Lecture 22 & 23. Thermoregulation: Dealing with Heat and Cold

Temperature regulation is interesting in its own right, but also because it emphasizes the ***relationships among physiological processes***. Over the next two lectures, will see that mechanisms of temperature regulation are closely related to osmoregulation and water balance, respiration, pH balance, body size, and ecology (habitat use). It's no accident that you don't see any lizards near the poles, or that most small animals (insects, for example) are ectotherms.

Temperature and Heat Capacity.

Temperature and heat are not the same thing.

Heat is form of energy, so it is measured in units of joules (or calories).

If a given amount of heat is added (removed) to an object, its temperature goes up (down) by an amount that depends on its ***specific heat capacity***, which is related to density.

- High heat capacity: absorbs heat with little change in temperature
- Low heat capacity: absorbs heat with greater change in temperature.

The heat capacity of water is much greater than the heat capacity of air. Restated, it takes more heat (energy) to raise a given volume of water by 1^oC than it does to raise the same volume of air by 1^oC.

E.g. You're camping and get caught in a storm. The air is -10^oC, but there is a stream with water at 1^oC. Should you get in the water?

Heat Flux: Pathways of Heat Gain and Loss

(Overhead: Pianka Fig 5.17)

Body heat = heat produced + heat gained - heat lost

$H_{tot} = H_{met} + H_{cond} + H_{conv} + H_{rad} + H_{evap} + H_{store}$

H_{met}: Heat produced by metabolic reactions. Examples - 58% of energy released by electron transport chain is trapped in ATP, so 42% released as heat. 75% of energy released from ATP in muscle goes to mechanical work of contraction, so 25% is released as heat.

In hot climate, this heat must be dumped somehow (more later).

To deal with cold, metabolic processes can be modified by natural selection to be more efficient as heat producers.

Metabolic heat producing specializations:

(Overhead: Fig 16-22)

1. Shivering: Work opposed muscles simultaneously, to obtain heat. Inefficient because 75% of the energy goes to mechanical work (opposed muscles, so no movement).

(Overhead: Fig 16-27)

2. Heater tissues in swordfish: Modified muscle cells that have lost myofibrils so that cannot do mechanical work. Energy that would have gone to work now goes to heat, so ↑ efficiency as heat producing tissue.

(Overhead: Fig 16-26)

3. ***Nonshivering thermogenesis*** in ***brown fat.*** Brown fat is brown because it has many capillaries (unlike most fat, which has little blood flow) and many mitochondria ⇒ both adaptations to ↑ ***rate*** at which the fat can be metabolized.

   Modified mitochondrial function increases ***efficiency*** of metabolic heat production. Mitochondrion is site of cellular respiration, in which protons flow through electron transport chain, normally to form ATP from ADP & P_i. Inner membrane of mitochondria in brown fat has ***thermogenin*** (a protein) inserted.

(Overhead: Fig 3-62)

Thermogenin is a proton transporter that blocks normal sequence of protons along E.T.C. Instead, protons combine with O_2 to give water and heat.

$4H^+ + O_2 \rightarrow 2H_20 + \text{heat}$ (highly exergonic rxn)

Thyroid hormones control deposition and use of brown fat.

H_{cond}: Heat gained or lost by conduction = direct transfer of kinetic energy from one molecule to another; the molecules themselves don't move.

Equation for heat flux by conduction illustrates three major points about thermoregulation by animals.

$$Q = \frac{kA(t_2 - t_1)}{L}$$

Q = heat flux (transfer) by conduction between 2 points
k = thermal conductivity (opposite of insulation)
t_2-t_1 = temperature difference between the 2 points
L = distance separating the 2 points
A = surface area over which conduction occurs
$(t_2-t_1)/L$ = ***temperature gradient***

To reduce heat flux by conduction, physics gives an animal three basic options:

1. Minimize the temperature gradient (thermoconform, or reduce surface temperature).

(Overhead: Fig 16-14)

2. Minimize the area over which a temperature gradient exists.
3. Insulate (minimize conductivity of area over which gradient exists).

H_{conv}: Heat transferred by the movement of gas or liquid that holds that heat.

E.g. wind chill: on windy day convection makes it harder to maintain body heat, because layer of air near body surface that is warmed is constantly blown away, maintaining maximum T_b - T_a temperature gradient.

(Overheads: Gill Fig 6-8 & 6-9 - piloerection & frizzled chickens with high BMR**)**

Adaptations to ↓ convection usually also ↓ conduction. E.g : Fur and feathers trap air, which reduces convective heat loss, and also gives layer with low conductivity.

H_{rad}: Heat emitted proportional to temperature in degrees K raised to 4^{th} power. Physics says all objects, living or dead, above 0^{o}K radiate heat in this way. Whether radiation causes a gain or loss of heat depends on temperature of animal's surface relative to environment.

(Overhead: Fig 16-19 - radiation vectors both ways**)**

Can affect heat flux by radiation through color and texture, which determine ***emissivity***.

H_{evap}: Heat lost by evaporation of body water.
Water has latent heat of vaporization = 585 cal/g H_20.
So evaporating 1 g (= 1ml = 1cc) of water consumes 585 cal of heat.
The specific heat capacity of body tissue is about 1 cal/^{o}C/g.
So evaporating 1 g of water can cool 585 g of tissue by 1^{o}C. So, a 60 kg animal can dump enough heat to cool body by 1 deg C by evaporating 0.1 liter H_2O.

(Overhead: Fig 8-9A & 16-39)

Sweating - specialized exocrine (ducted) glands extract water from blood by solute-coupled water transport across epithelium. Then release water through pore to be evaporated. Effectiveness depends on relative humidity of air.

(Overhead: Vaughan Fig 19-9)

Evaporative cooling by sweating (or panting) is not an option if water is limited. Recall camel example (under temporal heterothermy), as well as dik-diks in ohead.

Panting - same idea, but evaporation of water from nasal mucosa or mouth is increased. Thermoregulation by panting has important interactions with water conservation and pH regulation.

(Overhead: Fig 14-5 & 14-6)

Temporal counter-current water conservation in nose:

Inspiration — Air entering nasal passage is warmed. Warming increases its capacity to hold water. Water is evaporated from tissues of nasal cavity, cooling the tissues.

Expiration — Air has reached body temperature in lungs, which are moist (for gas exchange), so expired air exits lung warm, fully saturated. Air is cooled in nasal cavity, decreasing capacity to hold air, water is recovered.

Effectiveness of this mechanism can be increased by counter-current blood flow to nose, e.g. in Kangaroo rat (more on this later).

In extreme exercise, M.R. is high enough that exhalation is mainly by the mouth. This is less water-efficient, because expired air is not cooled as effectively. Test this by exhaling on your hand via nose and via mouth.

Counter-current brain coolers - the cool nasal cavity is exploited by some animals to avoid overheating the brain during burst of extreme activity (e.g. chasing prey or avoiding predators). Overheating brain is thought to limit chase distance in some large mammals, e.g. cheetah and their prey - including gazelles.

(Overhead: Vaughan Fig 19-7 & 19-8)

Carotid rete is a plexus of veins returning cool blood from nasal cavity, arranged around the carotid artery on its path to brain. Buffers brain temperature when body temperature rises during running. (Heat production by running gazelle increases 40x above resting.)

Panting & pH: Increasing respiration rate tends to increase elimination of CO_2.

$CO2 + H20 \rightarrow H2CO3 \rightarrow H+$ and HCO3-

If CO2 production by tissues exceeds CO2 clearance by lungs, the blood becomes acidic [H+ concentration rises, pH drops: recall that pH < 7 is acidic (high H+) and a pH > 7 is alkaline (low H+)].

If CO_2 is dumped very quickly, concentration of protons [H+] in the blood is reduced, so pH rises (becomes alkaline)
If blood pH increases, blood vessels constrict. (This constriction is what causes hyperventilating people to faint - blood flow to brain is reduced).
If pH reaches 8, mammal will die. Through mechanisms not understood, birds can tolerate this pH (necessary to maintain high respiratory rate needed for flight).

(Overhead: Fig 16-31)

Panting mammals have different solution to pH problem. Panted air is not moved across alveoli of lung, where CO_2 exchange takes place. Moves mainly in 'dead space' of nasal cavity, trachea, bronchii. Effect is increase in respiratory water loss & cooling, without ΔpH.

Sources of Heat and Temperature Regulation: A Trade Off

Two dichotomies, one based on ***source*** of heat, one based on type of temperature ***regulation***.

Charles Blagden (1775) Experiments and observations in a heated room. Phil. Trans. Roy. Soc. Lond. 65:111-123.

Source of Heat:

Endotherms: Produce much of body heat by metabolic processes. But also gain or lose heat from environment through passive (non-metabolic) processes. Can maintain core body temperatures up to 30^{o}C above ambient temperature, long term.

Ectotherms: Gain and lose body heat primarily from the environment. Body temperature tracks ambient temperature.

Regulation of Body Temperature:

(Overhead: Fig 16.16)

Homeotherms = thermoregulators. Maintain relatively constant core temperature.
Mammals regulate around 37 - 40^oC.
Birds regulate around 39- 43^oC (must have higher metabolic rate to sustain flight, so T_b is higher.)

(Overhead: Gill Fig 6-1)

37-43^oC is just below the temperatures that cause partial denaturing of enzymes. Denaturing requires synthesis of new enzymes, which is energetically costly.

Poikilotherms = thermoconformers. Allow core temperature to fluctuate.

The two dichotomies are not completely independent - most endotherms are relatively strict homeotherms, and most ectotherms are poikilothermic. Leads to casual classification as ***warm blooded*** (endothermic thermoregulator) or ***cold blooded*** (ectothermic thermoconformer).

Better to consider source and regulation separately. Ectotherms can use behavioral thermoregulation to hold core temperature constant in face of changing environmental temperature - so ectothermy is not always paired with poikilothermy.

(Overhead: Fig 16-17)

Endotherms sometimes allow dramatic shifts in core temperature (e.g. hibernating mammals) so endothermic does not always imply homethermic.

(Overhead: Fig 16-18)

These dichotomies are useful but are simplifications of reality ***Heterotherms*** regulate body temperature (T_b), but not tightly enough to make T_b independent of ambient temperature (T_a).

Two types of heterothermy:

(Overhead Fig 14-12)

- ***Temporal heterothermy*** - allow T_b to fluctuate under some conditions but not others.

(Overhead Fig 16-30)

- ***Regional heterothermy***- regulate T_b in core, allow extremities to thermoconform more than core

Under sufficiently extreme temperature, essentially endotherms will shift to regional heterothermy, shunting circulation and letting extremities cool in order to retain heat in core — this is an emergency response that limits losses to parts that might not be fatal to lose. Frostbite strikes the extremities first.

Heterothermy is basically a means of keeping core body temperature within acceptable limits.

Factors affecting the trade off between endothermic homeothermy and ectothermic poikilothermy

The fact that both systems are common (both are maintained by natural selection) indicate that neither system is unconditionally better than the other. Each has costs and benefits. Which mechanism is best for a given organism depends on several variables.

1. ***Body size.*** Endotherms generally maintain $37^oC < T_b < 43^oC$. Ambient temperature (T_a) is less than this for most environments at most times.

   So for endotherms in most environments, $T_b > T_a$. $T_b - T_a$ is the ***temperature gradient*** between the body and the environment. The rate of heat loss (energy loss) to the environment depends on the gradient, and the area over which the gradient exists (a big gradient need not cause major heat loss, if it occurs only in a small area).

   Heat loss $\propto$ Area $(T_b - T_a)$

   As body size ↓, surface area per kg of body mass (the surface/volume ratio) ↑

   Assume for now animal is a sphere with radius = r

   Surface = $4\pi r^2$
   Volume = $^4/_3\pi r^3$

   $S/V = 3/r$ $\Rightarrow$ as $r\uparrow$, $S/V\downarrow$. As $r\downarrow$, S/V ↑.

   So consider a spherical flea with r = 1 mm. S/V = 3/1 = **3**
   Compare with a spherical mountain lion, r = 100 mm, S/V = 3/100 = **0.03**

   Animals aren't actually spheres. A more realistic calculation uses

   $S = aV^{0.67}$ where a = coefficient that varies among taxonomic groups depending on shape.

(Overhead: Vaughan Fig. 19-3)

(The assumption that animals are spherical isn't as unreasonable as it first appears, because many animals adopt a ***posture*** that is nearly spherical when they are cold.)

(Overhead: Vaughan Fig 19-10)

Huddling is another way to ↓ S/V ratio and thus ↓ heat loss.

Combine the basic point that *S/V* ↑ as *r* ↓ with the equation for heat loss. Conclusion: for each gram of tissue that must be kept warm, the flea loses heat at 100 times the rate that the lion does.

An intuitive way of thinking about this is that a flea has no 'core' that is protected from the environment by the tissue around it, but a bigger animal does have a protected core. The bigger the animal, the bigger the core that is not threatened by heat loss to the environment.

(Overhead: Fig 14-12 again*)*

***Another effect of body size**:* even if the S/V ratio did *not* vary with body size, a given heat flux changes the temperature of a small object more than it would a large object.

So, body size is a constraint on endothermy. As size decreases, it is increasingly difficult (energetically) to maintain $T_b > T_a$. Smallest endotherm is the bumblebee hummingbird, at 2.2 grams (Smallest mammal is the masked shrew, 3.5 grams).

(Overhead: Vaughan Fig 19-4)

Endotherms can be as small as 2-3 grams only by maintaining high basal metabolic rate (BMR), so that rapid heat production offsets rapid heat loss. Below 5 g, the slope of BMR vs mass rapidly steepens. BMR that would support heat loss for body size <3.5 g is too high to maintain for mammals.

(Overhead: Gill Fig 6-10)

Bergmann's Rule: Within a species, body size increases as one moves toward the poles. Driven mainly by S/V relationship. Details of body size distributions (across longitudes) show that the pattern is due to thermoregulation — in woodpecker overhead, smaller birds at coast and along Mississippi Valley, where it is warm for the latitude.

2. Ambient Temperature

Ectothermic poikilothermy is simply not possible once temperature is low enough that thermoconforming would cause metabolic reactions to be too slow.

Endothermic homeothermy is easier to support when the T_b-T_a gradient is small, but it does allow animals to exploit environments too cold for ectotherms.

Ectotherms can allow T_b to cool even below 0^oC (more on this later), but not in the long run, because cooling renders them inactive. Eventually must warm up to forage.

3. Availability of Food (Energy)

(Overhead: Fig 16-25)

Endotherms use energy to regulate temperature. Consequently an endotherm has BMR in the wild that is up to 17x greater than BMR of similar size ectotherm.

If food (energy) is in abundant supply, endothermy may be maintainable. If energy is highly limited, it may be difficult to obtain sufficient food to be endothermic.

So ectothermic poikilotherms can exploit environments (or niches, more exactly) with sparse food (spatially or temporally). Good example of temporal sparseness of food - sit & wait predators like snakes, spiders, antlions: all ectotherms.

4. Availability of Water

Endothermic homeothermy is more difficult to support in arid environments for two reasons:

1. Endotherms use evaporative cooling via sweating or panting to cool themselves.

2. Endotherms have higher BMR (just discussed). Higher BMR $\rightarrow$ higher rate of respiration $\rightarrow$ more water loss via air passage over moist respiratory surfaces (must be moist for gas exchange).

- Ectothermic poikilotherms compose bigger proportion of desert communities: Poikilotherms better able to deal with water conservation
- Poikilotherms bear little cost by allowing $T_b = T_a$, because T_a is near range that endothermic homeotherms maintain anyway.

(Overhead: Gill Fig 6-15 - *interaction* of water conservation cost of endothermy with body size in birds)

5. Predation Risk

A cost of ectothermic poikilothermy is that mobility is constrained when ambient temperature drops. (Because of effects of temp on metabolic rate).

Consequently, poikilothermic prey are more vulnerable to homeothermic predators than homeothermic prey are. E.g: Lizards vs squirrels as prey of raptors in Serengeti, where it is relatively cold (about 15^oC) in the morning. Lizards get hammered.

Constrains poikilothermy to niches in which predation risk (by homeothermic predators) is not severe.

6. Aquatic/Terrestrial Environment

The heat capacity of water is high (compared to air), so any surface area exposed to water with a temperature gradient will rapidly lose heat.

Implies that aquatic organisms must be poikilothermic or very well insulated. Both solutions are used. Most permanently aquatic organisms are poikilothermic. Aquatic mammals have subcutaneous fat (blubber) or exceptionally dense and oily fur.

(Overhead: Fig 16-15)

Blubber is metabolically costly to maintain (it's fat) relative to feather or fur. But insulating value of blubber can be regulated by capillary flow.

Flow through blubber - insulation reduced.
Flow sub-blubber - insulation increased.

With fur/feathers, flow of blood is always beneath insulation. (Piloerection does alter insulating value of fur/feathers, but to lesser degree than in blubber.)

Fish and other water-breathing animals face a serious heat loss problem because water has high heat capacity ***and*** low oxygen content. Must move a lot of water over gas-exchange surfaces (gills) to get O_2. Air breathers can move less air over gas-exchange surface, and air has low heat capacity, thus possible to heat inspired air to body temperature. Energy cost of heating water (large volume, high heat capacity) would be too great $\Rightarrow$ water ***breathers*** constrained to poikilothermy (insulation can't solve this problem).

Heterothermic fish. Some fish (notably tuna) have evolved ***a counter-current heat exchange*** mechanism that allows a part of the body (red swimming muscle) to be kept above ambient temperature.

Arterial blood passing through gills is unavoidably cooled.

(Overhead: Fig 16-23)

Heterothermic fishes' circulatory system *routes cooled arterial blood (after gills) near the surface*, so core body heat isn't conducted to it (L maximized, in equation for conductive heat flux).

(Overhead: Fig 16-24A & p 604 part c & Gill Fig 6-14)

When this blood is routed into red muscle deep in body, it passes through ***rete mirabile,*** which is a counter-current heat exchanger — a system of veins and arteries running in opposite directions in contact with each other.

Cold arterial blood is warmed by passing venous blood, which has been heated up by metabolic activity in muscle. By passively moving heat from venous to arterial blood, some of the metabolic heat carried away by veins is returned to muscles.

(Overhead: Fig 16-24B)

Consequently, red muscles in tuna's core can be kept up to 15^{o}C above water temperature.

In bird example on ohead, heat is flowing from artery to vein, but principle is same. Same principle in brain coolers and in nasal blood supply, discussed above

Temperature effects on metabolic rate

Non-enzymatic rxns proceed faster as temp ↑ (due to Brownian motion).

Enzymes have optimal temperature range. In general, ↑ temp → ↑ rxn rate, up to point where partial denaturization begins (around 43^{o}C).

Quantify the effect of temperature on reaction rate with ***temperature quotient***, Q_{10}, which is simply the ratio of reaction rates at two temperatures that are 10^{o}C apart.

$$Q_{10} = \frac{\text{reaction rate at t+10}}{\text{reaction rate at t}}$$

To treat temperature quotient as a continuous variable (i.e. allowing ΔT to take values other than 10^{o}C), modify equation:

$$Q_{10} = (k_2/k_1)^{10/(t2-t1)}$$

t2 = temperature 2
t1 = temperature 1
k2 = reaction rate at t2
k1 = rxn rate at t1

(Overhead: Fig 16-9 and 16-19)

Enzyme catalyzed reactions have Q_{10} = 2 to 3. Reducing body temperature by 10_oC slows down metabolism by a factor of 2-3x.

Can replace k (reaction rate for a specific chemical reaction) with MR, the overall metabolic rate. Q_{10} for MR is also about 2-3, indicating that most of the effect of temperature on metabolic rate is due to changes in rate of enzyme catalyzed reactions.

Q_{10} for metabolic rate is not the same for all temperature ranges - see fig 16-9

Hypothalamic Control of Thermoregulation in Mammals

How are all of these thermoregulatory processes integrated and controlled?

(Overheads: Fig 9-5 & modified Fig 16-34)

Neurons in the hypothalamus are sensitive to temperature of blood supply. Hypothalamus also receives neural input from thermoreceptors elsewhere in the body.

(Overhead: Fig 1-3)

Hypothalamus has a set point (T_{set}) that works like thermostat.

If $T_b > T_{set}$, neural signals initiate cooling mechanisms (vasodilation of capillaries, sweating, panting, adjusting blood flow through counter-current heat exchangers, behavior regulation).

If $T_b < T_{set,}$ neural signals initiate warming or heat conservation mechanisms (vasoconstriction of capillaries, shivering, brown-fat thermogenesis, adjusting blood flow through counter-current heat exchangers).

(Overhead: Fig 16-36)

Thermostat is all-or-none device. Unlike a thermostat, negative feedback control by hypothalamus shows ***proportional control*** - a small deviation from T_{set} provokes a low intensity regulatory response. A major deviation from T_{set} brings out the big guns.