inspiration, as in reptiles, mammals and birds. Unlike the one-way tidal ventilatory pattern of most vertebrates, birds have a system of air sacs before and after the lung, which enables a one-way flow of air over the respiratory surface and allows a more efficient cross-current exchange system between the air and blood. The gas exchange system of arthropods consists of a series of air-filled tubes (tracheae) that infiltrate the body tissues and open to the external environment through spiracles at the body surface. Tracheal systems are generally not actively ventilated, relying on diffusion for gas exchange, a factor that limits the size of arthropods. The lungs of pulmonate snails are similarly diffusion driven.

Circulation

Small simple animals rely on diffusion to move solutes throughout their body. However, for larger and more complex animals the rate of diffusion is too slow so a circulatory system is needed for rapid transport of gases, nutrients, chemicals and waste products. Circulatory systems may be open, where the circulating fluid is not always contained in vessels and is at times in direct contact with tissue cells (*e.g.* arthropods), or closed, where the circulating fluid is always contained inside vessels (*e.g.* vertebrates; Fig 7). The circulating fluid is known as haemolymph (open systems) or blood (closed systems). It consists of plasma, a fluid containing water, ions and organic molecules, and various blood cells. These cells can be involved in transport of O_2 (erythrocytes), defence (leukocytes) or haemostasis (thromobcytes).

Blood and haemolymph flow is maintained by positive pressure created by the contraction of muscles in the body wall, or by the pumping of one or more hearts. Animal hearts are classified as neurogenic if they require an innervation for contraction (e.g. arthropods), or myogenic if the contraction is spontaneous (e.g. molluscs and vertebrates). The complexity of animal hearts varies from the simple tubular hearts of insects that push blood by peristaltic contractions of the muscular wall, to the multi-chambered hearts of molluscs and vertebrates. Chambered hearts have a varying number of muscular-walled compartments, which contract in a co-ordinated manner to circulate blood. Generally circulatory systems transport oxygenated blood from the respiratory surface(s) to the tissues and deoxygenated blood from the tissues to the respiratory surfaces. They can also be important in supplying nutrients to the tissues from the digestive system, transporting hormones from sites of synthesis to target cells, circulating cells of the immune system throughout the body, transporting heat, and generating a hydrostatic pressure.

Metabolism and digestion

The use of chemical energy is a fundamental characteristic of living animals. It is necessary to maintain cellular order and is vital to almost all physiological processes. Catabolic metabolism breaks down macromolecules for production of usable energy by cellular processes such as active transport, muscle contraction, ciliary movement, and production of heat, electricity or light. Most cellular reactions need 20-40 kJ of energy per mole of reactants, which is much less than the energy yield of the complete oxidation of a typical metabolic substrate. Therefore high energy phosphate compounds (phosphagens) are used as intermediary chemical energy stores. Adenosine triphosphate (ATP) is the most common phosphagen. Free energy is released by the hydrolysis of its terminal phosphate to form adenosine diphosphate (ADP) and inorganic phosphate (P_i) *i.e.* $ATP \leftrightarrow ADP + P_i + 30.5\ kJ\ mole^{-1}$. There is a cyclic formation of ATP from ADP (by cellular metabolism) and subsequent breakdown of ATP by energy-requiring processes.

Animals are heterotrophs, and as such are unable to synthesise their own organic compounds from inorganic molecules and so rely on other organisms for nutrients. Energy is obtained from nutrients such as carbohydrates, lipids and sometimes proteins (amino acids are required for protein synthesis but also produce energy when oxidised). Essential vitamins, minerals and fatty acids are also needed for proper cell functioning and must be also be obtained via the diet. Single-celled animals and sponges ingest food particles by phagocytosis. These are chemically and enzymatically reduced within a food vacuole to a few constituent substances (*e.g.* monosaccharides, fatty acids and amino acids) that are transported into the cytoplasm. Most multicellular animals have a digestive system specialised for extracellular digestion. Food particles enter the digestive system, where a series of physical and chemical digestive processes break down food particles into constituent molecules that are absorbed and distributed to the cells. These molecules can then be used for energy metabolism, or for cell maintenance or growth.

Metabolism may be aerobic or anaerobic. Aerobic metabolism is the oxidation of carbohydrates, lipids and proteins by oxygen to provide energy in the form of ATP. There are three major steps in the aerobic process; glycolysis, where glucose is converted to pyruvate with a net gain of 2 APT (and 2 $NADH/H^+$), the citric acid (or Kreb's) cycle, where pyruvate is converted to acetyl-CoA before undergoing a cycle of chemical reactions resulting in a further net gain of 2 ATP (and 6 $NADH/H^+$ and 2 $FADH_2$), and finally the electron transfer system. 95% of the ATP is generated by electron transfer, where electrons from $NADH/H^+$ and $FADH_2$ are transferred to electron carrier proteins, passing through several protein complexes and generating 34 ATP. Oxygen is the final electron receptor in the chain, and water is formed as the end product.

Anaerobic metabolism is an alternative to aerobic metabolism, but it is very inefficient by comparison, forming as little as 2 ATP per glucose molecule. Consequently most large and complex animals rely on aerobic metabolism to meet their resting requirements, but they may use anaerobic metabolism for supplemental energy *e.g.* during intense activity or anoxia. Build-up of lactate as an anaerobic end product of glycolysis is a major inhibitory factor in the long-term use of anaerobic metabolism in tetrapod vertebrates. However some (*e.g.* carp) can convert pyruvate to ethanol as the end product, which can be easily excreted to the environment and therefore does not inhibit glycolysis.

Many factors affect the metabolic rate (MR) of animals, including temperature, developmental stage, diet, photoperiod, taxonomy, habit, environment, activity and circadian rhythm. Body size is a major determinant of MR and is probably the best studied but least understood topic in animal physiology. Larger animals have a higher overall MR than small animals but have a lower MR per gram of body mass, so the relationship (eq 1) between mass (M) and MR

$$MR = a\,M^b \qquad (1)$$

does not scale isometrically (i.e. $b \neq 1$). Rather, $b < 1$ since small animals use proportionally more energy (*i.e.* per gram) than larger animals. This relationship is remarkably uniform for all animals, from single-celled protists to birds and mammals. Although there is some debate as to what the scaling co-efficient actually is (and why), b appears to generally fall between 0.67 (the value expected if MR scales with surface area) and 1 (the value if MR is proportional to mass); b is typically about 0.75. The intercept of the scaling relationship (a) is lowest for unicellular organisms, higher for ectothermic animals and highest for endothermic animals, but the slope is consistently about 0.75 (Figure 8).

Temperature relations

Body temperature has major significance for an animal's physiology. Temperature determines the state of matter and influences the rate of chemical reactions in biotic as well as abiotic systems. The body temperature of active animals generally ranges from -2°C (freezing point of seawater) to +50°C (where protein structure becomes unstable). This body temperature range can be even greater for animals in an inactive or dormant state; some can survive temperatures as low as -200°C or as high as 120°C!

All animals exchange heat with their environment. The vast majority of animals passively thermoconform to the temperature of their surroundings. However, some manipulate their thermal exchange to thermoregulate their body temperature within reasonably constant limits (typically 35 – 40°C) and maintaining an appreciable temperature gradient between themselves and the environment.

The thermal environment of an animal is complex. Heat exchange between an animal and its environment occurs by conduction, convection, radiation and evaporation/condensation (Fig 9). Conduction is direct heat transfer between two solid objects in physical contact. The rate of exchange depends on the area of physical contact, temperature difference, distance the heat must diffuse and thermal conductive properties. Convection is transfer of heat by fluid movement (liquid or gas), and depends on the surface area, the temperature differential between the fluid and the surface of the solid, and the thickness and conductivity of the convective boundary layer. Forced convection occurs if the fluid movement is a result of external forces (*e.g.* wind), while free convection is induced by the temperature of the object itself. Radiation transfers heat between two objects that are not in physical contact by electromagnetic waves. The higher the surface temperature of an object, the greater is the radiative heat loss. Animals both emit and absorb radiation. Environmental sources of radiation for animals are complex and include direct solar radiation, diffuse scattered radiation, reflected radiation and infrared radiation from surrounding objects and the ground. The structural and optical properties of an animal's surface are important determinants of its radiative heat load. Evaporative heat loss can be substantial because the latent heat of vaporization is about 2200 kJ g^{-1} (and condensation has an equivalent warming effect). Terrestrial animals lose heat via cutaneous and respiratory evaporation, and may have adaptations to reduce or augment this loss depending on environmental conditions.

Ectothermic animals have no physiological capacity to regulate their body temperature using internal metabolic heat production. They must either thermoconform to their environment, if their environmental temperature is relatively constant or if they can tolerate fluctuations in T_b, or use behavioural regulatory mechanisms to maintain a T_b that is somewhat independent of environmental temperature. For example many ectothermic reptiles remain largely independent of ambient temperature by using thermoregulatory behaviours such as basking, shuttling between warm and cool microhabitats and postural adjustments to keep T_b about 36 – 38°C. Endothermic animals, such as birds, mammals and some insects, have physiological control of body temperature (often 35 to 42°C). They utilize heat produced as a by-product of metabolism to maintain their high and constant T_b independent of ambient conditions. Insulating fur and feathers reduce heat flux between endotherms and their environment. Endotherms may also employ behavioural thermoregulatory strategies to reduce the energetic costs of endogenous heat production, especially when the gradient between T_b and T_a is large.

Further Reading

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Cross References

Respiration, Hormones, Endotherm, Ectotherms, Homeostasis, Homeotherms, Physiological Ecology, Plant Physiology, Temperature Regulation

Figures

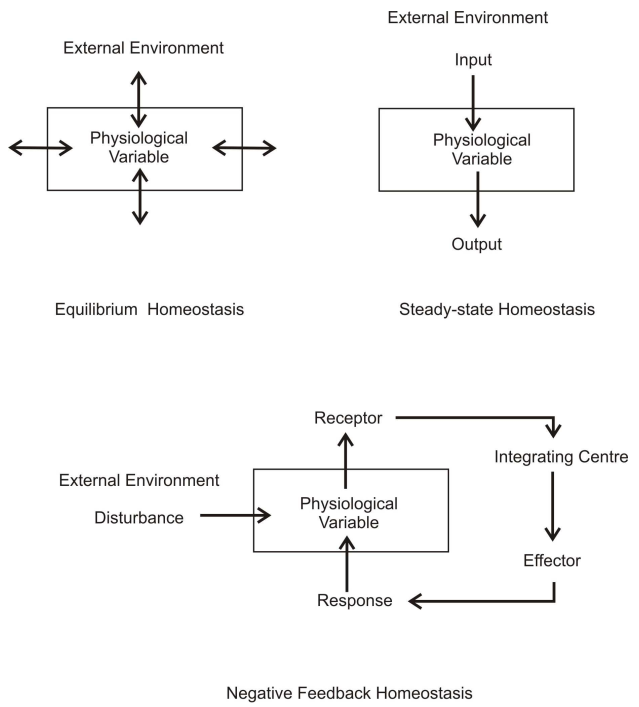

Figure 1. Schematic of equilibrium, steady-state and negative-feedback regulatory mechanisms

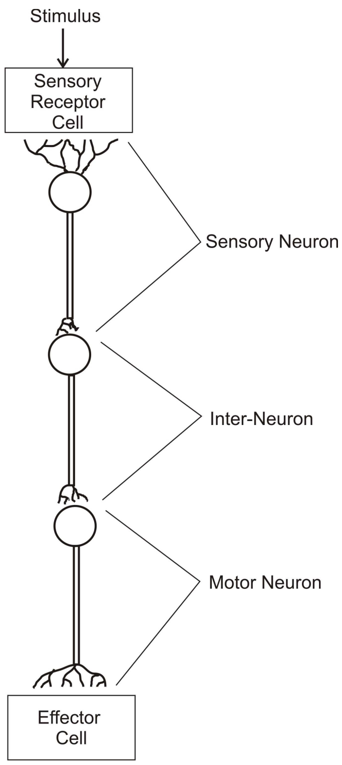

Figure 2: Schematic sensory-motor neuron system consists of a sensory neuron input, integrative and interpretative interneurone, and an effector motor neuron.

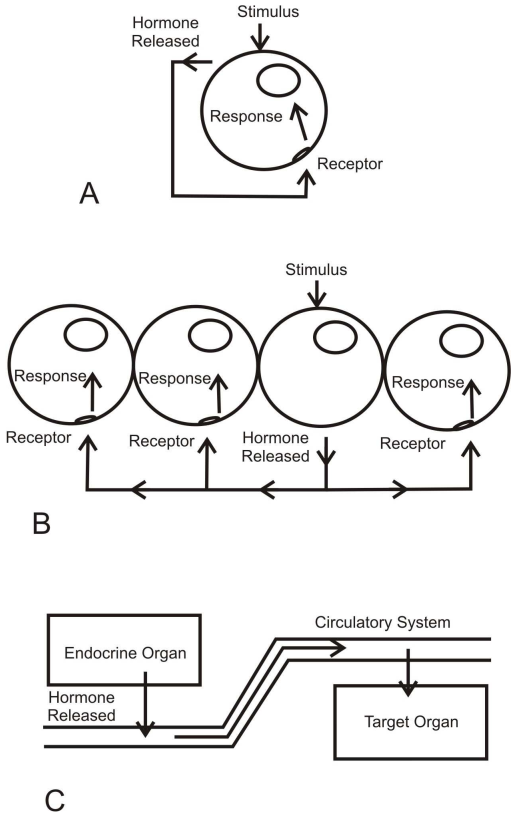

Figure 3: Hormone systems: A) autocrine hormones affect the cell that secreted them. B) paracrine hormones affect local tissues. C) endocrine hormones are transported in the circulatory system to affect distant organs.

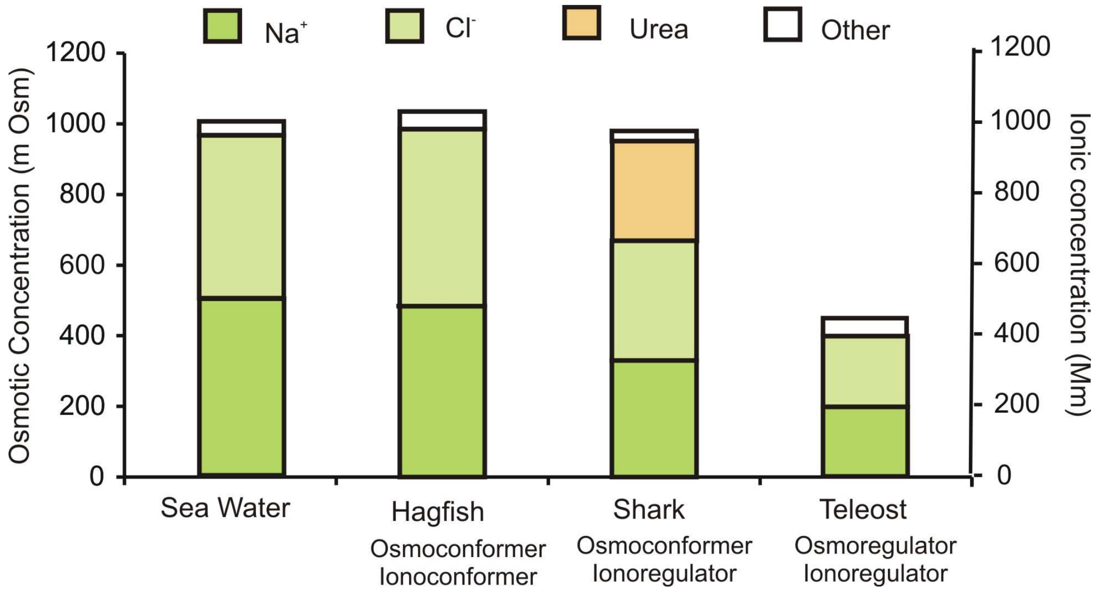

Figure 4: Patterns of intercellular ion and water regulation in vertebrate animals

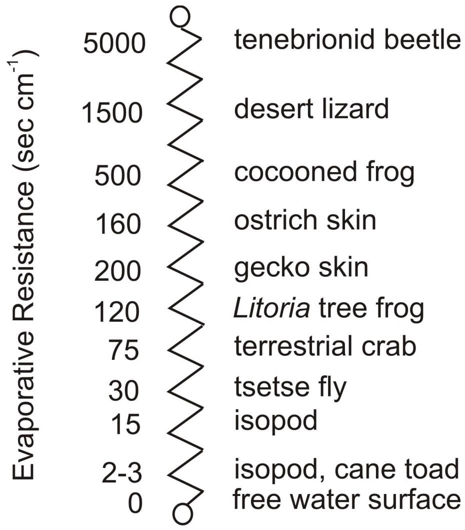

Figure 5. Scale of resistance to evaporative water loss, from about 0 sec cm^{-1} for a free-water surface to 5000 sec cm^{-1} or more for animals that are very resistant to EWL.

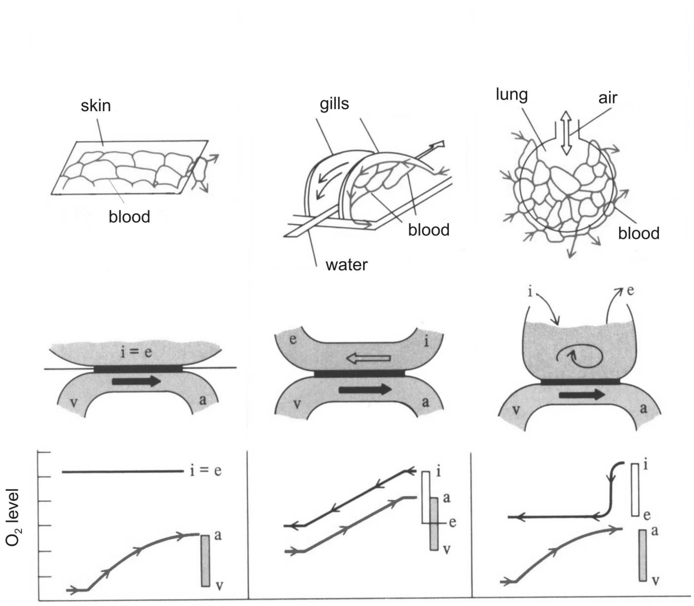

Figure 6. Schematic diagrams of respiratory gas exchange across skin, gills and lungs, showing patterns of fluid flow and O_2 exchange between the medium and blood, showing complete equilibration between the water (or air) and blood for skin exchange, typical countercurrent arrangement of water and blood flow for gills, and a tidal pool of air for lungs.

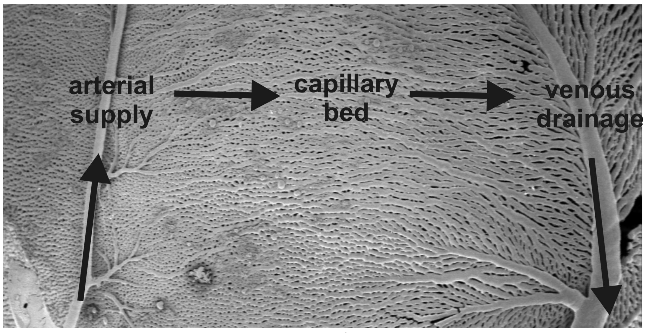

Figure 7. Vascular arrangement for a closed circulatory system, showing arterial blood supply, capillary bed and venous drainage, in the vascular supply to the eye of a marine toad (*Bufo marinus*). Photograph courtesy of T Stewart, J O'Shea and S Dunlop.

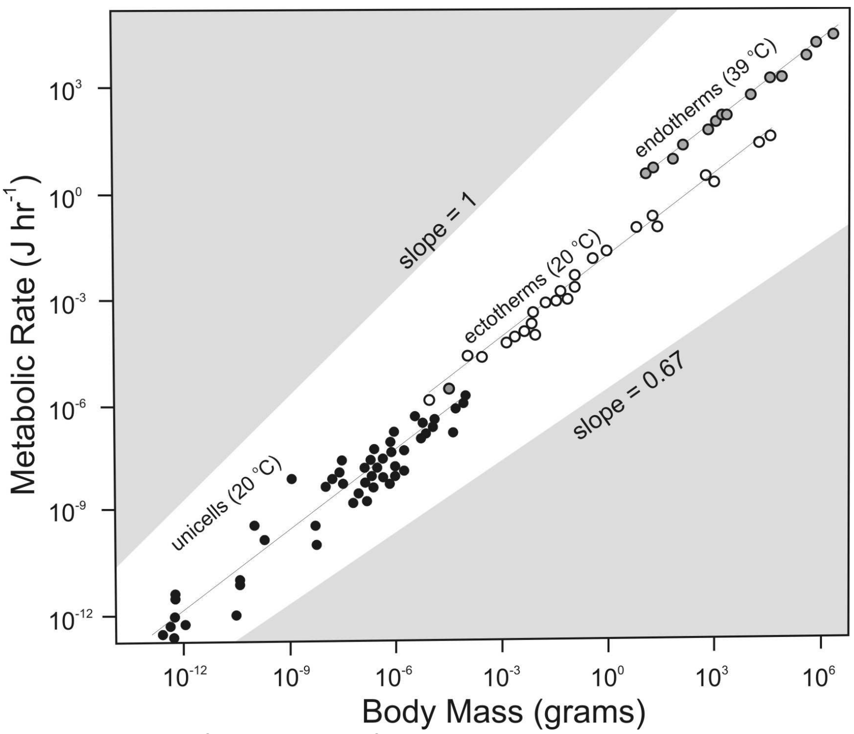

Figure 8. Scaling of metabolic rate for unicellular organisms, and ectothermic animals (at 20 °C) and endothermic mammals and birds (at 39 °C).

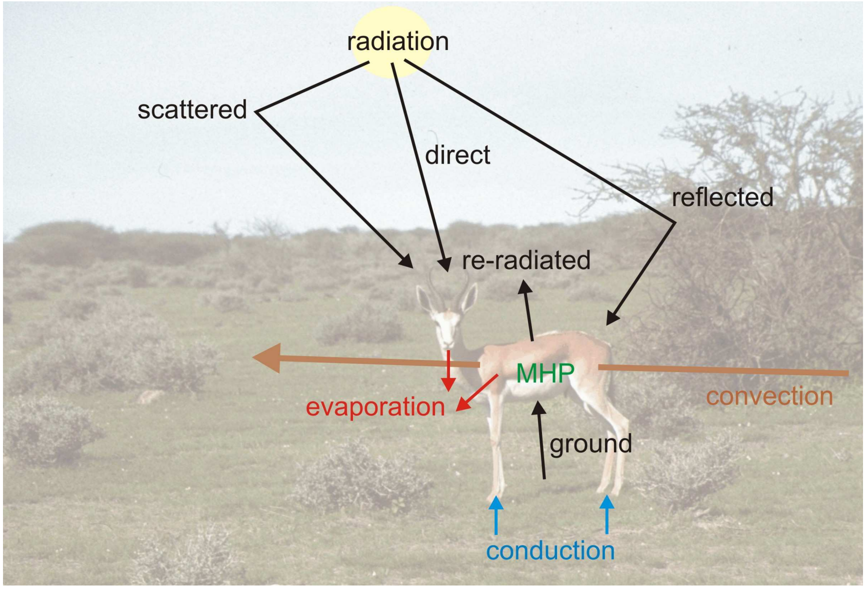

Figure 9. Avenues of thermal between an animal and its environment; conduction, convection, radiation and evaporation. Photograph by P Withers.

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