Ecosystems & Ecophysiology – Lecture 11

Thermoregulation

Objectives

1. Understand heat exchange between an organism and the environment by conduction, convection, radiation, and evaporation.

2. Know the heat balance equation, and how aquatic animals can thermoregulate by choice of microenvironment.

3. Describe how intertidal and amphibious animals can thermoregulate by modifying H_r, H_c, and H_e.

4. Know how the body temperature of an aquatic mammal is achieved by insulation and metabolic heat production.

5. Understand the action of countercurrent heat exchangers in aquatic mammals and in endothermic fish.

Thermoregulation

Animals can minimise effects of environmental temperature by keeping T_b constant, i.e. thermoregulation. Look first at the processes of heat exchange in more detail, then how they can be used for thermoregulation

1. Conduction. Occurs between physical objects in contact, including liquids & gases. The rate of heat transfer $\mathbf{Q = kA \cdot (T_2 - T_1)/L}$

Where k = thermal conductivity
A = area of contact
T_2-T_1 = temperature difference (therefore conduction is linearly related to temperature difference)
L = length of path between T_1 & T_2

Values of thermal conductivity (J s^{-1} cm^{-1} $^{o}C^{-1}$)

Copper	3800
Water	5.8
Muscle	4.6
Blubber	2.1
Fur	0.38
Air	0.25

Water is thus 20 x as conductive as air. The low value for fur is due to its air content, insulation of fur depends on a layer of air trapped next to the skin

Fur loses its insulation effect if the air cannot be held in place (under water). Blubber used by aquatic mammals, but much less effective so thicker layer

2. Convection. Facilitates conductive heat loss. Heat is transferred to a fluid (gas or liquid) by conduction, then warmed fluid is replaced by cooler. Convection thus keeps the temperature difference (T_2-T_1) high

3. Radiation. Occurs without physical contact between objects. All objects above 0 K (–273^{o}C) emit electromagnetic radiation. Intensity & wavelength emitted depend on the surface temperature:

1. Intensity, proportional to absolute temperature T^4 (power 4)

2. Wavelength decreases with increasing surface temperature. Emission spectra for objects at three temperatures:

a) Sun at 6000 K, peak in short waves - visible light & ultra violet
b) Red-hot metal at 1000 K, mostly infrared, some visible light (red)
c) Biological & environmental objects at 300 K, emit in the middle infrared (long waves)

Organisms are black bodies for infrared, i.e. with little reflection of long waves, absorbance 95-100%. Colour has no effect on emission or absorption of infrared, only affects absorption of visible light

■ **4. Evaporation.** Very effective as a means of heat loss as the heat of evaporation of water is high, 2.4 kJ g^{-1}. Joule is the SI unit, 4.18 J = 1 calorie

4.18 J is the quantity of heat needed to raise the temperature of 1 g of water by 1°C. (Specific heat capacity - actually from 14.5 to 15.5°C)

0.418 kJ would thus heat 1 g water from 0 to 100°C, but it would need nearly 6 x this amount of heat (2.4 kJ) to evaporate or boil the water away

■ **Heat balance equation**

Integrates the different processes of heat gain & loss:

$$\pm \mathbf{H_s} = \pm \mathbf{H_r} \pm \mathbf{H_c} - \mathbf{H_e} + \mathbf{H_{met}}$$

H_s = heat storage in body, + for T_b increase, – for T_b decrease
H_r = net radiative exchange, + for heat gain, – for heat loss
H_c = conductive & convective exchange, + for heat gain, – for heat loss
H_e = evaporative exchange, – as unidirectional, heat loss only
H_{met} = metabolic heat production, + as unidirectional, heat gain only

(Signs for H_r, H_c & H_e often reversed in books as put on the opposite side of the equation to H_{met}. Confusing as then + for heat loss)

Thermoregulation means minimising change of H_s, by altering the other four variables in response to environmental changes. Most work on terrestrial organisms, look at aquatic & intertidal here

Simplest is when all terms are effectively zero, animal is in equilibrium with thermal environment, regulates T_b by choice of microenvironment

■ Most aquatic animals show some thermal preference in the lab, e.g. sublittoral fish *Girella*, selected temperatures of 26°C. Major gradients of water temperature usually vertical rather than horizontal in wild

■ Lake-dwelling sockeye salmon *Onchorhynchus nerka* show diurnal vertical migration across the thermocline. Spend daytime in deep cold water (5°C), keep metabolic costs low during the inactive period

Migrate to surface to feed at dusk, can be more active in warmer surface water above thermocline (17°C), also feed at dawn. Then conserve energy by migrating back to deep water

■ Intertidal organisms experience greater range of temperature when emersed. Tropical mollusc *Chiton stokesii* in environment with rock surface temperatures up to 45°C in day

But selects crevice under rock in daytime, temperature between foot & rock is < 30°C, T_b less variable than if microenvironment use was random

Intertidal animals can also manipulate heat exchange to some extent. Low environmental temperatures are tolerated rather than avoided by thermoregulation (Lecture 12), but animals can avoid high T_b

■ 1. Decrease $+H_r$ by colour, often white compared to darker colour of sublittoral relatives. Light colour increases reflectance of the visible light in sunlight, so less energy absorbed

Also increase radiative heat loss by increased sculpturing of shell, increases surface area for emission of long-wave radiation

2. Increase $–H_e$ by evaporating water. Effective as high heat of evaporation, but limited by danger of desiccation

Aquatic ectotherms. H_r & H_e unimportant in water, but H_c large because of high conductivity of water. Body heat quickly lost unless well insulated

■ Inanimate objects cool & heat at the same rate. Animals can alter their rates of heating & cooling by conductivity changes. Useful in ectotherms entering water from land

Galapagos marine iguana basks on land, reaches 32^{o}C, but feeds in sea at 20^{o}C. Regulation possible by changes in heart rate & peripheral blood flow

Because although some heat moves directly from body core to skin, most is transported by forced convection in blood

Peripheral vasodilation on land, vessels in skin enlarge to increase blood supply & transfer of heat to body core. Vasoconstriction in water has opposite effect, minimises $–H_c$ in water. Heart rate also higher on land than in water

■ Heart rate higher at a given T_b during heating compared to cooling, hysteresis loop between heart rate & T_b

Result is that marine iguana heats on land twice as fast as it cools in water, minimises time needed for basking, maximises foraging time in water

Aquatic endotherms

Endotherms in water are vertebrates (no plants or invertebrates). Need thick insulation in water as blubber less effective than the air in fur

■ Layer can be several cm thick in a seal, cross section of body shows almost 60% of the area is blubber. So no small permanently aquatic endotherms

Sea otters don't have blubber, but very thick fur, constantly groomed to keep in the air insulation, also in marine birds, oily plumage repels water

■ Flippers need aerodynamic shape so cannot have thick blubber. They would give severe heat loss, except for countercurrent heat exchanger

■ Principle the same as countercurrent exchange in fish gill (Life Processes Lecture 22), except that exchange in the flipper is between two directions of blood flow in a closed system

Heat is retained within body core, not lost through uninsulated flipper to the water

■ H_{met} increases as the water becomes cooler, to offset greater conductive heat loss (despite insulation). Linear relationship to T_a, as rate of conduction is directly proportional to temperature difference

Metabolic rate does not decline to intercept of zero. There is a minimal level or basal metabolic rate (above the lower critical temperature T_{lc}), of general metabolic processes other than thermoregulation or activity

Also endothermy in some fish. Resting metabolic rates of ectotherms too low to give much metabolic heat, typically only 1/10th basal rates of endotherms

But activity increases metabolic rate by 10 x (in both ecotherms & endotherms). So an active ectotherm may have a similar metabolic rate to a resting endotherm, with potential for heating

Usually little increase of T_b as ecotherms are not insulated, only high T_b in large fish & reptiles. Leatherback turle (900 kg) maintains $T_b > 25^oC$ in water at 7^oC, partly due to large size & thus relatively low surface area

Huge size also permits relatively thick layer of superficial tissues with reduced circulation, acts as insulation (muscle only 2 x as conductive as blubber)

27 species of fish are endothermic; tunas & lamnid sharks (mako, great white). Problem of gills, countercurrent exchange would transfer heat out of blood as effectively as oxygen into blood

No possibility of keeping T_b high throughout body, so regional heterothermy

■ Aerobic swimming muscles (red, high myoglobin), positioned either side of the vertebral column in skipjack tuna. Have become internalised (normally superficial in fish, for greater mechanical advantage)

These red muscles are at higher temperature – shown by isotherms. Viscera & brain are also > T_a in some species, but < muscle temperature

■ Smaller tuna species (skipjack & yellowfin) show elevation of T_b above T_a, but no regulation – parallel lines with slope = 1

■ Bluefin tuna shows both elevation of T_b and slope < 1.0, i.e. it regulates body temperature as well

■ Arteries to the red muscles pass under skin (cutaneous), then dive into muscle where they divide into many small vessels

These vessels mingle with small veins leaving the muscle in a countercurrent heat exchanger – the rete mirabile or wonderful net

■ Small vessels have relatively thick walls, else there would be exchange of oxygen as well as heat, & no oxygen would reach the muscles

Exchanger keeps heat in the muscles, heat exchange veins → arteries. Viscera & brain may be heated by blood from muscles, but rest of body is cold

Advantage is greater muscle activity & so swimming performance in predatory fish. Expanded geographic range into cool temperate oceans compared to similar ectothermic fish

■ Major innovation of the tuna is not countercurrent flow as such, but the cutaneous supply to the muscles. Arteries & veins to organs usually run parallel & close in vertebrates

Gives some countercurrent exchange even in ectothermic fish. But since the blood supply is from central vessels, acts to keep heat of muscles from body core, & heat is lost through the skin

Tuna also have central blood vessels, but supply to the red muscles is from cutaneous vessels. Heat therefore kept within muscles, not lost through skin

■ Billfish (swordfish *Xiphias*, & marlin) have a specialised heater organ. Also in butterfly mackerel (related to tuna), by convergent evolution

Modified extrinsic eye muscle, heats blood flowing to brain. Blood passes through carotid rete countercurrent heat exchanger to retain heat in brain, then heater organ, then brain

Advantage is greater sensory perception. Swordfish active over a range of T_a up to 19^{o}C across the permanent thermocline, pursuing squid prey

Heater cells myofibrils but have many mitochondria, up to 2/3 of muscle volume (cytochromes give brown colour). Also sarcoplasmic reticulum, heat production stimulated by Ca^{2+} release from this

■ Similar in principle to Brown Adipose Tissue (BAT) in mammals, the only other tissue adapted solely for heat generation. Mostly occurs in temporal heterotherms for rapid heat production after torpor

BAT also has high mitochondria & brown colour from cytochromes. Works by uncoupling the electron transport chain from ATP production

Electrons pass along the electron transport chain in inner mitochondrial membrane, & pump protons out into the intermembrane space (Life Processes Lecture 21)

■ In normal tissues protons re-enter matrix of mitochondrion through ATP synthase enzyme in membrane. Energy released by protons moving down their concentration gradient produces ATP (chemiosmosis)

Inner mitochondrial membrane in BAT is permeable to protons, so these bypass the ATPase. Heat produced but ATP not synthesised – uncoupled

System in swordfish is different, it is coupled to ATP production. The ATP is then used by the enzyme calsequestrin, which returns Ca^{2+} to the sarcoplasmic reticulum

Ca^{2+} then released again, in a futile cycle, only net result is catabolism of carbohydrates & lipids to produce heat