

Goals:

- Understand the concepts of heat balance and of temperature regulation
- Learn the basic ways animals exchange heat with their environment
- Appreciate the heterogeneity of the thermal environment on a micro-scale

I. Introduction

- A. Temperature regulation (i.e., to control T_b) requires that an animal
1. **Monitor** environmentally or physiologically induced (e.g., activity) deviations of T_b from some internal reference (thermostat or "set-point")
 2. Then activate **adjustments** (behavior or physiology or both) that oppose or compensate for that deviation. This is "**negative feed-back control.**"
- B. Simple heat balance equation governs the amount and direction of heat transfer between animals and their environments (SN 253)

$$\text{heat production } (\dot{E}) + \text{heat in} - \text{heat out} = \text{heat stored}$$

1. To raise T_b , heat gains (i.e., production + heat in) must be > heat losses (thus heat stored > 0). To lower T_b heat loss must be > heat gain (heat stored < 0).
 2. If and only if heat gains = heat losses (i.e., heat stored = 0), will T_b not change.
 3. [The concept is just like balancing a bank account at the end of a month.]
- C. Heat transfer is influenced by type of animal (ectotherm vs. endotherm), its size and color, and by environmental conditions (e.g., hot or cold).
- D. Heat exchange is very different for animals on land vs. in water. Why?
1. Ambient temperature fluctuations are of much greater magnitude on land.
 2. But specific heat capacity and conductivity much greater in water. Hard, therefore, to maintain a T_b that is elevated above water temperature.

II. How is heat transferred between animals and environment? SN 247-253

- A. But first, review (1st lecture) basic – and very important principles – of heat transfer
1. **Heat** is a form of energy, and heat content is proportional to the total kinetic energy of a system. In contrast, **temperature** measures the average kinetic energy of the system.¹
 2. When two objects that are in contact are at different temperature, the **net** heat flow is from the warmer object to the colder object.
 3. The greater the difference ("gradient") in temperature between the two objects, the greater the rate of heat exchange (= flux).
 4. The greater the surface area in contact, the greater the heat flux.
 5. The physical properties of the objects will also influence the rate of flux.
- B. **Conduction** -- heat transfer (to/from) between bodies in direct physical contact.
1. Heat is conducted in if animal is cooler than its environment, and vice versa.
 2. Magnitude of heat conduction depends primarily on area of contact, temperature differential, and the conductivity of materials

¹ So, if one combines two liters of water, each at 50°C, the temperature remains the same, but the heat content (thus energy) is doubled.

- a. Water, blood, and tissue have high conductivities, air and fur low.
 - b. Thus heat easily conducted in water and within an animal's body, but not so easily between air and body -- especially in furred animals.
 3. Formally $Q = C A (T_b - T_a)$, where Q = rate of heat flow, C = conductivity, and A = surface area. Good insulators have low values for C .
 - [4. Hard for fish to maintain high T_b since C is high and gill area (A) is huge.]
 5. Conduction much less important in most terrestrial than for aquatic animals, because little skin surface in contact with ground and because C_{air} is small.
- C. **Convection** -- transfer of heat (to/from) by bulk movement of particles (air, blood)
1. Not surprisingly, the magnitude of heat flux depends on the temp. differential², a "convection coefficient" (h), plus the exposed surface area.

$$Q = h A (T_s - T_a)$$
 2. All surfaces have boundary layer of air, a transition zone for the temperature differential³. The thicker the boundary layer, the lower the convection coefficient (in effect, a thick boundary layers provides "insulation")
 - a. Wind ("forced convection") maintains a steep gradient between air and skin and also reduces the thickness of the boundary layer, thereby increasing heat transfer ("wind chill factor" for endotherms).

$$h \propto (u)^{1/2}$$
, where u = wind speed
 - b. Boundary thickness is proportional to (diameter)^{1/2} of the animal's body, thus very small animals have thin boundary layers and are relatively susceptible to convection. Thus, $h \propto 1/(d)^{1/2}$. (be able to plot this relationship).
 - c. Insulation (fur, feathers) of endotherms lowers h , thus lowers convection.
 3. Blood circulation transfers heat by convection within an animal's body.
- D. **Radiation** (heat in or out of body)
1. Transfer of electromagnetic energy. → **All objects above 0 K emit radiation.** Amount emitted increases with surface temperature (T^4) and with "emissivity" of an object: (most animal skin has an emissivity of about .97, whereas an "black-body" is 1.0). Warm objects emit more radiation than cold objects.
 2. Animals receive as well as emit radiation. Net heat flow to or from animal depends on whether its skin is colder or warmer than objects in its view.

$$Q \propto (T_b^4 - T_{env}^4)$$
 3. Wavelengths emitted depend on surface temperature of the emitter. Solar radiation (relatively hot) at earth's surface is predominately short wave (mainly visible, near IR), whereas radiation from animals and the environment (relatively cold) is at much longer wavelengths (IR), which we can't see.
 4. Radiation incident on animal is reflected, absorbed, or (rarely) transmitted
 - a. Animals absorb about 60% to 85% of incident radiation
 - b. Absorptivity is a function of skin color, but only in visible wavelengths.⁴

² The temperature gradient here (and also in conduction) is skin (not core) temperature minus T_a .

³ The boundary layer of air around endotherms is heated by conduction from the skin. This heated air rises, and is replaced by cooler air ("free convection"). Thus skin heat is first conducted to the boundary layer of air, then convected away.)

⁴ Thus one cannot predict absorption in UV or IR from knowledge of an organism's color (e.g., skin of Blacks and Caucasians are both highly absorptive in mid-infrared).

5. Absorptivity, but **not** emissivity, of radiation depends on skin color. [However, note that dark ectotherms will absorb more radiation and hence become warmer. Having a higher skin temperature, dark animal will thus emit more radiation than light animal (Stefan's Law). But this is a property of having a higher temperature, **not** of color per se. At night, dark and light ectotherms will have same T_b and emit same amount of IR.]
6. Color more important to heat balance of large animals than small. Why? Small animals have small boundary layers and are strongly influenced by convection. Large animals have large boundary layers, and their heat balanced is thus only slightly influenced by convection -- but is significantly influenced by radiation.
7. All else equal, a large ectotherm in sun heats relatively slowly but will have higher equilibrium T_b than will a small animal.

E. Evaporation (heat loss only)

1. Evaporation is the **only** means by which animals can readily lose heat (other than by seeking cold microclimate), and it is very effective. Evaporation of water from body surface (skin, lungs) causes heat loss (at 35°C, 2.4 kJ or 580 cal to vaporize 1 g H₂O -- this is a large amount of heat -- more than 5x that required to heat 1 g water to the boiling point). There is some physiological control over evaporative heat loss (panting, sweating).
2. The amount of evaporation depends (surprise!) on the gradient in water vapor density between air and animal.
3. Gradient is high for "wet-skinned" animals (e.g., frogs, slugs) in dry environment. Thus easy to cool evaporatively (until they run out of water, of course!).
4. Gradient is low in humid environment -- hence endotherms risk of overheating if ambient temperatures are also high. In dry environments (large gradient), evaporation can be high.⁵

F. Metabolism -- heat production by animal (i.e., a **heat-gain mechanism only)**

1. Ectotherms produce too little heat to influence heat balance except during very vigorous exercise -- generally whatever heat they produce by metabolism is lost by evaporation, so doesn't impact heat balance. Also, insulation is very poor, so can't easily store heat. [Exceptions: "hairy" moths, large pythons.]
2. Endotherms have high metabolic rates and good insulation (low "h"), so their metabolism is a major factor in their overall heat balance.
3. In cold environment ($T_b - T_a$ is large), thus heat loss is large, endotherm **must** increase metabolism or work (i.e., metabolic heat production via shivering or exercise thermogenesis) to balance heat loss (otherwise "heat storage" would be negative, and T_b would drop).
4. At "moderate" ambient temperatures, metabolism reaches a minimum value -- "thermal neutral zone" is the range of ambient temperatures where insulative, postural, and circulatory adjustments alone maintain stable T_b using only "resting" rates of heat production.
5. At temperatures above the "upper critical temperature," metabolism again increases. In part because T_b may be raised and because animal must activate heat loss mechanisms (sweating & panting), which require energy. This

⁵ Evaporation is obviously most effective for desert animals, yet desert animals can't "afford" to lose the water, which is hard to replace. So, most desert animals have relatively impermeable skins. Curiously, however, desert cicadas extremely permeable skins. The resultant heat loss keeps them from overheating, but where do they get water? Cicadas feed on plant "juices" -- so always have a ready supply of water.

increases metabolism, but net heat loss is greater (not always -- in humid environment, evaporation is slow and animals have high risk of hyperthermia).

6. Lower critical temperature is lower in large endotherms. Why?

III. The thermal environment in nature is heterogeneous

- A. **From an animal's perspective, the thermal micro-environment is spatially (and temporally, of course) very heterogeneous.** So weather station data, which imply homogeneity at a given site, are therefore misleading. Climate varies dramatically on a micro-scale. Such environmental heterogeneity can be exploited by animals and enable them to control T_b (ectotherms) or reduce heat/cold stress (endotherms).
- B. Because of differences in size, shape, color, orientation, physiology, **the “temperature” of any given spot will be different for different animals.** Thus a dark lizard will find a given (sunny) perch “hotter” than will a light lizard.

IV. Biophysical methods quantify the thermal environment *from an animal's perspective**

- A. Biophysical models (mathematical) of heat transfer accurately predict body temperatures of ectotherms at any site in the environment. Similar models accurately predict heat loads (conversely wind chills) on endotherms.
- B. They require information on microclimates (T_a , radiation loads, wind speeds, etc.) and on animals (size, color, insulation, orientation). They then integrate all sources of heat fluxes (e.g., metabolism, convection, radiation -- heat flux from different sources is additive) and predict body temperatures of ectotherms, heat loads on endotherms, potential times of activity, etc. Very useful, very accurate.
- C. Alternatively, one can make physical replicas of animals (usually hollow copper **models**, painted appropriate color) to predict equilibrium body temperatures of ectotherms or heat loads on endotherms (heated taxidemic mounts). Very convenient and simple to use. If lots of these are distributed into the environment can create a "thermal" map of the habitat from a specific animal's perspective.
1. Predicted T_b of ectotherms is its **“operative environmental temperatures”** (T_e).
 2. Predicted heat loads on endotherms are called “standard operative temperatures” or T_{es} . Why would T_{es} be different from T_e ? Consider the impact of wind chill and of insulation.